

UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

Solos e seus efeitos na vegetação da Caatinga brasileira
Soils and their effects on Brazilian Caatinga vegetation

Alexandre Tadeu Brunello

Tese apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Doutor em Ciências, obtido no Programa de Pós-Graduação em Biologia Comparada.

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Orientador: Prof. Dr. Tomas F. Domingues
Coorientador: Prof. Dr. Jonathan J. Lloyd

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1. Solos 2. Solos do semiárido 3. Caatinga 4. Pedogênese 5. $\delta^{15}\text{N}$ do solo 6.
Biomassa acima do solo 7. Atributos funcionais 8. Gradientes climáticos 9.
Gradientes edáficos

*I dedicate this thesis to my parents, **Rita and Carlos**, not only for all their support and love during all stages of this challenging work but also throughout life.*

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“While the lack of water threatens population growth in arid and semiarid regions, the lack of water is the natural state, and the state that imparted the unique properties to arid and semiarid soils. It is also the lack of water that makes arid and semiarid places some of the most open, least developed places on Earth, and some of the last ‘wild’ places for future generations to enjoy and study.”

Monger, Martinez-Rios and Khresat

Resumo

BRUNELLO, A. T. **Solos e seus efeitos na vegetação da Caatinga brasileira [tese]**. 2022. Doutorado em Biologia Comparada – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 2022.

As propriedades do solo foram negligenciadas por muito tempo em estudos que tentam particionar a influência potencial de múltiplos fatores nas propriedades da vegetação. Essa falta de uma abordagem sistemática sobre como os solos influenciam a vegetação é bastante evidente em estudos com foco em florestas tropicais sazonalmente secas (FTSSs). Uma amostragem intensiva de solo e vegetação em 29 parcelas de estudo em todo o domínio da Caatinga sazonalmente seca (isto é, uma abordagem de comparação geográfica) permitiu avaliar variações em várias propriedades do solo entre três afiliações geológicas [ou seja, sedimentar (S_{SED}), metamórfica (S_{MET}) e cárstica (S_{KAR})] e investigar até que ponto essas propriedades se relacionam com variações na biomassa lenhosa acima do solo (AGB_W), atributos funcionais ponderados pela comunidade e índices de diversidade funcional. As propriedades do solo variaram sistemicamente entre as afiliações geológicas, com algumas propriedades, no entanto, exibindo variação substancialmente maior do que outras. Por exemplo, as métricas associadas ao intemperismo, como capacidade efetiva de troca de cátions (I_E) e reserva total de bases (\sum_{RB}), diminuíram de acordo com $S_{KAR} > S_{MET} > S_{SED}$, enquanto as concentrações totais de fósforo no solo ($[P]_T$) foram relativamente mais altas nas áreas S_{KAR} . Além disso, a distribuição dos principais cátions trocáveis (ou seja, Ca, Mg, K, Na e Al) no complexo sortivo do solo refletiu seus respectivos materiais de origem, com teores de cátions básicos sendo geralmente maiores nas áreas S_{KAR} e S_{MET} . Em contraste, os níveis de alumínio trocável foram geralmente mais altos nas áreas S_{SED} . A dinâmica do nitrogênio (N), abordada pelos valores de $\delta^{15}N$ do solo, foi modulada principalmente por forças climáticas [isto é, índice de aridez (AI) e sazonalidade da precipitação (ψ)]. No entanto, um papel para I_E sobre os valores de $\delta^{15}N$ do solo também foi sugerido, especialmente nos locais mais úmidos. A AGB_W foi influenciada tanto pelo solo quanto pelo clima. Por exemplo, a precipitação média anual (P_A) e a fertilidade do solo (representada por cálcio) influenciaram positivamente os valores de AGB_W . Além disso, as interações entre o déficit hídrico climático de longo prazo (CWD) e tanto à $[Ca]_{ex}$ quanto o teor máximo de água disponível no solo (θ_P) sugerem que a AGB_W na Caatinga é determinada por interações complexas. As propriedades do solo também foram relacionadas às propriedades funcionais da comunidade, com diâmetro máximo do fuste ponderado pela comunidade (CWM_{dmax}), densidade da madeira ponderada pela comunidade (CWM_{wd}), riqueza funcional (F_{Ric}), equitabilidade funcional (F_{Eve}) e divergência funcional (F_{Div}) sendo todas influenciadas pelas propriedades do solo. Nesse sentido, foi encontrada uma relação inversa entre cátions básicos do solo e CWM_{wd} . Em contraste, os cátions básicos do solo influenciaram positivamente CWM_{dmax} . Por fim, várias métricas nutricionais do solo influenciaram positivamente o índice F_{Ric} , enquanto apenas alguns elementos influenciaram inversamente os índices F_{Eve} e F_{Div} . Acredita-se que essas relações reflitam as compensações da vegetação entre o investimento no crescimento secundário e as estratégias de economia da água. Coletivamente, esses resultados fornecem informações sobre as múltiplas maneiras pelas quais os solos podem afetar a estrutura e o funcionamento da vegetação.

Palavras-chave: 1. Solos 2. Solos semiáridos 3. Materiais de origem do solo 4. Caatinga 5. Pedogênese 6. $\delta^{15}\text{N}$ do solo 7. Biomassa acima do solo 8. Atributos funcionais 9. Gradientes climáticos 10. Gradientes edáficos

Abstract

BRUNELLO, A. T. **Soils and their effects on Brazilian Caatinga vegetation [thesis]**. 2022. Doctoral degree in Comparative Biology – Faculty of Philosophy, Sciences and Letters of Ribeirão Preto, University of São Paulo, Ribeirão Preto, 2022.

Soil properties have long been overlooked in studies that attempt to disentangle the potential influence of multiple drivers on vegetation properties. This lack of a systematic approach to how soils influence vegetation is markedly evident in studies focusing on seasonally dry tropical forests (SDTFs). An intensive soil and vegetation sampling in 29 study plots across the seasonal dry Caatinga domain (that is, a geographic comparison approach) allowed evaluating variations in several soil properties among three geological affiliations [that is, sedimentary (S_{SED}), metamorphic (S_{MET}) and karst (S_{KAR})], and investigating to which extent these properties relate to variations in above-ground woody biomass (AGB_W), community-weighted mean traits and functional diversity indexes. The soil properties varied systemically among geological affiliations, with some properties, however, showing substantially higher variation than others. For example, weathering-associated metrics such as effective cation exchange capacity (I_E) and total reserve bases (\sum_{RB}) were found to decrease following $S_{KAR} > S_{MET} > S_{SED}$, while total soil phosphorus concentrations ($[P]_T$) were relatively higher at the S_{KAR} sites. Moreover, the distribution of main soil exchange cations (that is, Ca, Mg, K, Na, and Al) in the soil sorptive complex reflected the original soil parent materials, with soil base cations being generally higher at the S_{KAR} and S_{MET} sites. In contrast, exchangeable aluminium levels were generally higher at the S_{SED} sites. Nitrogen dynamics, addressed by soil $\delta^{15}N$ values, was found to be primarily modulated by climatic forces [that is, aridity index (AI) and the seasonality of the precipitation (ψ)]. However, a role for I_E on soil $\delta^{15}N$ values was also suggested, especially at the wetter sites. The AGB_W was found to be influenced by both soil and climate. For instance, mean annual precipitation (P_A) and soil fertility (represented by calcium) positively influenced AGB_W levels. Furthermore, interactions between long-term climatic water deficit (CWD) and both $[Ca]_{ex}$ and the maximum plant-available soil water content (θ_P) suggest that AGB_W in Caatinga is driven by complex interactions. Soil properties were also related to community functional properties, with all community-weighted mean maximum stem diameter (CWM_{dmax}), community-weighted mean wood density (CWM_{wd}), functional richness (F_{Ric}), functional evenness (F_{Eve}), and functional divergence (F_{Div}) being influenced by soil properties. In that regard, an inverse relationship was found between soil base cations and CWM_{wd} . In contrast, soil base cations had a positive influence on CWM_{dmax} . Finally, several soil nutritional metrics positively influenced F_{Ric} , while only a few elements inversely influenced both F_{Eve} and F_{Div} metrics. These relationships are thought to reflect vegetation trade-offs between investment in secondary growth and water-economy strategies. Collectively, these results provide information on the multiple ways through which soils can affect vegetation structure and functioning.

Keywords: 1. Soils 2. Semiarid soils 3. Soil parent materials 4. Caatinga 5. Pedogenesis 6. Soil $\delta^{15}N$ 7. Above-ground biomass 8. Functional traits 9. Climatic gradients 10. Edaphic gradients

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List of symbols and abbreviations

- S_{SED} – designates soils or sites associated with sedimentary parent materials
- S_{MET} – designates soils or sites associated with metamorphic parent materials
- S_{KAR} – designates soils or sites associated with karstic parent materials
- S_{LAC} – low-activity clay soils
- S_{HAC} – high-activity clay soils
- S_{ARE} – arenic soils
- AGB – above-ground biomass
- AGB_w – above-ground woody biomass
- CWM – community-weighted trait means
- Sand_f – soil sand fraction
- Silt_f – soil silt fraction
- Clay_f – soil clay fraction
- [Ca]_{ex} – soil exchangeable calcium
- [Mg]_{ex} – soil exchangeable magnesium
- [K]_{ex} – soil exchangeable potassium
- [Na]_{ex} – soil exchangeable sodium
- [Al]_{ex} – soil exchangeable aluminium
- Σ_B – soil sum of bases
- Σ_{RB} – soil total reserve of bases
- NCR_T – soil total nutrient capital reserves
- I_E – effective cation exchange capacity
- BS% – soil base saturation
- m% – soil aluminium saturation
- pH_{H₂O} – water-measured soil pH
- pH_{KCl} – KCl-measured soil pH
- $\delta^{15}N$ – the ratio between the two N stable isotopes (^{15}N : ^{14}N)
- [Ca]_T – soil total calcium
- [Mg]_T – soil total magnesium
- [K]_T – soil total potassium
- [Na]_T – soil total sodium
- [P]_T – soil total phosphorus
- [Fe]_T – soil total iron

[Mn]_T – soil total manganese
[Zn]_T – soil total zinc
[C]_T – Soil total carbon
[C]_N – Soil total nitrogen
C/N – soil or plant C: N ratio
 T_A – Mean annual temperature
 T_{MAX} – Mean temperature of the warmest month
 P_A – Mean annual precipitation
AI – Aridity index
ETP₀ – Potential evapotranspiration
CWD – Long-term climatic water deficit
CWD_{adj} – Long-term climatic water deficit with a positive sign
 θ_v – texture-associated volumetric water content
 $W_{\theta v}$ – texture-associated volumetric water content weighted across soil profile
 θ_p – Maximum plant-available soil water
 R_{EF} – Measured effective rooting depth
 Ψ – Precipitation seasonality (used once for soil matric potential)
a – annum
Ma – mega annum
MEM – Moran Eigenvector Map
OLS – Ordinary least squares
LMM – linear mixed model
SWC – Spatial weighting matrix
AICc – Corrected Akaike Information Criterion
 W – Akaike weights
 I – Global Moran's I
VIF – Variance Inflation Factor
RIV- Relative importance value
CPRM – Geological Survey of Brazil
IBGE - The Brazilian Institute of Geography and Statistics
RSG – Reference Soil Group
IUSS – International Union of Soil Science
WRB – World Reference Base
SiBCS – Brazilian System of Soil Classification

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Introduction

Despite the prevailing focus of the present-day tropical ecology research still being on moist evergreen forests and to a lesser extent on savanna formations, seasonally dry tropical forests (hereafter SDTFs) (PENNINGTON; PRADO; PENDRY, 2000) have an unquestionable ecological and floristic importance. Seasonally dry tropical forests comprise a wide range of plant physiognomies (MURPHY; LUGO, 1986), generally consisting of trees and/or shrubs with varying height and canopy closure levels, and with almost all plant species shedding their leaves during the dry season (SAMPAIO, 1995).

Globally, SDTFs are relatively less studied than other tropical biomes (SANTOS et al., 2011; BECKNELL; KUCEK; POWERS, 2012), although the predominant water limitation in this type of biome is a strong ecological force that drove the evolution of a unique dry-adapted flora (PENNINGTON; PRADO; PENDRY, 2000; FERNANDES et al., 2022). Furthermore, a considerable part of the available studies did not consider soil properties. For example, Becknell, Kucek, and Powers (2012) were able to only evaluate climatic variables as explanatory variables of above-ground biomass over an extensive meta-analysis that included 44 pant-tropical studies of SDTFs. The absence of edaphic variables in that study was due to inconsistency among protocols for soil analyses or due to the total lack of soil data. In the study by Becknell, Kucek, and Powers (2012), the need for measurements of soil covariates that could potentially explain the biomass stocks of SDTFs was also highlighted.

In Brazil, the bulk of SDTFs is found within the Caatinga biome borders, which virtually coincides with the Brazilian semiarid region. This seasonal dry biome occupies an area of approximately 862,818 km² and has marked environmental heterogeneity (IBGE 2019a; 2019b), which is particularly notable when considering the landforms and various soil parent materials found in the region.

Historically, Caatinga has attracted less attention compared to other biomes in the region (SÄRKINEN et al., 2011; ALBUQUERQUE et al., 2012), with the study by Santos et al. (2011) providing a series of scores from the '*semiquantitative index describing biodiversity survey efforts and knowledge status*' that support the so-called 'Caatinga negligence', especially compared to other Brazilian regions. Although this situation appears to be improving over the last few years, with several studies being published in important journals of international circulation, the need for the adoption of methodologically consistent protocols remains noticeable. This relative lack of standardised surveys also applies to soils, as there are

not many studies reporting on systematic variations in soil properties and how these properties can account for variations in vegetation structure and functioning in the region.

Concerning the Caatinga soils themselves, the mosaic pattern of its spatial distribution (Figure 1.3, Chapter 1) is known to be the product of long-lasting intricate evolutionary geotectonic processes (AB' SABER, 1974; SAMPAIO, 1995; OLIVEIRA, 2011). These processes largely determined the chemical, physical, and mineralogical properties of soil, and despite their marked spatial variability, they have been classically categorised into discrete groups to reflect their geological origin. For instance, several studies in ecology and botany classify Caatinga plant communities as 'Crystalline Caatinga', 'Sedimentary Caatinga' and 'Karst Caatinga' (QUEIROZ, 2006; QUEROZ et al., 2017; FERNANDES et al., 2022). Importantly, soils that overlay these geological substrates have more or less predictable properties, where 'crystalline soils' are generally assumed to be less weathered (that is, low to intermediate pedogenetic development), while 'sedimentary soils' are generally assumed to be more weathered (that is, advanced pedogenetic development). Soils from karst areas usually show particular properties. This is because the limestones and dolomites typically found, often gave rise to soils with high base saturation and high soil pH, ultimately controlling several biogeochemical processes. It should be noted, however, that (micro)relief variations can cause marked differences in physicochemical and geochemical properties in these soils, as shown for karst soils of the Apodi Plateau, NE Brazil (OLIVEIRA et al., 2018).

Most importantly, geologically-derived soil properties are expected to influence vegetation composition, structure, and functioning in multiple ways. For instance, soil properties should influence vegetation not only by providing essential resources (that is, water and nutrients), but also by acting as an environmental selecting species according to their edaphic suitability (FERNANDES et al., 2022). Furthermore, soil properties have already been shown to influence wood anatomical characteristics (see, e.g., QUESADA et al., 2012; LIRA-MARTINS, 2017), potentially accounting for variation in many other plant traits (JAGER et al., 2015).

Therefore, this thesis develops upon the idea that geology, in addition to promoting biogeographical shifts (FERNANDES et al., 2022), is a major determinant of soil properties in the semiarid Caatinga. In turn, soil properties are expected to account for variations in vegetation properties, including stand-level above-ground woody biomass, community mean traits and functional diversity indexes, both latter investigated in this thesis.

Understanding how climate, soil chemical and physical properties, and their complex interactions altogether determine vegetation structure and ecosystem functioning is critical to

improving our general knowledge and predicting how global changes may affect the Brazilian Caatinga biome.

Aims and objectives of the thesis

The brief introduction above put forward the outstanding environmental heterogeneity of the Caatinga, which is further detailed in Chapter 1. Despite valuable efforts in recent years, the need to improve our understanding of how environmental factors influence the composition, functioning, and structure of vegetation remains noticeable.

Therefore, the main objectives of this thesis are as follows:

1. Provide a detailed approach for Caatinga soils with particular reference to the study sites of the Nordeste Project (details in Section 2.2), aiming to contribute to soil science in the target region and semiarid regions.
2. Investigate to what extent environmental drivers (that is, soil and climate) influence vegetation properties of stands belonging to geologic-edaphically distinct environments.
3. Provide baseline soil information for future research in the established permanent plots.

Thesis outline

Chapter 1 - Literature review

Chapter 2 – Several soil properties were analysed, along with the potential influence of climate on selected soil properties. The analyses were performed in the context of sites associated with distinct geological affiliations (determinants of soil parent materials), that is, soils derived from sedimentary parent materials (S_{SED}), soils derived from metamorphic rocks (S_{MET}), and soils derived from rocks typically found in karst environments (S_{KAR}).

Chapter 3 – The influence of climate and soil on above-ground wood biomass (AGB_W) was evaluated through a linear mixed-effect model (LMM), along with multi-model inference and a model-averaging approach. Additionally, bivariate relationships were explored considering the entire dataset together and evaluated geological categories separately. Finally, relationships between several soil properties, community-weighted means of plant functional traits, and functional diversity indexes were explored.

Chapter 4 – Conclusions

Chapter 1

Literature review

Chapter 1 – Literature review

1.1 Seasonally Dry Tropical Forests (SDTFs)¹

SDTF is a broad term that represents a globally extensive and still less studied biome compared to their tropical humid forests counterparts (PENNINGTON; LEWIS; RATTER, 2006; SANTOS ET AL., 2011; BECKNELL; KUCEK; POWERS, 2012). Although there is no consensus to define SDTFs (SIYUM, 2020), seasonal climatic patterns and long dry periods are elements that are commonly present in bioclimatic definitions of SDTFs. To provide a classical definition, as adopted by Murphy, and Lugo (1986), the term SDTFs encompasses a wide range of vegetation formations, from tall forests in wetter places to cactus scrub where rainfall is reduced, with the annual precipitation levels usually falling within 0.25 to 2.0 m, with 4-7 months with less than 0.1 m precipitation (MURPHY; LUGO, 1986)². Deciduousness is a conspicuous trait of SDTFs, with most woody plant species shedding their leaves during dry periods, which usually is more pronounced as rainfall decreases (MOONEY; BULLOCK; MEDINA, 1995). As a result, leaf litter often accumulates on the forest floor during drier periods, but also because direct sunlight on the forest floor leads to very low humidity levels and decomposition rates (QUEIROZ, 2006). Xeromorphic traits are also common in SDTFs plants, e.g. the replacement of leaves by spines and the crassulacean acid metabolism (CAM) (SAMPAIO, 1995). The latter is mostly represented by the leafless Cactaceae and Euphorbiaceae families. In addition, ecosystem processes such as net primary productivity take place only during a restricted wet season, i.e., plant growth is markedly seasonal (QUEIROZ, 2006).

Regardless of employed definitions, there is agreement that SDTFs coverage is decreasing worldwide (OCÓN et al., 2021). Also, despite the controversies to estimate the actual extent of these formations, it is noteworthy that these ecosystems have a considerable role in the global carbon budget, with semiarid biomes significantly participating in inter-annual carbon cycle inter-annual variations (POULTER et al., 2014). They also harbour many unique species (SÄRKINEN et al., 2011; DRYFLOR, 2016). More than 50% of the global SDTFs are located within South America, with the other remnants in North America, Central America,

¹There is no consensus term. For example, Queiroz et al. (2017), following UNESCO'S (1973) classification for global vegetation, proposed the term Seasonally Dry Tropical Forests and Woodlands (SDTFWs). The addition of the term 'woodland' would encompass the plethora of dry woody physiognomies found in the neotropics.

²Such thresholds may vary according to the bioclimatic definition adopted (ÓCON, 2021).

Eurasia and Africa (MILES et al., 2006). Figure 1.1 shows the SDTFs distribution across the Neotropics.

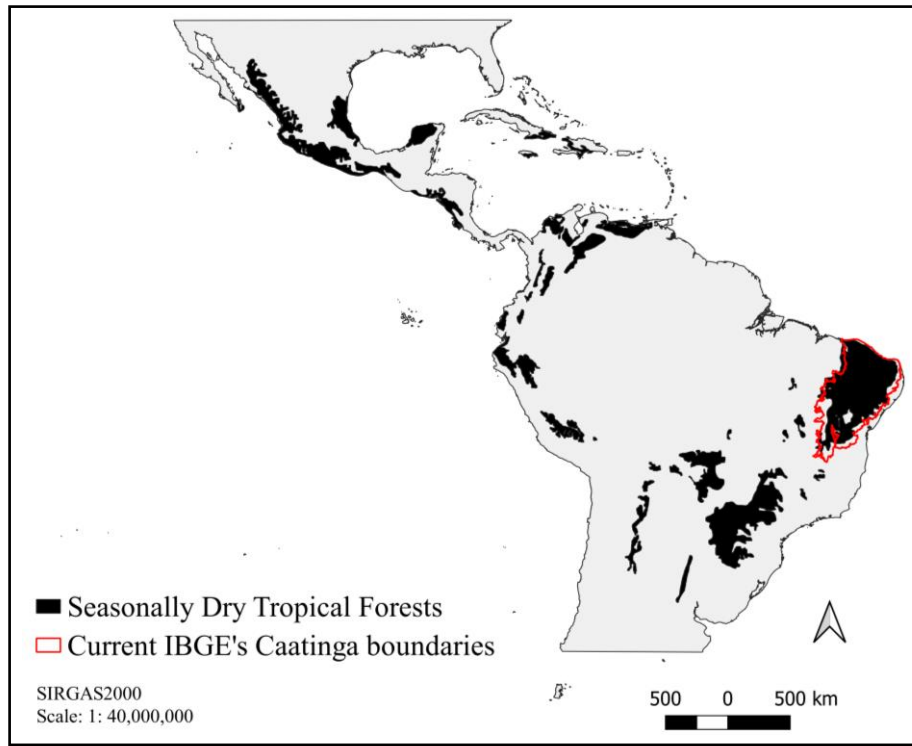


Figure 1.1: Seasonally Dry Tropical Forests distribution in the Neotropics. Redesigned from DRYFLOR et al., 2016. Shapefiles of SDTFs and the Neotropical region were downloaded from the DRYFLOR website (<http://www.dryflor.info/data>). The Brazilian Institute of Geography and Statistics' (IBGE) current Caatinga boundaries' shapefile was downloaded from the IBGE's website (<https://www.ibge.gov.br/>).

In South America, these formations occur scattered in disjunct patches. The Brazilian Caatinga is the largest and most continuous nucleus of SDTFs in the New World (QUEIROZ, 2006; QUEIROZ et al., 2017, FERNANDES; CARDOSO; QUEIROZ, 2020), followed by areas known as the Missiones and the Piedmont Nuclei (PRADO; GIBBS, 1993), and areas nearby Venezuela and Colombia coasts (PENNINGTON; PRADO; PENDRY, 2000; DRYFLOR, 2016). Smaller and isolated patches occur scattered with variable plant community structure and composition, largely depending on abiotic conditions (PENNINGTON; PRADO; PENDRY, 2000). Taken together, the unique characteristics of SDTFs, their ecological importance and current levels of climatic and anthropogenic threats, draw attention to the need for a better ecological and biogeochemical understanding as well as the preservation of these ecosystems. Because Caatinga's SDTFs and their relationships with the environment will be focussed on throughout this work, a brief biotic and environmental characterisation is provided in the following section.

1.2 The Brazilian Caatinga

Even before the arrival of naturalists in Brazil, indigenous groups had already named the typical vegetation growing in Northeastern Brazil “*Caatinga*”, which means “whitish forest” in Tupi indigenous language. This is thought to reflect the whitish leafless vegetation aspect during the dry waterless periods (AB’SÁBER; MARIGO, 2011). The word Caatinga names the bulk of SDTFs in Brazil, also naming one of the Brazilian biomes, which occupies an area of ca. 862,818 km², representing about 10.1% of the Brazilian territory according to the Brazilian Institute of Geography and Statistics (IBGE, 2019a)³. This biome occurs in all Northeastern Brazil states and is present in the upper part of Minas Gerais state (Southeastern Brazil). Considering the region's observed latitudinal range (ca. 3° to 18° S), the climate is considered azonal since it differs significantly from other regions with the same latitudinal range (AB’SÁBER, 1974). The complex atmospheric circulation largely explains the azonal climate of Caatinga, which is caused by multiple meteorological phenomena (MOURA et al., 2019). In conjunction with orographic effects (i.e. the moisture interception by high plateaus or mountains), the Caatinga region occurs predominantly across a semiarid climate, with scattered wetter environments, or “exception landscapes” (AB’SÁBER, 1974). As a result of the complex circulation and relief effects patterns, the annual mean precipitation (P_A) is erratic in time and space, usually ranging from 0.25 – 1.0 m, often concentrated in 3 – 5 months (OLIVEIRA, 2011). Drought years often occur and droughts lasting 3-5 years have been recorded each 30 – 40 years (SAMPAIO, 1995). Rainfall generally decreases from the Caatinga boundaries to the interior while the temperature rises (SAMPAIO, 1995). At the biome boundaries, the mean annual precipitation is roughly about 1.0 m a⁻¹, coinciding with the so-called “Drought Polygon,” or the 1.0 m isohyet (ANDRADE-LIMA, 1981).

Moreover, in Caatinga, the cloud frequency is usually low so the total annual solar radiation is typically high (OLIVEIRA, 2011). Such high-intensity solar radiation results in high potential evapotranspiration rates (E_p), usually ranging from 1.5 – 2.0 m a⁻¹. Therefore, E_p rates in most cases overcome annual rainfall levels (P_A), resulting in negative water balances of 7 – 11 months year-round (MENEZES et al., 2012). Thus, the P_A / E_p ratio is commonly < 0.65, which characterises the semiarid climate. Furthermore, the high coefficients of variation of rainfall (usually higher than 30%) can be even more critical in conditioning the ecosystem functioning across the region (SAMPAIO, 2010). Considering that many ecological processes

³ The Caatinga area may vary from author to author according to the criteria adopted.

occur closely synchronised with adequate water supply, precipitation seasonality is of great importance in these environments (MURPHY; LUGO, 1986), influencing several vegetation features such as canopy coverage, seedling mortality, successional and evolutionary courses (MARKESTEIJN ET AL., 2010; APGAUA et al., 2015).

Some classical overviews of Caatinga have been presented over the past decades (AB'SABER, 1974; ANDRADE, 1977; ANDRADE-LIMA, 1981; SAMPAIO, 1995; DE ALBUQUERQUE et al., 2012). From these reviews, it can be said that the Brazilian Caatinga stands out in terms of geodiversity (including landforms, rocks, sediments and soil types), which along with the typical semiarid climate, gave rise to an adapted biodiverse and structurally distinct flora. In this context, the geographical soil distribution of Caatinga is commonly referred to as “mosaic” (see, e.g., MEIADO et al., 2012). This terminology can be extended to other components of the ecosystem, such as the complex geological arrangement and the vegetation, also commonly mentioned as a ‘mosaic of plant physiognomies’. Furthermore, the unique phytogeographical characteristics of the region appear indisputable among South American SDTF nuclei, as the region harbours several “Caatingas” (AB'SÁBER, 1974), and many phytophysiognomies have been described and reviewed by some authors (e.g., ANDRADE-LIMA, 1981; VELLOSO et al., 2001; MORO et al., 2014). However, the dry tropical deciduous thorn woodland (Caatinga *sensu-stricto*) or *Savana Estépica* in the IBGE definition is estimated to occupy ca. 63% of the Caatinga territory, followed by ecotones and vegetation enclaves (22.6%), deciduous forests (8.0%) and semideciduous forests (2.1%). Savannas and evergreen dense and open forests are also represented to a minor extent throughout the region (IBGE Environmental Information Database, BDIA, Vegetation theme, 2022).

The current knowledge of Caatinga soils is the result of the efforts of several soil scientists and institutions, such as the National Soil Survey and Conservation Service (SNLCS), currently EMBRAPA soils. The latter has continued the work started in 1947 when the first systematic soil survey was conducted in Brazil (FAVORIM; LAFORET; ARCANJO, 2021). However, much still needs to be done in terms of systematic soil studies that enable our understanding of soil properties and how these properties relate to vegetation structure, functioning and composition.

Beyond their nutritional role, soil characteristics also play a paramount role in the ecosystem water budget, being ultimately the link between rainfall and the available water potentially provided to the ecosystem (WELTZIN et al., 2003; JARAMILLO; MURRAY-

TORTAROLO, 2019). But because SDTFs are, intuitively, water-limited ecosystems, soil properties have long been overlooked.

In this scenario, and given that one of the main objectives of this thesis is to provide a detailed approach to Caatinga soils, it is first necessary to describe Caatinga geology and geomorphology, because these largely determine soil properties. From a general standpoint, it may be expected that, as the rainfall levels decrease in a certain region, the climate factor loses strength in determining soil properties, whereas geology (parent materials) and relief assume a more influential role in determining these properties (ARAÚJO FILHO, 2011; ARAÚJO FILHO et al., 2017).

1.3 Geodiversity of Caatinga

The Brazilian Caatinga is characterised by considerable geological variability, with rock ages ranging from the Paleoproterozoic Era (3600 – 3200 Ma⁴) to the Quaternary (2.58 Ma to the present). Since the 1970s, huge efforts have been made to leverage the mining activities in Brazil through the *RADAM* and *RADAMBRASIL* Projects of the Geological Survey of Brazil (CPRM), Petrobras, universities and several public and private entities. This has yielded diverse maps and a huge volume of data, including the physicochemical properties of rocks (HASUI, 2012).

Brazil was first geologically compartmentalised in the pioneering works of Almeida et al. (1977; 1981), who separated the major geological unit (i.e. the South American Platform) into discrete structural provinces. In simple words, these provinces consist of large continuous domains, with particular composition along with a shared evolutionary geotectonic history and a clear distinction from the surrounding provinces (ALMEIDA et al., 1977; 1981). Although there are several distinct schemes for separating geological provinces (e.g. ALMEIDA et al. 1977; SCHOBENHAUS; NEVES, 2003; ALKIMIM; MARTINS-NETO, 2004), the current scheme adopted by the IBGE considers 13 structural provinces plus the Cenozoic coverage over the Brazil territory. This scheme is mainly based on ALMEIDA et al. (1977) and incorporates some inputs from other authors. Among these provinces, six (plus the Cenozoic coverage) occur in Caatinga, that is, São Francisco, Borborema, Parnaíba, Recôncavo Tucano-Jatobá, Coastal Province and Continental Margin (referred to as only “Coastal Province” in Figure 1.2),

⁴Ma = Mega age, i.e. millions of years; 1,000 Ma = 1 Ga

Mantiqueira and Cenozoic coverage (Figure 1.2). As already mentioned, these provinces are chiefly differentiated according to the nature of their crystalline basement or sedimentary rocks (in the last instance, soil parent materials), considering similarities in structures, tectonic plates, and evolutionary geotectonic history (ALMEIDA et al., 1977; 1981). It is noteworthy that, irrespective of each province's specific characteristics, much of their structural evolution has interdependent relationships (ALMEIDA et al., 1981). A brief characterisation of geotectonic processes and geological structural provinces comprised in Caatinga follows.

The São Francisco Province corresponds to its namesake São Francisco Craton in extension and geotectonic characterisation (ALMEIDA et al., 1977; IBGE, 2019b). Materials of various ages overlie the basement of this province. However, where the basement is exposed, it is as old as the Archean (4000 – 2500 Ma; ALMEIDA et al., 1977), with subsequent complex events determining the province characteristics, including the collisional Brasiliano orogeny (or Brasiliano cycle) dated from the late Neoproterozoic (670 – 550 Ma) (SCHOBENHAUS; NEVES, 2003). As a result, the South American continent was amalgamated into the African continent, forming the “São Francisco-Congo/Kasai-Angola” shield. These lumped continents were much later spread during the Pangea's supercontinent splitting (MABESOONE; NEUMANN, 2005), with massive magma amounts being released during these intricate events, allowing the formation of highly migmatitised granitic-gneissic complexes (ALMEIDA et al., 1977). Also covering a considerable part of the crystalline basement, representative structures composed of metasediments, metavolcanics, metamorphosed mafic (magnesium and iron-rich rocks), and ultramafic (high iron content; low silicon, potassium and sodium contents) rocks also occur (MABESOONE; NEUMANN, 2005) in the province, dictating the nature of the soil parent materials. The presence of sedimentary basins across São Francisco Province is also remarkable, such as the Espinhaço Supergroup, an intracratonic *sag* basin (thick accumulations of sediments) that shows old Mesoproterozoic (1600 – 1000 Ma) sedimentary structures, chiefly formed by arenites and quartz-sericite schist (DUSSIN; DUSSIN, 1995). The Borborema Province occupies an extensive part of the Caatinga region and was formed during the ancient Brasiliano Orogeny. In simple words, the province's basement is a mosaic resulting from the amalgamation of microcontinents from the Paleoproterozoic (2500 – 1600 Ma) (MABESOONE; NEUMANN, 2005). In addition, the Borborema province also comprises sedimentary basins formed during the Cretaceous, where aborted rifts were filled with sediments (ALMEIDA et al., 1977; MABESOONE; NEUMANN, 2005). Regarding the main lithotypes, the Borborema Province exhibits rocks as old as the Archean and, predominantly,

Paleoproterozoic rocks, overlain by metasedimentary, metavolcanic granitoid intrusions, associated with the Cariris Velhos Cycle (1100 – 930 Ma) (HASUI, 2012). Other products include diabase dykes (sheets of rock formed in a fractured pre-existing rock) from the Cretaceous Period, alkalic-basaltic volcanic, and other thin sediment layers from the Tertiary and Quaternary that may occur locally (ALMEIDA et al., 1981). Thus, a great range of rock types is found throughout the Borborema Province.

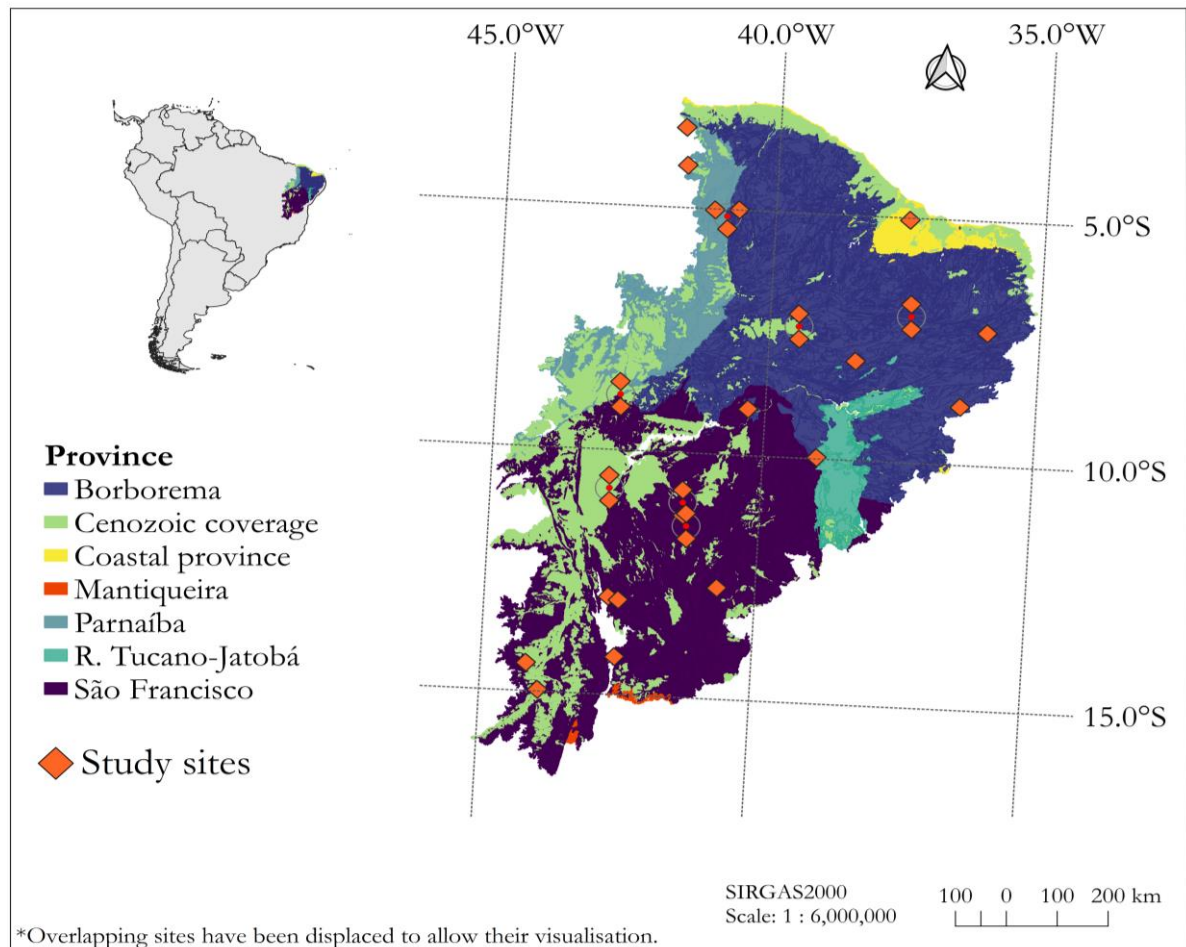


Figure 1.2: Geological provinces encompassed in Caatinga and study sites. Upper left) South America with emphasis on the Caatinga domain. Right side) structural geologic provinces encompassed in the region. Study sites of this thesis are shown as orange diamonds. Shapefile source: IBGE's Environmental Information Database – BDIA (theme geology). Map design: Brunello, A. T.

Along with Paraná Basin and the Amazonas Basin, the Parnaíba Province is one of the large, essentially sedimentary Brazilian basins which virtually overlaps the homonym Parnaíba sedimentary basin, which is essentially formed by Paleozoic strata, occupying ca. 650,000 km² in Piauí, Maranhão and Tocantins, Ceará and Pará states (ALMEIDA et al., 1977; 1981; DA CONCEIÇÃO et al., 2016). The geological strata found throughout the province resulted from

coastal and neritic sedimentation, originating sandstones with different grain sizes and conglomeratic associations, followed by thin arenites, siltites and shales, totalising a layer of about 700 m (ALMEIDA et al., 1977; 1981). The region has undergone marine regressions and transgressions episodes along the Devonian Period, resulting in an accumulation of arenites from the seawater (MABESOONE; NEUMANN, 2005; ALMEIDA et al., 1981). Despite the sedimentary origin, the Precambrian basement is also exposed in the northern part of the province. After long-lasting sedimentation (both marine and fluvial), the region has undergone an uplift, with other successional sedimentation events and basaltic magmatism (ALMEIDA et al., 1977). Enormous exposures of sedimentary rocks can be encountered in the region, such as in the Cabeças Formation in the *Parque Nacional das Sete Cidades* (IBGE, 2019b). The geological wealth of the region includes fossil plant-bearing sites, such as the Pedra do Fogo Formation, where large gymnosperm woods were recorded, associated with sedimentary sandstones, siltstones, cherts and limestones (DA CONCEIÇÃO et al., 2016).

The Recôncavo-Tucano Jatobá Basin consists of extensive sedimentary coverage that partially overlain part of the originally proposed Borborema and São Francisco provinces (IBGE, 2019b). It is estimated that 85% of the basin is in Bahia state. The basin's history goes back to the breakup of the Gondwana supercontinent) when aborted rifts (aulacogens) emerged (BIZZI; SCHOBENHAUS; MOHRIAK, 2003). During this event, the formation of sedimentary basins was enabled, sequentially forming coupled uplifted basins in the South-North direction from Bahia until the Pernambuco states. Caixeta et al. (1994) described the main lithostratigraphic units (i.e. types of strata or rock layers) present in the basin, from where it can be highlighted the overall occurrence of sandstones and shales with variable grain size and colouration, along with kaolinitic conglomerates, arkose and calcareous also present to a minor extent. Overall, a relief-correlated sandstone has been accumulated in this basin (MABESOONE; NEUMANN, 2005).

The Coastal Province and Continental Margin circumscribes the South American Platform divergent margin, directly associated with the ancient Gondwana supercontinent splitting and the rise of the Atlantic Ocean (ca. 140 Ma B.P.) (IBGE, 2019b). Physiographically, the Coastal Province usually exhibits a gently elevated relief closer to the coast, chiefly composed of alluvial and marine deposits. Moving west, the relief becomes higher, represented mainly by tablelands, with a significant presence of continental and marine sediments until the province's boundaries, where the crystalline basement is reached (ALMEIDA et al., 1977; 1981). The continental margin translates into the immersed part of the province, where many

sediment types are found, particularly associated with materials from different sedimentation events (MILANI; THOMAZ FILHO, 2000).

The Mantiqueira Province occupies a modest 0.2% of the Caatinga territory and results from the late Neoproterozoic (SCHOBENHAUS; NEVES, 2003). The province's territory is predominantly mountainous, with altitudes usually ≥ 1500 a.s.l., which indicates that the relief strongly influences the soil through its rejuvenation originating from erosive processes. Schematic geological cross-sections have shown many crystalline or sedimentary lithologies occurring throughout the province (IBGE, 2019b). Within the main lithotypes found in the northeastern portion of the province, there are alkaline rocks, pelitic to psefitic (i.e. finer to coarse grains) sediments, limestones, mafic volcanic rocks, and other sediments with a variable degree of metamorphism (from greenschist to amphibolite) (ALMEIDA et al., 1977; 1981).

Finally, the Cenozoic Coverage occurs mostly in the southern part of the Parnaíba province and on the western side of the São Francisco Province. To a lesser extent, it occurs in the region's northern boundary and small inlays within the other provinces. In a simple definition, the Cenozoic coverage represents the sedimentary filling of continental basins during the last 66 Ma in the Cenozoic (IBGE, 2019b). Therefore, geological characteristics (including both landforms and parent materials types) largely control edaphic properties. Following this rationale, Araújo (2011), Araújo et al. (2017) and Araújo et al. (2019), based on the Northeast Agroecological Zoning (SILVA et al., 1993), compartmentalised the region into nine landscape units and described the main soil types associated within each type landscape.

In terms of geomorphology, some predominant landforms can be recognised across the Caatinga region: the relief across interplanaltic lowland depressions (locally known as “Depressão Sertaneja”), which is mostly gently undulating, assigned by the intense, long-lasting pediplanation process under semiarid conditions. These processes date from the Cenozoic (Tertiary to Quaternary) and are still active (BEEK; BRAMAO, 1969). As a result, Precambrian crystalline rocks were exposed (i.e. granites, gneisses, and schists), leaving only residuals vestiges (i.e. inselbergs, tablelands, uplands, and mountains) from the younger rocks (BEEK; BRAMAO, 1969; AB'SABER, 1974). Although the soils in these “depressions”⁵ commonly have silty to clayey texture and high fertility, they are commonly shallow, stony, and susceptible to erosion under certain conditions (VELLOSO et al., 2001).

⁵ The expression “flatten surfaces” instead of “*Depressão Sertaneja*” is adopted by some authors.

Regarding main soil types found across broad geological types, Leptosols, Regosols and Luvisols, i.e. soils with low medium pedogenic development, account for a considerable part of crystalline terrains, whereas Arenosols, Ferralsols and Acrisols are soil groups commonly formed in sedimentary terrains, which, in general, are well-weathered, deep, sandy, along with fast-draining conditions (SAMPAIO, 1995, ARAÚJO FILHO, 2011). For example, kaolinitic yellow Ferralsols, developed from Cretaceous ferruginous sandstones, are widespread in the *Chapada do Araripe* (BEEK; BRAMAIO, 1969). Although these characteristics predominate, exceptions may occur across the sedimentary portion of Caatinga. For example, in “*Complexo de Campo Maior*, a mosaic of ecotones located in the Piauí state, shallow, acidic, finer-textured, and poorly-drained Plinthosols predominate (VELLOSO et al., 2001).

Other sedimentary formations that are important to the Caatinga flora are the aeolian relict continental dunes and karstic formations. The former was encompassed in the list of the ecoregions (so-called *Dunas do São Francisco*; VELLOSO et al., 2001). There, disjunct dunes form the landscape, with Arenosols (Neossolos Quartzarênicos) predominating. Such Arenosols are usually deep and poor in nutrients due to their essentially quartzose (SiO_2) composition. In addition, there are some residual elevations across the *Dunas do São Francisco* region, where scattered litoric soils (i.e. Leptosols) and rock outcrops can be found (VELLOSO et al., 2001). Karstic environments occur discontinuously in discrete patches across the Caatinga region, specifically in areas between Rio Grande do Norte and Ceará (Jandaíra Group) and also in Bahia and Minas Gerais states (Bambuú Group). Soils derived from karst tend to be characterised by high base saturation levels due to their original calcium-rich parent materials. Taking the Apodí Plateau as an example, where a vast flattened karst landscape occurs, calcitic and dolomitic limestone rocks often give rise to Cambisols (OLIVEIRA et al., 2018). Vertisols with, to a minor extent, Chernozems and Leptosols also occur (ARAÚJO FILHO, 2011; ARAÚJO FILHO et al., 2017). Soils that originated from karstic materials are exceptions among sedimentary environments due to their high fertility (SAMPAIO, 2010; ARAÚJO FILHO, 2011) and the marked presence of high-activity clays. Soils formed from these materials can assume a wide range of characteristics and fall into different soil groups due to the intensity of pedogenetic processes, with a variable degree of calcite accumulation in the soil profile. These processes are known to be intrinsically related to climatic conditions and topography (BACHMAN; MACHETTE, 1977).

1.4 Classification systems and soil diversity of Caatinga

The great geodiversity of Caatinga, along with its semiarid climate has resulted in the previously mentioned patchy “mosaic of soils”, which can be observed in Figure 1.3. The figure also shows the distribution of soil types across the region. The nomenclature used in Figure 1.3 refers to Reference Soil Groups (RSGs). This term is adopted in the World Reference Base for Soil Resources (WRB-FAO soil classification system) for classifying soil types based on diagnostic horizons, diagnostic properties and diagnostic materials (IUSS⁶ WORKING GROUP WRB, 2015). The WRB system consists of two hierarchical levels, i.e., RSGs are the first level (the system has 32 different RSGs in total), and principal and supplementary qualifiers are the second level. Principal qualifiers are ranked in order of importance from right to left before the RSG without brackets, whereas the supplementary qualifiers are placed alphabetically ordered with brackets after the RSG (IUSS WORKING GROUP WRB, 2015). The WRB system was developed to strictly reflect soil-forming processes and was developed to accommodate as far as possible other national systems, such as the Brazilian Soil Classification System (SiBCS; SANTOS et al., 2018). In the SiBCS system, the classification is based on diagnostic attributes and diagnostic horizons and, similarly to the WRB system, was built in hierarchical categorical levels. However, the SiBCS system has six hierarchical categorical levels, *viz.* orders, suborders, great groups, subgroups, families and series. The higher hierarchical levels are based on properties that reflect soil genesis or associated properties (SANTOS et al., 2018). Thus, the correspondence between SiBCS orders and RSGs is more or less straightforward, but it should be noted that some RSGs are not classified in the Brazilian system. Moreover, in the SiBCS, Leptosols, Regosols, Arenosols and Fluvisols of the WRB system are lumped together as “Neossolos”, with the second hierarchical categorical level being “Litólico”, “Regolítico”, “Quartzarênico” and “Flúvico”, respectively. In this work, I adopted the WRB system mostly because it is intended to serve as a common denominator at the international level (IUSS WORKING GROUP WRB, 2015). Table 1.1 provides the approximate general correspondence between the first and second hierarchical levels of SiBCS and RSGs of the WRB system:

⁶ International Union of Soil Sciences

Table 1.1: Approximate correspondence between first levels in the SiBCS and WRB-FAO systems. Adapted from Brazilian Journal of Soil Science (RBCS, 2022).

SiBCS (2018)	WRB (IUSS, 2015)
Argissolos	Acrisols; Lixisols; Alisols
Cambissolos	Cambisols
Chernossolos	Phaeozems; Kastanozems Chernozems (a few)
Espodossolos	Podzols
Gleissolos	Gleysols; Stagnosols (some)
(Gleissolos Sálícos)	Solonchaks
Latossolos	Ferralsols
Luvisolos	Luvisols
Neossolos	—
(Neossolos Flúvicos)	Fluvisols
(Neossolos Litólicos)	Leptosols
(Neossolos Quartzarênicos)	Arenosols
(Neossolos Regolíticos)	Regosols
Nitossolos	Nitisols; Lixisols or Alisols
Organossolos	Histosols
Planossolos	Planosols
(Planossolos Nátricos)	Solonetz
(Planossolos Háplicos)	Planosols
Plintossolos	Plinthosols
Vertissolos	Vertisols
Not classified in Brazil	Cryosols Anthrosols; Technosols Andosols Umbrisols Gypsisols Durisols Calcisols Albeluvisols

Considering Brazilian soils, the Caatinga region exhibits unparalleled soil diversity (or pedodiversity), meaning that several soil types might occur across the landscape scale. Despite the outstanding soil diversity of Caatinga, six soil groups (i.e. Leptosols, Regosols, Arenosols, Fluvisols, Ferralsols, and Acrisols) account for 68.8% of the region. An individual review of each RSG is not provided here, but for the interested reader, excellent accounts of Caatinga soils are available in national exploratory soil surveys (JACOMINE et al., 1971; 1972a; 1972b; 1973a; 1973b; 1975; 1976; 1977; 1979; 1983; 1986) as well as in Araújo Filho (2011), Araújo Filho et al. (2017; 2019), Jarbas et al. (2010), IBGE (2019b). Excellent global soil reviews are available in Driessen et al. (2001) and the World reference base for soil resources (2015).

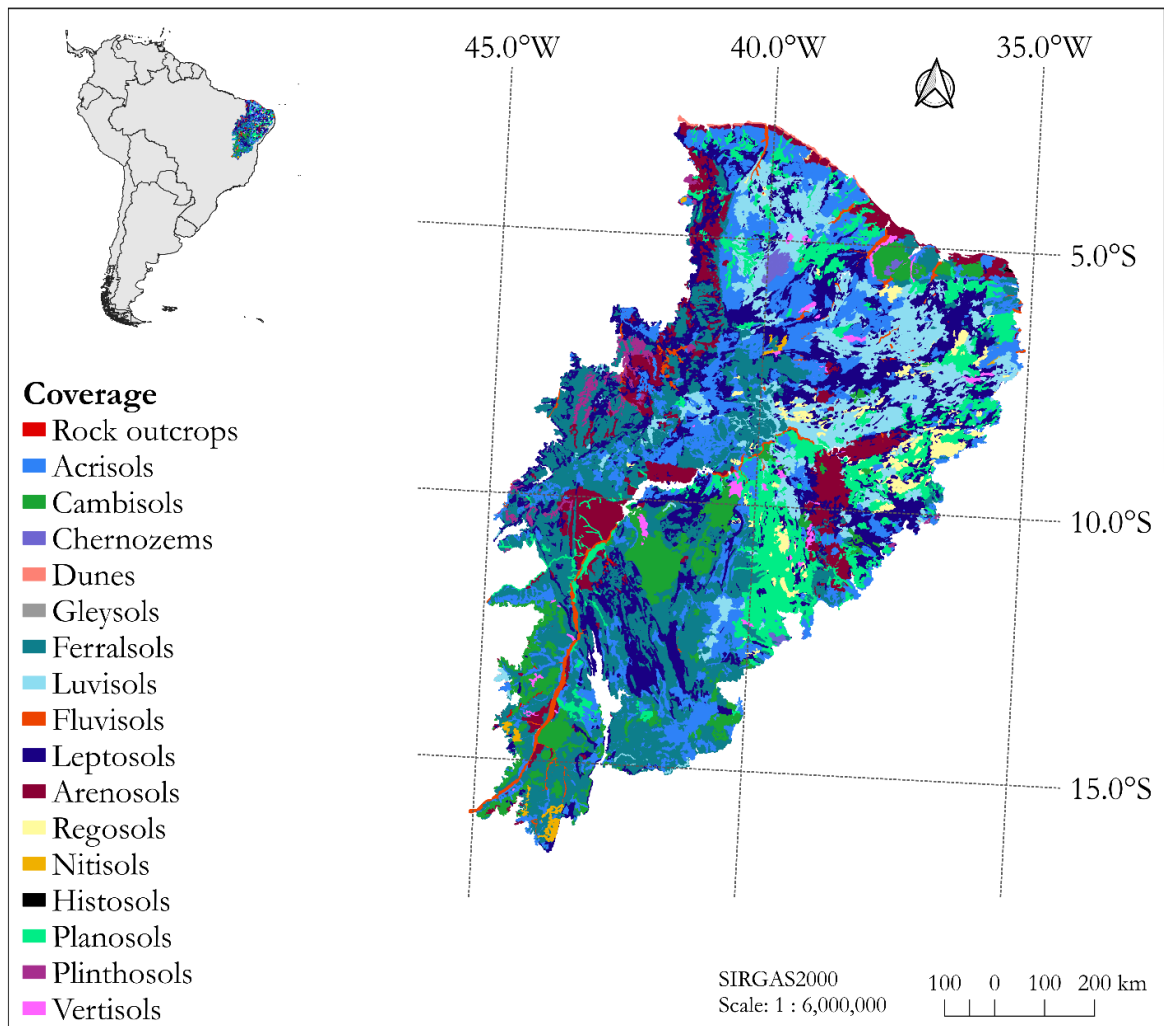


Figure 1.3: Distribution of reference soil groups (RSG) across the Caatinga region. RSGs were adapted from their equivalents from the Brazilian soil classification system (SiBCS). Shapefile source: IBGE's Environmental Information Database – BDIA (theme pedology). Map design: Brunello, A. T.

Regarding other non-included soil groups in Figure 1.3, it is unlikely that other soil orders occur significantly throughout the region. Nevertheless, the existence of specific environments or microenvironments may give rise to less common soil groups. For example, Souza et al. (2022) described five Umbrisols at Borborema Plateau highlands (> 1,000 m a.s.l). These soils showed unusual high soil organic carbon (SOC) contents under relicts of semideciduous forests and Rupestrian Grasslands. In addition, anthropogenic soils analogous to the Amazon *Terra Preta de Índio* can be found in some regions of paleoenvironmental interest such as Anthrosols found in Paraíba state (SOUZA et al., 2020), with the authors also suggesting the inclusion of “Antrosolos” in the SiBCS.

1.5 Geology and soil diversity across Caatinga

The diverse geological history of Caatinga has resulted in a large diversity and spatial variability of soils (Figure 1.3). Proportional coverages of RSGs overlain genetically distinct rock types and geological structural provinces were calculated from vector-based thematic maps available in the IBGE's Environmental Information Database – BDIA; (<https://bdiaweb.ibge.gov.br/>). From these calculations, it results that 40.81% of the Caatinga soils overlain metamorphic rocks, where Acrisols, Leptosols, Ferralsols and Planosols (see Table S1.1). Sedimentary terrains account for 28.64% of the Caatinga land area (of which 30.34% are karst zones). Sedimentary terrains are mapped as being mostly overlain by Ferralsols, Arenosols and Leptosols. Karst areas are mainly constituted of Cambisols. Interestingly, Ferralsols were also reported in some karst environments under specific conditions related to terrain physiography and drainage (FERREIRA, 2013). Igneous plutonic terrains account for 14.47% of the territory, where the most representative soil group are Acrisols, Leptosols, Planosols, Luvisols and Ferralsols. Igneous volcanic terrains account for only 0.03% of the area, where the most representative soils are Leptosols, Vertisols, Luvisols, and Acrisols. Finally, 16.05% of the Caatinga soils develop from coverages of the Cenozoic age, where Ferralsols and Arenosols account for about 74% of the soils (absolute and relative RSGs coverages for each geological affiliation type are shown in Table S1.1).

Soils from igneous plutonic and volcanic terrains were not sampled as part of this study. An interesting pattern can be highlighted from the geology *versus* RSGs across geological structural provinces (Table S1.2). In general, a few soil groups (RSGs) account for 70-90% of all soils in each province. For example, in Borborema Province, where the most recent part largely overlain the crystalline core of Caatinga, Leptosols and Luvisols (i.e. low to intermediate pedogenic stages) account for over 50% of the soils. Ferralsols alone occupy nearly 50% of the Cenozoic Coverage domain, which is mostly represented by sediments that have undergone weathering over the last 66 Ma in the Cenozoic Era (IBGE, 2019b). Arenosols occupy alone approximately 50% of the Recôncavo-Tucano-Jatobá basin's area, which makes full sense from the geological standpoint. This is because this basin mostly consists of massive sandstone deposits that accumulated in an aborted rift (CAIXETA et al. 1994; BIZZI; SCHOBENHAUS; MOHRIAK, 2003). Soil-geology associations can be observed in the supplementary 'heat' Tables S1.1 and S2.2, where genetic rock categories and geological provinces, were crossed with RSGs, respectively.

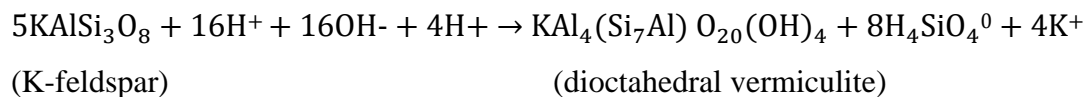
Divergent (or slightly divergent) terms are not uncommon in publications mentioning the fertility of Caatinga soils. So, regarding the predominance of “fertile”, “relatively fertile” or “infertile” soils, and considering geologically distinct parent materials as a determinant force (noting that several exceptions are expected to occur), one can roughly say that Caatinga soils are predominantly fertile as nutrient-rich materials (including carbonate rocks) should occupy around 64% of the Caatinga land. Indeed, most of the Caatinga soils are located in the crystalline basement (DA SILVA; LEAL; TABARELLI, 2017), which has undergone raising and erosion until the Tertiary (SAMPAIO, 1995). Crystalline terrains (referring to metamorphic + igneous plutonic) were calculated to account for 55% of Caatinga’s territory.

1.6 Mineralogy and weathering in Caatinga soils

As detailed in Section 1.3, the complex geological history of Caatinga has resulted in the formation of several disparate soil parent material types (or rock types) that can be found across the geological provinces. The resistance of these parent materials to weathering depends strongly on their mineralogical composition. Goldich (1938) showed that the main rock-forming minerals [namely olivine, augite, hornblende, biotite, Ca-plagioclases (anorthite), Na-plagioclases (albite), orthoclases (potassium-rich or K-feldspar), muscovite and quartz] have variable levels of stability (FONTES, 2012), which follows their respective melting points. Thus, minerals that crystallise first (mafic or ferromagnesian minerals; ↓Si; ↑Fe; ↑Mg; arrows indicating higher and lower concentrations) tend to be much less resistant to weathering than those that crystallise later (felsic minerals; ↑Si; ↑Al). Within the felsic minerals, however, Ca-plagioclases (Anorthites) are less resistant to weathering than orthoclases. These two groups were also described by petrologists as “Bowen’s reactions” series or continuous series of ferromagnesian (mafic) minerals and the discontinuous series of felsic minerals (BOWEN, 1928).

In addition to the intrinsic resistance (or vulnerability) of parent materials to weathering, climatological characteristics also influence weathering intensity. While thermal stress and mechanical weathering are mostly associated with the fragmentation of rocks and the formation of sand and silt particles, clays are formed through chemical weathering (RIGHI; MEUNIER, 1995; WEIL; BRADY, 2016). Within soil particles, sand and silt hold relatively lower specific surface areas (SSA) than clay, but store considerable amounts of weatherable primary minerals such as feldspars, apatite and micas. Conversely, clay particles have a much higher SSA, but store no weatherable minerals. (PALM et al., 2007).

As anticipated, clay particles are formed through climate-mediated chemical weathering (RIGHI; MEUNIER, 1995) and can be broadly separated into 1: 1 aluminosilicate clays (or low-activity clays, LAC) and 2: 1 aluminosilicate clays (or high-activity clays, HAC) (RIGHI; MEUNIER, 1995; QUESADA et al., 2020). The predominance of these types of clays in a given environment will be determined by both the composition of parent materials composition and climate. In soils of semiarid regions, the relatively low and erratic annual rainfall rates, associated with high potential evapotranspiration rates (so high as 2.0 m a^{-1} in Caatinga) exert a great influence on both leaching, weathering, and chemical reactions involved (ARAÚJO FILHO ET AL., 2017; 2019; RIGHI; MEUNIER, 1995). In this respect, an associated important process is the partial hydrolysis. For example, the reaction below shows the partial hydrolysis of a K-feldspar:



In the reaction above, the K-spar is hydrolysed releasing soluble silica and potassium, but also forming a 2: 1 dioctahedral vermiculite, a secondary clay mineral (RIGHI; MEUNIER, 1995; FONTES, 2012). A general sequence of clay minerals transformations can be exemplified as in the following sequence: illite \rightarrow vermiculite \rightarrow smectite, with these transformations proceeding until the depletion of silica and potassium and a concomitant reduction in the surface charge density over time (WILSON, 1999). Partial hydrolysis occurs in soils where leaching occurs at its minimum rates, thus providing specific conditions (i.e. high concentration of base cations and relatively higher soil pH) for the formation of 2: 1 smectite, as long the parent materials contain enough levels of base cations (RIGHI; MEUNIER, 1995).

However, 1: 1 clay minerals, mostly represented by kaolinite in several Caatinga soils (MELFI et al., 1983), also occur significantly in Caatinga where losses of bases are more intense and/or where the parent materials intrinsically have greater proportions of 1: 1 clay minerals, such as rocks rich in felsic minerals (ARAÚJO FILHO ET AL., 2017).

Importantly, clay mineralogy strongly influences the soil surface charge density, ECEC (effective cation exchange capacity) soil structure and water storage properties (PALM et al., 2007; SANCHEZ, 2019; QUESADA et al., 2020). Regarding the latter, HAC particles are contractible (shrink-swell clays or expansive clays), potentially absorbing plentiful amounts of

water during swelling, but shrinking as the water content decreases⁷. Low-activity clays, however, do not swell as a result of water absorption and generally hold less water than HAC soils. Gaiser, Graef, and Cordeiro (2000) have shown the importance of clay mineralogy along with SOC and soil texture in determining the capacity of soils of semiarid regions to retain water at different matric potentials, with HAC soils potentially storing greater water amounts as opposed to LAC soils. Additionally, numerous Fe and Fe and Al (oxy)hydroxide species, typical of Ferralsols, may occur at different proportions across Caatinga soils depending on soil parent material compositions. Ferralsols of sedimentary domains are thought to have undergone more intense weathering in former wetter conditions (ARAÚJO ET AL., 2017). Likewise kaolinite, these compounds are variable-charge clays and usually, their ECEC is about 3 – 10 cmol_c kg⁻¹ (SANCHEZ, 2019). Considering that Ferralsol is the predominant soil type of Caatinga (covering ca. 24% of Caatinga's land), variable-charge clays are expected to strongly influence the biogeochemical behaviour of these soils. Moreover, in Caatinga, soil mineralogies dominated by Fe and Al (oxy) hydroxide species are thought to be more relevant in sedimentary soils with more intensively weathered.

The high sand contents present in several soils of Caatinga make it inappropriate to approach them in terms of clay activity. Rather, the quartz-dominated mineralogy of these soils requires a specific category for them. Quesada et al.(2020) classified a broad suite of soils into “LAC”, “HAC” and “Arenic” to study soil carbon concentrations and stabilisation mechanisms in the Amazon. The latter term is used in the WRB system to describe soils “*having a layer ≥ 0.3 m thick, within the ≤ 1.0 of the mineral surface...*” or in the major part of shallower soils. Therefore, given that the WRB soil classification system is based on soil-forming processes, RSGs can be clustered into LAC, HAC and Arenic categories (QUESADA ET AL., 2020). Thus, RSGs corresponding to more intensively weathered soil such as Ferralsols and Acrisols are typically classified as LAC soils, whereas soils with low to intermediate pedogenetic development such as Leptosols, Cambisols, Luvisols, Alisols, are usually classified as HAC. It is of note that exceptions may occur such as infertile rocky Leptosols (being LAC rather than HAC) that can be found in Caatinga under specific conditions. In Quesada et al.(2020) study, LAC, HAC and Arenic (the latter comprising Arenosols and Podzols) soils had marked differences in terms both in terms of both ECEC and SOC stabilisation mechanisms.

⁷ The *shrink-swell* behaviour in Caatinga's Vertisols (which usually show large cracks when dry) are commonly portrayed as the predominant landscape of Caatinga.

1.7 Properties of Caatinga soils

1.7.1 Soil reaction and cation availability

There is a general perception that Caatinga soils are fertile, being commonly mentioned as “fertile”, “nutrient-rich” or “relatively fertile”. This general perception is associated, in part, with the idea that the typical low rainfall levels lead to minimum leaching rates, which in turn lead to a maintenance of cations in the soil as well as other nutrients. This rationale certainly applies to a significant proportion of Caatinga soils, where in addition to relatively higher contents of the base cations, soil pH (or soil reaction) tends to be relatively high allowing the presence of exchangeable aluminium (Al^{3+}) in low solubility forms. base cations levels (i.e. Ca^+ , Mg^+ , K^+ , Na^+) can be extremely variable in Caatinga soils, which is thought to reflect the composition of their parent materials. For example, Araújo et al. (2017) summarise the sum of base cations (\sum_B) values recorded in representative soils of Caatinga. In their compilation, the maximum \sum_B values of many soil groups were about $50 \text{ mmol}_c \text{ kg}^{-1}$. In addition, Arenosols and Ferralsols had maximum \sum_B values below $5 \text{ mmol}_c \text{ kg}^{-1}$. On the other hand, clay-rich Vertisols and clay-enriched sub-horizons of Luvisols had maximum \sum_B values reaching 400 and 250 $\text{mmol}_c \text{ kg}^{-1}$, respectively.

Despite the relatively high \sum_B values that can be found in Caatinga soils, one should also consider that a considerable part of these soils derives from previous weathered and nutrient-poor parent materials (SAMPAIO, 1995; SAMPAIO, 2010; ARAÚJO, 2011; ARAÚJO et al., 2017). In many of these soils, Al^{3+} is likely to predominate in the soil sorptive complex. Specifically, in Caatinga, soil groups having markedly contrasting chemical characteristics can be found at relatively short distances, with parent materials being a major determinant. For example, RATKE et al. (2020) found marked differences in the properties of soils belonging to the *Gurguéia* watershed in the Piauí state. In their study, soil types reflected original parent materials, i.e. sandstones gave rise to Ferralsols and an Acrisol, gneiss gave rise to a Cambisol and different alluvial sediments originated a Vertisol and an Arenosol. Moreover, soil parent materials had a sharp relationship with soil chemical properties. Namely, soils formed from sandstone or their sediments (Arenosols and Ferralsols) were associated with relatively lower organic matter concentrations, low density of permanent charges, high acidity and high aluminium levels RATKE et al. (2020).

Acidity is a natural characteristic of most Brazilian soils and is related to several potential negative effects on plant establishment and growth. For example, high aluminium

concentrations in acidic soils may be the cause of limitations for root growth (DELHAIZE; RYAN, 1995). Aluminium toxicity may also interfere with cell division, DNA replication, root respiration, enzyme functioning, and plasma membrane function, with implications for water and nutrient uptake, transport and use (BOJÓRQUEZ-QUINTAL et al. , 2017). It has been shown that many plants, especially those exposed to high Al^{3+} levels, developed mechanisms to tolerate aluminium toxicity, which can be separated into two categories: exclusion and resistance to aluminium (avoiding the entrance of Al^{3+} through cell membranes) and internal mechanisms that neutralise Al^{3+} effects. A fuller revision of these mechanisms is available in Bojórquez-Quintal et al. (2017), but some of these mechanisms involve changes in the rhizosphere pH, changes in cell's membrane properties, excretion of metabolites, and internal mechanisms such as aluminium chelation in the cytosol (mostly with organic ligands) and vacuolar compartmentalisation of Al^{3+} . These mechanisms seem to be better studied for Cerrado plants, where soil Al^{3+} levels usually stand out, with a recent work (OLIVEIRA et al. , 2019a) showing that 77.4% of native trees and shrubs species (among 31 species) have shown mechanisms of Al^{3+} avoidance through exclusion as opposed to accumulating this element in their tissues (the remaining species).

Evaluating the influence of soil and climate on the discrimination of plant physiognomies comprised in Caatinga, Oliveira et al. (2019b) found that soil cations, represented by both base and Al^{3+} saturation and exchangeable potassium (K), were the most important soil attributes. In their work, the occurrence of Cerrado species was tightly associated with higher Al^{3+} saturation levels. According to the authors, such a high concentration of Al^{3+} in the soil also acts as a barrier to the occurrence of SDTFs. In addition, the occurrence of Caatinga *stricto sensu* stands was associated with higher contents of exchangeable potassium, which was attributed to relatively higher levels of 2 : 1 clay minerals and the presence of K-bearing primary weatherable minerals.

Other than these considerations, Al^{3+} tolerance mechanisms may take place in the discussion of biome transitions. It was hypothesised that in the eventual absence of fire and predominance of sufficiently fertile soils, Cerrado formations might be, if propagules are available, colonised by species of semideciduous, dry forests or even evergreen forests (BUENO et al. , 2018). However, if the underlying soils are aluminium-rich, which is thought to be primarily associated with the nature of parent materials, Cerrado species (generally adapted to high Al^{3+} levels) would be expected to outcompete and dominate the vegetation over time (DEXTER et al., 2018).

1.7.2 Carbon

The soil organic carbon (SOC) contents result from the net balance of organic matter inputs to the soils and its relative decomposition (or mineralisation) rates (SMECK, 1985; BRUUN; ELBERLING; CHRISTENSEN, 2010; SINGH et al., 2018). Notwithstanding, soil general fertility, texture, mineralogy (BRUUN; ELBERLING; CHRISTENSEN, 2010), moisture and climate also are expected to influence losses and accumulation of SOC (QUESADA et al., 2010; QUESADA et al., 2020). It is noteworthy that soils with pH 7.3 or higher potentially contain some inorganic (pedogenic) carbon in the form of carbonates and bicarbonates (SANCHEZ, 2019), which might be the case for many Caatinga soils, especially those developing calcite-rich karst environments.

Due to the relatively low plant biomass formation and, consequently, low organic matter inputs, the uppermost layers of Caatinga soils tend to hold lower average total organic carbon (in both native and human-modified stands) in comparison to other Brazilian biomes (MENEZES et al., 2012). Within Caatinga soils, and contrary to the authors' expectations, Menezes et al. (2021) did not find significant differences in SOC stocks among the most representative soil orders of Caatinga, which were more affected by the type of coverage and land use. Biomass production (i.e. the elementary SOC source) itself might be conditioned by several environmental drivers as will be discussed later in this thesis. So here I will focus on the factors that could potentially control SOC levels in the studied soils.

Parent materials and pedogenic stage are expected to influence soil carbon contents (QUESADA et al., 2010), who found systematic variation in SOC contents across a pedogenic age gradient (reflected by soil types) in forest soils. Nevertheless, soil texture and mineralogy, along with climatic variables are also known to influence SOC levels. Fine-textured soils (i.e. loamy and clayey soils) have a higher specific surface area in comparison to sandy soils (PALM et al., 2007). For this reason, SOC is much more prone to being encapsulated into aggregates of clayey and loamy soils, providing physical protection against mineralisation, which should occur at a much faster rate in sandy soils (SANCHEZ, 2019).

As regards soil mineralogy influences on SOC, although Bruun, Elberling, and Christensen (2010) have found contrary tendencies, soils with abundant high activity clays (e.g. smectite group) are expected to hold a greater potential to protect SOC than low-activity clays (e.g. kaolinite). This is assumed to be due to the relative higher soil surface specific area found in the former class (SINGH et al., 2018). Also of note is that Fe and Al (oxy)hydroxides tend

to associate with clay minerals (e.g. kaolinite), yielding a high capacity to absorb and stabilise organic matter and providing additional protection against biological degradation (BALDOCK; SKJEMSTAD, 2000). Quesada et al. (2020) have shown a significant role of clay to explain SOC storage in highly weathered soils such as Ferralsols and Acrisols, which was assigned to the relatively uniform kaolinitic mineralogy of these soils. On the other hand, less weathered soils (such as Cambisols, Alisols and Plinthosols) had their SOC mainly associated with organo-mineral complexes. In Quesada et al. (2020) study, sandy soils carbon contents were slightly influenced by clay and silt contents, this likely being associated with particulate organic matter. Those authors did not find, however, relationships between SOC and woody productivity, neither above-ground biomass nor temperature and precipitation regimes. Despite related questions that will be addressed in this work, a comprehensive analysis approaching carbon stabilisation mechanisms remains to be undertaken for Caatinga soils.

Soil temperature, moisture and frequency of wetting-drying cycles may also influence SOC. As the temperature rises, an increase in SOC mineralisation can be expected (SANCHEZ, 2019; SINGH et al., 2017) as a result of increased microbial activity. Wetting and drying processes may potentially destroy soil aggregates, but this process should be more important for smectite-rich soils than soils rich in Al and Fe (oxy)hydroxides, which bind SOC much more effectively (SANCHEZ, 2019). In addition, sudden wetting of soils at the onset of rainy seasons may provoke microbial cell lysis, thus releasing nutrients and carbon. These processes are of large importance for soils of semiarid regions due to abrupt changes in soil water status (JARAMILLO; MURRAY-TORTAROLO, 2019).

1.7.3 Nitrogen cycle and causes of soil isotopic discrimination

In contrast to many essential nutrients that originate primarily from soil parent materials (SMECK, 1985), N is primarily derived from biological atmospheric N₂ fixation (BNF) (SPRENT, 2009) and atmospheric deposition (SWAP et al., 1992). Also of note is that the N cycle in soils is mostly associated with organic pools as opposed to phosphorus, the latter usually distributed among organic and inorganic pools (SANCHEZ, 2019). Thus the particular characteristics of the N cycle is of great importance for water-limited ecosystems since the relative availability of nitrogen may depend on biologically-mediated mineralisation rates. Globally, soil gross nitrogen mineralisation (GNM) was shown to be positively correlated with microbial biomass, soil total carbon, soil total nitrogen and mean annual precipitation and

negatively associated with soil pH and bulk density (ELRYS et al., 2021). It seems reasonable, however, to expect that, in semiarid environments, mineralisation rates are mostly limited by climatic aspects, including rainfall total amounts, seasonality patterns and temperature regimes. Microbial cell lysis due to the sudden increase in soil water potential at the onset of rainy seasons has been proposed as an important process of nutrients release in semiarid ecosystems (DIRZO; YOUNG; MOONEY, 2011; JARAMILLO; MURRAY-TORTAROLO, 2019).

A review of the main pathways associated with inputs, outputs and transformations of soil N in SDTFs provides evidence for an “open” N cycle, which is consistent with high N losses commonly measured in these ecosystems (GEI; POWERS, 2014). The authors also noted, however, that most works undertaken in these ecosystems focussed only on the very dry or wettest end of the rainfall spectrum (i.e. $P_A > 1.8$ m). Moreover, although valuable endeavours have been made to improve knowledge of nutrient cycling in SDTFs in the last years, future efforts would be best directed towards the understanding of the role of water availability on nutrient dynamics and integrative approaches encompassing species to ecosystems levels (GEI; POWERS, 2014).

Another key component of the nitrogen cycle in semiarid environments is the wide presence of Leguminosae. Leguminosae (potentially N₂ fixers) is the most species-rich plant family of SDTFs (PENNINGTON; LAVIN; OLIVEIRA-FILHO, 2009), including Caatinga (QUEIROZ, 2006), but BNF may be limited by different factors, such as the absence of rhizobium infestation (absence of nodules), and/or low BNF efficiency due to shortage of other nutrients (SILVA et al., 2017). A field/experimental study has shown that BNF in Caatinga was associated with P-deficiency rather than the absence of rhizobia bacteria infestation (SILVA et al., 2017), which draws attention to the coupling of cycles of essential nutrients. A BNF study in four fragments of native Caatinga (FREITAS et al., 2010) showed that although species of high BNF capability were present (i.e. *Mimosa tenuiflora*, *Mimosa arenosa* and *Piptadenia stipulacea*), the estimated annual quantities added to leaves biomasses through BNF were relatively low (2.5 to 11.2 kg ha⁻¹ yr⁻¹). This was assigned to low proportions of plants that effectively fix N₂ in these communities. The authors also highlighted, however, that these quantities might reach much higher values in regenerating stands such as 130 kg ha⁻¹ year⁻¹. Gei, and Powers (2014) also noted that, despite the high observed overall diversity and abundance of Fabaceae in SDTFs, the biologically fixed N in these ecosystems should be modest.

Natural abundances of ^{15}N (expressed by $\delta^{15}\text{N}$) provide valuable information on soil nitrogen dynamics. This is because $\delta^{15}\text{N}$ integrates a wide range of N transformations over time (HÖGGER, 1997; SANTOS et al., 2022). In general, SDTFs are assumed to have higher N availability in comparison to humid ecosystems (ARANIBAR et al., 2004; SILVA et al., 2017), and measurements of natural abundances of $\delta^{15}\text{N}$ in both soil and leaves have been used to infer the “openness” of the N cycle and the proportion of biologically fixed N (ARANIBAR et al., 2004; FREITAS et al., 2010; RIVERO-VILLAR et al., 2021). This is because when plants are fixing atmospheric N_2 , where the isotopic signature is 0‰, it tends to lower $\delta^{15}\text{N}$ values. On the other hand higher $\delta^{15}\text{N}$ foliar signatures tell that nitrogen most of the N consumed by plants primarily comes from ^{15}N -enriched soil pools where heavy ^{15}N has accumulated due to the process of isotopic discrimination (SWAP et al., 1992; HÖGGER, 1997).

Patterns of soil ^{15}N enrichment have been extensively studied for tropical humid and temperate forests compared to semiarid regions, with tropical forest soils showing, on average, $\delta^{15}\text{N}$ values 8‰ higher than their temperate counterparts (MARTINELLI et al., 1999). In humid forests, nitrogen availability, expressed by isotope and non-isotope data, has been shown to vary primarily with rainfall at a regional scale. At a landscape scale under the same rainfall conditions, however, soil type and texture were shown to be the main driver of N availability (NARDOTO et al., 2008). Moreover, in forest soils, there is evidence that $\delta^{15}\text{N}$ enrichment patterns are associated with changes in P availability across the pedogenetic development. This process is suggested to ultimately affect N dynamics in soils through intricate stoichiometric controls (QUESADA et al., 2010). In addition, it has been suggested that a trade-off between water and nutrients availability should influence isotopic signatures of N in soils, where nutrients may become more important when water is not a limiting factor (SWAP et al., 2004), which is consistent with findings of QUESADA et al. (2010). Furthermore, potential effects of soil cation exchange capacity have been hypothesised to potentially influence isotopic discrimination against ^{14}N , though evidence for this effect was minimal (MARTINELLI et al., 1999). Studies in humid regions, however, where environmental conditions are markedly different than arid and semiarid regions, seem to not contribute significantly to the patterns observed in soils of the latter, where relationships between soil properties and ^{15}N enrichment patterns are far understudied.

Among the available studies, Swap et al. (2004) showed foliar $\delta^{15}\text{N}$ values increasing according to a water limitation gradient (P_A ranging from 0.2 m a^{-1} to 1.3 m a^{-1}) in southern Africa. The strong linear relationship found ($r^2 = 0.54$; $p < 0.01$) was somewhat surprising for

the authors since their study region included manifold soil types, land use history and changes and distinct vegetation composition. Similarly, Aranibar et al. (2004) showed a negative correlation between precipitation levels (i.e. increasing aridity) and both soil and plant $\delta^{15}\text{N}$ values in the Kalahari region, Southern Africa. The latter study, however, also pointed out that the inverse relationship found between plant $\delta^{15}\text{N}$ values and precipitation was even stronger in the sandy soils of 'Kalahari sands' (> 90% of sand) when compared to the results of Swap et al. (2004) for entire southern Africa. This result suggests a role for soil texture in isotopic discrimination. In addition, the authors also found a trend for higher soil $\delta^{15}\text{N}$ values with aridity in wetter years, which was suggested to be related to increased mineralisation of old recalcitrant N pools in these unusual years. Collectively, these studies indicate that the N cycle is strongly affected by rainfall total amounts and annual variability in arid and semiarid environments, along with environmental finer-scale factors such as soil texture and general fertility.

Indeed, further evidence suggests that not only climate has a major influence on N isotopic signatures in semiarid environments, but a suite of soil properties can potentially be important. For example, soil $\delta^{15}\text{N}$ values are influenced by soil organic matter (SOM) stability. In this respect, Craine et al. (2015) suggest that, in addition to relatively high rates of fractionating gaseous N loss commonly associated with clayey soils, clays are capable to stabilise relatively greater amounts of soil organic matter. Thus, high soil $\delta^{15}\text{N}$ values commonly found in semiarid environments can be hypothesised to result from the presence of stable ^{15}N -enriched organo-mineral complexes (CRAINE et al., 2015). Soil pH can also potentially isotopic discrimination processes. Because soil pH affects soil microbial activity, soil microbial biomass and community structure (ACIEGO PIETRI; BROOKES, 2008), this may in turn affect mineralisation rates in soils, with higher soil pH generally associated with high soil $\delta^{15}\text{N}$ values. This can be explained by higher microbial activity at higher pH resulting in higher SOM decomposition and increased N transformations in the soils. Ammonia volatilization is also favoured in soils with high pH (HOULTON; MARKLEIN; BAI, 2015). Therefore, any environmental factor that can potentially affect N transformations in soils is likely to define different isotopic signatures of N in soils. Furthermore, it has been suggested that a trade-off between water and nutrients availability should influence isotopic signatures of N in soils, where nutrients may become more important when water is not a limiting factor (SWAP et al., 2004), which is consistent with the findings of Quesada et al. (2010).

A recent study showed that patterns of $\delta^{15}\text{N}$ enrichment in Caatinga soils have a major climatic control (SANTOS et al., 2022). However, soil clay content and soil pH also had a

positive and negative relationship with $\delta^{15}\text{N}$ values, respectively. The study of Santos et al. (2022) was undertaken along almost the entire longitudinal length of the Pernambuco state, covering distinct physiographic regions (i.e. *Zona da Mata, Agreste e Sertão*) and the soil type was Alisol (common to all physiographic regions studied). Moreover, in that study, the highest $\delta^{15}\text{N}$ values were recorded in soils of *Sertão*, where relatively low and erratic rainfall levels, in conjunction with high temperature and alkaline soil reaction, led to favourable conditions for the N transformation reactions in the soils, which in turn yielded higher $\delta^{15}\text{N}$ values in these soils. Other potential factors driving isotopic behaviour in semiarid environments are poorly understood. Given the high environmental heterogeneity of Caatinga, it is likely that isotopic discrimination is influenced by manifold factors.

1.7.4 Phosphorus

In general, Caatinga soils have been recognised as P deficient (SILVEIRA; ARAÚJO; SAMPAIO, 2006). However, because Caatinga encompasses a wide range of soil parent materials and stages of pedogenic development, P contents and bioavailable forms (or fractions) are expected to vary significantly across these soils. For example, soil total P contents in Caatinga soils were found to range from 123 to 155 mg kg⁻¹ (TIESSEN; SALCEDO; SAMPAIO, 1992), 80 to 390 mg kg⁻¹ (FRAGA; SALCEDO, 2004), 260 to 390 mg kg⁻¹ (ARAÚJO; SCHAEFER; SAMPAIO, 2004), 52 to 1625 mg kg⁻¹ (SILVEIRA; ARAÚJO; SAMPAIO, 2006). The latter study evaluated 69 soils encompassing the most common soil orders found in the region. The highest total P contents were found in Fluvisols, Vertisols, Luvisols, and Cambisols; intermediate contents in Acrisols, Leptosols and Ferralsols; and lowest contents in Regosols, Planosols and Arenosols. Despite the high variation found in soil total P concentrations among the main soil orders of Caatinga, the majority of soils in Silveira, Araújo and Sampaio (2006) study had total P concentrations ranging from 100 to 200 mg kg⁻¹.

Along with common weathering indexes (PARKER, 1970; FIANTIS et al., 2010), soil total P has been for decades used as an index of weathering stage (e.g. WALKER; SYERS, 1976; CROSS; SCHLESINGER, 1995; QUESADA et al., 2010; PORDER; HILLEY, 2011). All these authors found relationships between soil total P and weathering levels. In soil science, however, it is well established that total P itself does not inform much about the P-availability for plants and microorganisms (VITOUSEK; SANFORD, 1986; SANCHEZ, 2019).

In addition, only a few studies have employed more detailed approaches to assess P availability in Caatinga soils using classical P fractionation methods such as the sequential Hedley and coworkers' method (HEDLEY; STEWART; CHAUHAN, 1982). Silveira, Araújo, and Sampaio (2006) found marked variability in soil total P as well as its distributions into organic and inorganic forms between and within the main soil groups of the Caatinga. In general, the largest proportion of P was found in the residual fraction (usually considered biologically non-available) and smaller proportions (7 – 12%) in labile fractions (P extracted with anion exchange resin and sodium bicarbonate, usually considered the most bioavailable forms).

Salcedo (2006) reviewed the main mechanisms controlling the availability of P to plants in soils of the Brazilian semiarid region. It is of note that P inputs to soil systems originate almost entirely from phosphate-bearing primary minerals, particularly apatites (WALKER; SYERS, 1976; SMECK, 1985; QUESADA et al., 2010). Considering that the Caatinga holds a vast range of rock types, the variation in the concentration of soil total P should reflect the variation in parent material P concentration. Porder and Ramachandran (2012) led a global compilation assessing the concentration of P in several rock types, noting a 30-fold variation in P concentration. For example, P varied from 120 mg kg⁻¹ in many ultramafic rocks to > 3000 mg kg⁻¹ in several alkali basalts. Furthermore, silica-rich rocks showed a lower concentration relative to iron-rich rocks. In sedimentary rocks, P concentrations were strongly governed by the grain sizes [i.e. higher in siltstone (finer grains) and lower in sandstone (coarser grains)]. A previous work, assuming a global generic rock classification encountered, on average, 1300 mg kg⁻¹ of P in igneous and metamorphic rocks, 750 mg kg⁻¹ in schists, 350 mg kg⁻¹ in sandstones and lower 180 mg kg⁻¹ in calcareous rocks (JACKSON, 1969, *apud* SALCEDO, 2006). In Porder and Ramachandran's compilation, limestones and dolomites P concentrations were comparably low to sandstones (medians of 500 and 567 mg kg⁻¹ for limestones and dolomites, respectively) and even less for other carbonate rocks (median = 290 mg kg⁻¹). Despite the relatively low P contents commonly found in limestones and dolomites, high soil total P concentrations in karst-derived soils are not rare, which may be attributable to the formation of low-solubility calcium phosphates (PANSU; GAUTHEYROU, 2006). Bioavailable forms, however, may be present in relatively small amounts (FERREIRA et al., 2016).

A recent global analysis found that variations in soil total P are largely explained by the combination of soil organic carbon concentrations, parent material, mean annual temperature, and soil sand content (HE et al., 2021). Under similar climatic conditions (i.e. soil and rock P

measured in adjacent sites), however, Porder and Ramachandran (2012) found that parent materials alone explained 42% of the variation in soil P. Considering the typical low mean annual precipitation (P_A) levels of Caatinga, it can be expected that soil P should be related, to a large degree, to parent rock P levels. One comparison between soil total P as related to original parent material in Caatinga was made in Araújo, Schaefer, and Sampaio (2004), where P fractions of toposequences of Luvisols were compared to their underlying saprolites concentrations, which were greater downslope. Quantifying and comparing soil and rock P can contribute to the understanding of regional and global P variations (PORDER; RAMACHANDRAN, 2012).

In general, phosphate-bearing primary minerals are present as weatherable minerals held in the soil sand and silt fractions, whereas secondary phosphorus minerals are formed as discrete clay particles (SANCHEZ, 2019). Depending on the soil mineral assemblage, sand particles may or not contain several plant-available nutrients (including P). This is of great importance for Caatinga, where sandy soils occur to a large extent, especially considering geomorphological units such as the arenite-dominated Recôncavo-Tucano-Jatobá Basin (Figure 1.2) and other geological units where sandstones or unconsolidated sands are the main parent materials. As a single mineral usually predominate (i.e. quartz) rather than other primary silicate minerals (e.g. feldspar), the sand fraction often contains few plant-available nutrients (WEIL; BRADY, 2017). In addition to the negative relationship commonly found between quartz and P contents in rocks, sandy soils are more prone to P losses through leaching (HE et al., 2021).

Moreover, phosphate anions are retained in the soils only for a short time either because they become immobilised by microorganisms or plants or converted into phosphate secondary minerals (SMECK, 1985; SANCHEZ, 2019). Regarding the latter process, it is generally considered that three main forms of phosphate active secondary minerals are formed (ordered from most to least soluble forms): (Ca)-bonded phosphate, (Al)-bonded phosphate and (Fe)-bonded phosphate, and with the proportion of these minerals being ultimately determined by soil pH (SMECK, 1985; GUO et al., 2000). In other words, as the soil weathers and becomes more acidic, phosphate anions tend to be bounded in less soluble Al and Fe compounds.

Other geochemical processes are also important to release P into the soils. On the one hand, intense leaching of bases associated with high precipitation regimes may catalyse soil acidification in wetter ecosystems – therefore releasing (Ca)-bonded phosphate into soil solution (SMECK, 1985; WEIL; BRADY, 2017). On the other hand, this process should be less important in a semiarid ecosystem. SALCEDO (2006) pointed out that the geological substrate

(i.e. igneous, metamorphic or sedimentary rocks) is of great importance to understanding P pools and dynamics. In general, it is assumed that slightly weathered soils originating from crystalline terrains should be expected to contain higher (Ca)-bonded phosphate, whereas more intensively weathered soils, common in sedimentary terrains, are expected to contain higher amounts of (Fe) and (Al)-bonded phosphorus forms (TIESEN; SALCEDO; SAMPAIO, 1992).

Another geochemical process that also affects P availability in soils is phosphate sorption. In highly weathered acid tropical soils (e.g. Ferralsols), the large proportion of iron and aluminium (oxy)hydroxides species associated with medium to fine-textured particles are responsible for high phosphate fixation rates (SANCHEZ; UEHARA, 1980; GARCIA-MONTIEL et al., 2000). Phosphate anions become bonded to reactive soil clay surfaces through ligand exchanges, i.e. phosphate anions replace hydroxyl groups present in (oxy)hydroxides surfaces (SANCHEZ, 2019). With “soil ageing”, these phosphate anions can penetrate the mineral matrix of the soil, forming extremely insoluble compounds. In Caatinga soils, P sorption is more important in sedimentary areas, such as in highly weathered Ferralsols of the São Francisco and Parnaíba geological provinces (see Supplementary Table S.2.1).

In summary, phosphorus sorption processes are strongly controlled by three main soil bulk properties, *viz.* texture, SOM and mineralogy. And specifically, sandy soils, which are extensively represented in Caatinga, should not present phosphate sorption issues, with a low sorption capacity allowing any phosphate anions present in the soil solution to move downwards the soil profile. Regarding the influence of mineralogy on P sorption, multiple scenarios should exist (or coexist) in Caatinga since diverse mineral species do occur in its soils, e.g. 2: 1 clay mineral (specially smectite group), 1: 1 clay mineral (kaolinite), seldom hydroxy-interlayered vermiculite (HIV) as well as oxidic fractions such as goethite, hematite and gibbsite (ARAÚJO FILHO et al., 2017). It is worth mentioning that the discrimination of mineral types is significantly influenced by climatic characteristics such as temperature and rainfall distribution (RIGHI; MEUNIER, 1995), with the semiarid climate of the Caatinga region indirectly influencing P sorption processes as described above, via an influence on soil mineralogical properties.

An additional property that influences P sorption is soil organic carbon (SOC). This is because the negatively charged radicals of SOC compete with phosphate anions for free hydroxyls present at the sesquioxides surfaces. Thus, the higher the SOC, the lower the chance of phosphate anions being sorbed into the soil mineral matrix (MOSHI; WILD; GREENLAND,

1974). The SOC levels of Caatinga soils have been found to be, on average, relatively lower than soils of other Brazilian biomes (MENEZES et al., 2012), perhaps due to relatively low organic matter inputs to the soils.

A considerable portion of the available P is taken up by plants and immobilised by microorganisms. At some point, this P will return to the soil in the form of organic P compounds (P_O). It is believed that P_O plays a paramount role in some more highly weathered P-deficient tropical soils (TIESSSEN; SAMPAIO; SALCEDO, 2001). Measurements of both labile and more recalcitrant P_O forms in Caatinga have found values ranging from 13% to 60% of the total P (TIESSSEN; SALCEDO; SAMPAIO, 1992, SILVEIRA; ARAÚJO; SAMPAIO, 2006). This buildup of P_O is not generally considered to be the result of the soil-forming process (SANCHEZ, 2019). Rather, an accumulation of P_O relates to the ability of some soils to accumulate organic matter (SOM), as evidenced by the relatively fertile Fluvisols and Vertisols sampled by Silveira, Araújo and Sampaio (2006). In those soils, the plant biomass production rates were high, which in turn were reflected by higher SOM and P_O contents as compared to the less fertile soils in their dataset.

Finally, the activity of soil microorganisms is subject to seasonal patterns as it is mediated by the temperature and moisture of the uppermost layers of Caatinga soils. For this reason, the biomass of microorganisms and their enzymatic activity should vary over the year, including the production of alkaline and acid phosphatases, in turn impacting the rates of mineralisation of organic P as well its storage in the microorganisms' biomass and release across wet and dry seasons (JARAMILLO; MURRAY-TORTAROLO, 2019).

1.7.5 Micronutrients

There has been little research about the role of micronutrients influencing tropical dry ecosystems functioning, with the availability of micronutrients in Caatinga soils and associated biogeochemical processes virtually unknown. Nevertheless, these nutrients may account for some part of the variation in the vegetation (SAMPALIO, 2010), also likely acting in specific biogeochemical processes. Biondi et al. (2011) evaluated the natural contents of metallic micronutrients (i.e. Fe, Mn, Zn, Cu, Ni and Co) in benchmark soil of the Pernambuco state and found significant relationships between these nutrients and the clay fraction in both surface and subsurface horizons of these soils. The soil organic matter, however, was correlated with most micronutrients only in surface horizons. In addition, the contents of such metallic

micronutrients in most evaluated soils were found to be relatively lower than soils of other Brazilian regions, which was assigned to the predominant presence of mafic rocks (i.e. containing iron-magnesium minerals) of the latter. Nevertheless, despite variations in rock types among the physiographic regions (*Zona da Mata*, *Agreste* and *Sertão*) evaluated in their study, the authors concluded that deficiencies of Fe, Mn and Zn are less likely than Cu, Co and Ni, especially where less advanced weathering and richer parent materials take place.

In addition to the natural concentrations of micronutrients in Caatinga soils, studies considering the contents of these nutrients in plant tissues and their relative biological efficiencies uses are also scarce in Caatinga. Albuquerque et al. (2018), studying tree and shrub species in Acrisols belonging to the geo-environmental unit of the Borborema Plateau, found significant differences in the plant use efficiency of micronutrients following the decreasing order: $Mn > Cu > Zn > Fe$. Moreover, efficiencies levels varied among species, suggesting that some species may perform better than others in edaphically distinct environments, therefore accounting for relatively higher biomass production.

Micronutrients may also affect ecosystem properties through other indirect effects on biogeochemical processes. For example, KASPARI et al. (2008) showed that fertilisation with micronutrients enhanced significantly leaf-litter decomposition in a lowland Panamanian forest. Similarly, a short-term laboratory experiment has demonstrated an increase in leaf-litter decay of tropical dry forests (TDF) species driven by micronutrient supplementation (POWERS; SALUTE, 2011). In addition to mediating biogeochemical processes, micronutrients (B, Cl, Cu, Fe, Mn, Mo, Zn and Ni) are essential for plant development. The individual role of micronutrients for plants has been stressed in several works (e.g. RÖMHELD; MARSCHNER, 1991; ABREU; LOPES; SANTOS, 2007; BLOOM; SMITH, 2015; WEIL; BRADY, 2017) and will not be detailed here. Nevertheless, it is worth mentioning that all these micronutrients influence both plant structure and metabolism, with many being required for the successful completion of the plant's life cycle (BLOOM; SMITH, 2015).

A few underlying factors that control the concentration and availability of micronutrients in soils are as follows: (1) Mineralogy - similarly to other (macro)nutrients, the main source of micronutrients is the dissolution of primary weatherable minerals present in sand and silt fractions (e.g. feldspars, micas) (SANCHEZ, 2019); (2) Soil pH - except for molybdenum (Mo), the availability of the micronutrients decreases as soil pH increases. Generally speaking, slightly acid soils (soil pH_{H_2O} ranging from 6 to 7) are the most optimal for micronutrients uptake; (3) Soil organic matter (SOM) - organic matter is usually micronutrient-

rich so low SOM contents may imply a micronutrients shortage (SHUMAN, 2018); (4) Soil texture – coarser-textured soils (e.g. Arenosols) are susceptible to endure micronutrient paucity mostly because these soils generally are associated with low SOM (LÜ et al., 2016) and low ionic retention capacity; (5) Redox status (waterlogged vs aerated soils) is also known to control micronutrients availability (SHUMAN, 1991). For example, Fe, Cu, and Mn should be much more available in waterlogged soils rather than dry oxidated soils. However, waterlogged conditions should have only local importance in exceptional landscapes (AB’SÁBER, 1974) such as floodplains (“brejos”) adjacent to hillsides and “Chapadas” of Caatinga.

In the context of global drylands (i.e. dry sub-humid, semiarid and arid regions), there is some evidence that increases in aridity may limit the availability of metallic micronutrients (Fe, Cu, Mn, and Zn). It has been argued that independent of soil parent materials, increased aridity may affect negatively plant production, leading to lower organic matter inputs in the soils (MORENO-JIMÉNEZ et al., 2019). In addition, aridity-driven limited weathering and changes in soil reaction (i.e. increased soil pH) may also lead to a potential reduction in micronutrient supplies. Because organic matter holds several micronutrients in complex colloidal organic compounds (WEIL; BRADY, 2017) a reduction in SOC contents may represent a limitation in the availability of these nutrients. Concerning the latter effect, it is well-studied that the solubility and availability of most micronutrients are greater in acid conditions so that an increase in soil pH may influence the form of these elements in the soils, from free ionic forms to hydroxy ions until very stable and insoluble oxides or hydroxides (SHUMAN, 1991; ABREU; LOPES; SANTOS, 2007; WEIL; BRADY, 2017).

1.7.6 Soil water availability and effective rooting depth

Several studies have pointed out that soil water availability (or soil moisture availability) is crucial in determining several ecosystem properties (e.g. CHATURVEDI; RAGHUBANSHI, 2014, GAVIRIA; TURNER; ENGELBRECHT, 2017; TERRA et al., 2018). For example, soil water availability significantly influences the survival of seedlings (MCLAREN; MCDONALD, 2003), tree mortality owing to hydraulic failure (VILAGROSA et al., 2012), and long-term terrestrial carbon uptake (GREEN et al., 2019). Extended periods of water deficit may push many species towards their physiological limits, even though it is well-documented that species living in these ecosystems usually possess mechanisms to help them tolerate water shortage effects. For example, drought-deciduousness and/or root systems that are capable to

exploit the soils at different depths in search of water (OLIVEIRA et al., 2014), in addition to other traits described in Section 1.1.

Within the factors controlling soil water availability, soil texture is generally assumed as the most important property influencing water retention in soils. As a rule of thumb, finer-textured soils tend to hold more water than fast-draining coarser textured soils (JENNY, 1980). Furthermore, texture indirectly influences soil water-holding capacity since it determines soil bulk density, pore size and distribution (PALM et al., 2007). This, in turn, influences the water movement through soils. A second factor that significantly influences soil water retention is clay mineralogy (Section 1.6), which influences, to a large degree, soil properties such as aggregate stability, structure and porosity (TISDALL AND OADES, 1982; PALM et al., 2007).

Soil organic matter (SOM) is the third soil bulk property that contributes to the soil's hydraulic properties. Interacting with the previously discussed properties, SOM affects soil water storage and release (PALM et al., 2007), for at least two reasons: (1) Organic matter enhances soil structure and enlarges the potential water reservoir (FRANCHINI et al., 2009). (2) Organic matter also is widely known to enhance soil aggregation, cohesion and permeability (BRONICK; LAL, 2005; SCHJØNNING et al., 2018).

The soil properties described above strongly influence the amounts of water that can be stored at different matric potentials (ψ_M). For plants, the most important matric potentials reflecting soil water availability are the field capacity (FC) - which represents the maximum water content in the soil after drainage ceases (often assumed as $\psi_M = -0.10$ to -0.30 kPa); permanent wilting point (PWP) - the lower limit for plant water absorption ($\psi_M = -1,500$ kPa); and plant-available water capacity (AWC) - the plant-available water (interval between FC and PWP in which plants can extract water).

In addition to *in situ* soil properties, terrain physiographical characteristics, e.g. depth to impervious layers to water drainage (e.g. rock or hardpans) influence the size of the water reservoir [the maximum plant-available soil water (θ_P)], in turn influencing the ecosystem-level water availability. In general, shallow soils (e.g. < 1.0 m deep), if not replenished in time through rainfall, are expected to supply water for plants only for a few weeks, while deep soils (≥ 2.0 m) might store water for long periods as long as the root system can exploit a large volume of soil (SAMPAIO, 2010).

Only a few studies have been published reporting on soil water availability in both natural and human-modified environments of Caatinga (e.g. GÜNTNER AND BRONSTERT,

2004, PINHEIRO et al., 2017, ALCÂNTARA et al., 2021), but some works in other tropical biomes also shed some light on this discussion. For example, Lloyd et al. (2015) showed through numerical simulations that the presence of shallow impermeable layers might actually be beneficial for the soil water budget as long the reductions in water losses are not being fully compensated by negative effects (e.g. strong runoff and erosion) in the case of heavy rainfall events. Costa et al. (2022) showed that a shallow water table (WT) might be beneficial during moderate drought by buffering water shortage. Nevertheless, that work also showed that during severe drought, forests with shallow WT (dominated by species with shallow root systems and intolerant-drought traits) might endure negative effects such as increased mortality.

In addition to the overall soil water holding capacity of soils, a variety of ecosystem properties such as nutrient availability, vegetation type and climate also influence root growth (GUSWA, 2010). By equating the marginal cost of carbon to invest in deeper roots compared to the benefit of these roots to continued transpiration, Guswa (2010) found deeper roots in ecosystems where the potential evapotranspiration was nearly equal to rainfall rates, which is consistent with a global analysis of roots distribution for terrestrial biomes (JACKSON et al., 1996). This is because, in wetter ecosystems, water is regularly found near the surface, whereas in drier ecosystems, there is usually no water at depth (GUSWA, 2010). Schenk; Jackson (2002) found deeper rooting depths in water-limited ecosystems compared to their wetter counterparts, also noting that the deeper 95% rooting depths were found in sandy soils *versus* clayey soils and across shallow organic horizons relatively to deeper organic horizons. Pinheiro et al. (2013) found effective root depths ranging from 0.6 to 0.78 m in non-restrictive Caatinga soils with 65% of the cumulative root biomass in the soil upper 0.3 m, an intermediate value for tropical deciduous forests and savannas (JACKSON et al., 1996). It is thus readily apparent that climate plays a marked role in root development and dynamics, which then interact with species characteristics and other soil properties (e.g. aluminium levels and overall fertility) in determining the capacity of roots to exploit the soil in search for water and nutrients.

1.8 Above-ground woody biomass (AGB_w)

Above-ground biomass (AGB) is a pivotal property of terrestrial ecosystems, reflecting manifold ecosystem services including carbon uptake and storage (POORTER et al., 2015). More often than not, studies that focus on environmental controls on AGB in Caatinga (as in seasonally dry tropical forests worldwide), have tested only climate variables rather than soils

and potential soil-climate interactions. This is either because of the lack of the requisite *in situ* soils or because of inconsistent soil sampling protocols and laboratory analyses across sites. The largest collection of standardised soil information is available in the Brazilian System of Soil Information (EMBRAPA, 2022). Oliveira et al. (2019) using EMBRAPA's soil data set showed that, rather than climate or soil separately, a combination of soil and climate predictors, performed better in separating plant physiognomies comprised in the Brazilian semiarid zone.

A notable characteristic of Caatinga region AGB is that the region is highly human-modified (SOUZA et al., 2019; CASTANHO et al., 2020a). Souza et al. (2019) pointed out that AGB can be a multi-driven characteristic in a given ecosystem, especially where human disturbances took place. The authors tested species richness, successional stages, plant functional composition, rainfall, soil fertility, and grazing impacts as potential biomass drivers in Caatinga and found a high variation between stands ($28.48 \pm 23.32 \text{ Mg ha}^{-1}$) mostly explained by successional stage, species richness and rainfall. Castanho et al. (2020a) compiled information from 104 published data reporting on Caatinga AGB values and found a variation between 5 – 118 Mg ha^{-1} across a variety of plant physiognomies. Furthermore, through a satellite product, Castanho et al. (2020a) estimated that around the year 2000, over 50% of the Caatinga region had AGB levels as low as $< 2 \text{ Mg ha}^{-1}$ (accounting for ca. 1% of total Caatinga's AGB), 20% of the region had AGB in the range of 40-80 Mg ha^{-1} (accounting for 55% of the region's total AGB), and only 7% of the region had AGB ranging from 80 to 130 Mg ha^{-1} , representing another 31% of the region's total AGB of the region (the remaining AGB was in stands with 2-40 Mg ha^{-1}).

These results illustrate the high spatial variability of AGB in Caatinga, reflected by at least three hierarchical levels, i.e. macro, meso and micro-variability, these being with climate and soil effects, current land-use of a given stand and the successional age, respectively (CASTANHO et al., 2020a). Therefore, any inferences concerning AGB in Caatinga must necessarily specify which factors are being tested.

Nevertheless, when referring to natural stands (i.e. without significant disturbances, at least in a few last decades), a common distinction often made is “Dense Caatinga” and “Open Caatinga”. The former generally refers to those stands with closed (or nearly closed) canopies, whereas the latter refers to those stands with intermediate regeneration levels or those with natural limitations for plant growth such as very limited soil depth (MENEZES et al., 2021). Commonly, AGB values between Dense and Open Caatingas vary significantly. For example, Menezes et al. (2021) reported average AGB values of 42.3 ± 6.2 and $22.7 \pm 6.0 \text{ Mg ha}^{-1}$ for

Dense and Open Caatingas, respectively (using a conversion factor of 0.47 since the authors provided C stocks values). Also noted in Menezes et al. (2021) discussion is that, on average, AGB values of old-growth Dense and Open Caatingas tend to be lower compared to other SDTFs in South America. This was attributed to the Brazilian Caatinga region being markedly drier than other places in the continent, with water being a major limiting factor in this semiarid ecosystem. That said, one should also bear in mind that water availability does not depend on precipitation itself, but on rainfall seasonality and soil water storage characteristics.

Concerning studies reporting on potential constraints for above-ground woody biomass in SDTFs, Becknell, Kucek; Powers (2012), examining 44 SDTFs worldwide have shown that mean annual precipitation (P_A) itself explained over 50% of the above-ground biomass in old-growth SDTFs. This finding is consistent with other research supporting that biomass accumulation is related to rainfall gradients (BROWN; LUGO, 1982; POORTER et al., 2016; MOORE et al., 2018). However, it is noteworthy that some studies, beyond considering P_A itself, also considered other water availability metrics, such as climatic water deficit (CWD). Indeed, it seems sensible that water availability does not depend on precipitation itself but the final water budget. For example, Poorter et al. (2016) showed that biomass accumulation in regeneration forests resulted from water availability (represented by lower climatic water deficit and higher rainfall). Some works have, however, looked at the influence of soil properties on vegetation characteristics of SDTFs at local scales. For example, PEÑA-CLAROS et al. (2012) found a considerable role of soil nutrient status on a suite of forest properties. Interestingly, the detected soil chemistry effects were more pronounced in drier than moister forests, contrary to the authors' predictions. De Souza et al. (2019) showed the influence of small-scale heterogeneity of soils influencing standing biomass, sprouting rates, and community composition. Maia et al. (2020a) have found interactions between soil and climate variables (i.e. texture, precipitation seasonality and precipitation in the driest quarter), accounting for variations in both above-ground woody biomass and species richness. Most studies, however, covered limited geographical ranges and further research upon larger spatial scales is needed to disentangle the most influential environmental controls influencing the structural properties of Caatinga's SDTFs, across the biome.

1.9 AGB_w, functional diversity and soil properties

Alternative hypotheses have already been tested in the sense of disentangling standing AGB_w drivers and related dynamic processes in dry forests (i.e. recruitment, mortality, and growth of surviving trees). Prado-Junior et al. (2016) tested four contrasting hypotheses that could potentially explain these dynamics and found that the initial standing AGB_w was the most influential factor that determined all AGB_w-associated demographic processes in mature stands. Initial standing AGB_w translates into the “vegetation quantity hypothesis” (LOHBECK et al., 2015). The premise of this hypothesis is that the quantity of vegetation is the most influential factor in determining ecosystem processes, as opposed to the quality of the vegetation. Lohbeck et al. (2015) also found that the amount of vegetation in a site is the most important driver of ecosystem process rates, that is, wood and litter productivity and litter decomposition. Interestingly, despite showing relatively similar results, the studies of Lohbeck et al. (2015) and Prado-Junior et al. (2016) were carried out under very different conditions (that is, the former in wetter successional forests and the latter in dry mature forests). Thus, if it generally applies to dry Caatinga forests, any environmental force driving the initial standing AGB_w may indirectly influence dynamic processes.

Regarding other hypotheses that potentially explain variations in AGB_w, the soil fertility hypothesis, which is comprehensively tested in this thesis, has already been tested in a multitude of studies in humid (e.g. LAURANCE et al., 1999; ROGGY et al., 1999; CLARK; CLARK, 2000; QUESADA et al., 2012) and dry ecosystems (Section 3.1, Chapter 3).

The mass ratio hypothesis (or biomass ratio hypothesis) is based on the idea that the predominant traits in a given community exert a dominant role on ecosystem processes, therefore contributing more significantly to primary production (GRIME, 1998). This could potentially reflect greater biomass accumulation over time. In practice, functional traits are considered the mechanistic connection between plant species assembly and ecosystem functioning (LOHBECK et al., 2015; DÍAZ et al., 2006).

The niche complementarity hypothesis (TILMAN et al., 1997), reflected by the community functional richness (F_{Ric}), is thought to be driven by multiple factors, such as positive symbiotic interactions, improved use of limiting resources, decreased diseases, herbivory, and positive feedbacks in nutrient cycling (TILMAN; ISBELL; COWLES, 2014).

Soil properties have already been shown to influence the functional composition of plant communities. For example, Quesada et al. (2012) found a negative relationship between many soil nutrients and stand-level wood density in humid forests, which was primarily attributed to

water economic strategies. Furthermore, low-density trees were associated with higher turnover rates on physically unfavourable soils (QUESADA et al., 2012). Lira-Martins (2019) also found low wood density values associated with potassium and sodium leaf contents in humid pantropical forests, suggesting that these relationships were mainly mediated by an inverse relationship between parenchymatic tissues and wood density, the former associated with water, nutrients and carbohydrates storage. However, these patterns seem to be less studied in seasonally dry environments. In a recent study, Angelico et al. (2021) found evidence that soil fertility influences tree growth and wood anatomical characteristics in individuals of *Enterolobium contortisiliquum* (Vell.) ('Tamboril'), a species that occurs widely in Brazil, including several areas in Caatinga (CARVALHO et al., 2003). For example, Angelico et al. (2021) found that soil fertility positively influenced stem diameter, tree height, storage compounds associated with parenchymatic cells, fibre walls, and diameter of intervessel pits, these being associated with low values of wood density. The authors also highlighted the need to establish reliable relationships between soil conditions and species wood anatomical features, this strongly reflecting water-economic strategies and nutrient uptake.

The distribution of a given trait value (or a set of trait values) over the niche space can be summarised into orthogonal axes, these representing functional diversity indexes (MASON et al., 2005). Specifically, functional richness (F_{Ric}) represents how much of a multivariate-trait space is filled in a given community; functional evenness (F_{Fve}) reflects the degree to which the basal area is distributed across the multivariate-trait space; and functional divergence (F_{Div}) indicates if the basal area is concentrated at the extremes of the multivariate-trait space (that is, high F_{Div}) or if the basal area is concentrated towards the center of the multivariate-trait space (*sensu* MASON et al., 2005). In this context, determining the influence of soil properties on specific functional traits, as well as its derived functional diversity metrics, is part of the object of study of this thesis.

Supplementary Table S1.1: Reference soil groups (RSGs) coverages according to broad geological types. Total area and fraction cover refer to the proportion of the Caatinga land covered by each RSG. Colours represent relative coverage proportions of each RSG within geologic affiliations, whereby warmer colours means relatively higher coverages whereas cooler colours represent relatively lower coverages. Calculations based on BDIA/IBGE. Coverage values in km².

RSG	Coverages	Fraction cover	RSG	Igneous Plutonic	Fraction cover	RSG	Igneous Volcanic	Fraction cover
Ferralsol	77,223.91	0.56	Acrisol	26,040.73	0.21	Leptosol	71.72	0.29
Arenosol	24,480.95	0.18	Leptosol	25,491.54	0.21	Vertisol	60.98	0.24
Acrisol	8,969.72	0.07	Planosol	20,301.29	0.16	Luvisol	39.47	0.16
Cambisol	7,532.86	0.05	Luvisol	18,034.44	0.15	Acrisol	28.28	0.11
Leptosol	5,066.62	0.04	Ferralsol	15,692.94	0.13	Arenosol	21.60	0.09
Planosol	4,074.14	0.03	Regosol	8,925.05	0.07	Ferralsol	15.03	0.06
Fluvisol	3,565.04	0.03	Cambisol	4,753.65	0.04	Planosol	7.26	0.03
Vertisol	1,465.68	0.01	Nitisol	1,297.19	0.01	Fluvisol	3.88	0.02
Urban areas/water bodies	1,413.76	0.01	Arenosol	1,259.44	0.01	Nitisol	0.90	0.00
Plinthosol	1,260.78	0.01	Urban areas/water bodies	907.04	0.01	Urban areas/water bodies	0.26	0.00
Luvisol	992.80	0.01	Rock Outcrops	404.84	0.00	Plinthosol	0.13	0.00
Dunes	743.46	0.01	Fluvisol	330.91	0.00	Rock Outcrops	0.00	0.00
Gleysol	363.43	0.00	Vertisol	300.64	0.00	Cambisol	0.00	0.00
Nitisol	232.35	0.00	Chernozem	172.65	0.00	Chernozem	0.00	0.00
Regosol	199.59	0.00	Plinthosol	94.30	0.00	Dunes	0.00	0.00
Histosol	15.50	0.00	Gleysol	6.90	0.00	Gleysol	0.00	0.00
Chernozem	12.21	0.00	Dunes	0.00	0.00	Regosol	0.00	0.00
Rock Outcrops	7.91	0.00	Histosol	0.00	0.00	Histosol	0.00	0.00
Total area	137,620.71	1.00	Total area	124,013.55	1.00	Total area	249.50	1.00
RSG	Metamorphic	Fraction cover	RSG	Sedimentary	Fraction cover	RSG	Total	Fraction cover
Acrisol	76,007.22	0.22	Ferralsol	65,662.85	0.27	Ferralsol	205,594.32	0.24
Leptosol	73,597.36	0.21	Leptosol	48,437.54	0.20	Leptosol	152,664.79	0.18
Luvisol	70,562.45	0.20	Arenosol	36,805.05	0.15	Acrisol	142,262.13	0.16
Planosol	53,799.10	0.15	Acrisol	31,216.20	0.13	Luvisol	93,915.53	0.11
Ferralsol	46,999.59	0.13	Cambisol	29,392.66	0.12	Planosol	88,218.36	0.10
Cambisol	8,751.97	0.03	Planosol	10,036.58	0.04	Arenosol	64,795.43	0.08
Regosol	7,854.81	0.02	Fluvisol	5,749.94	0.02	Cambisol	50,431.14	0.06
Urban areas/water bodies	2,896.70	0.01	Luvisol	4,286.38	0.02	Regosol	17,538.35	0.02
Chernozem	2,728.08	0.01	Plinthosol	4,210.12	0.02	Urban areas/water bodies	13,297.11	0.02
Arenosol	2,228.40	0.01	Vertisol	3,218.79	0.01	Fluvisol	10,266.29	0.01
Vertisol	1,822.35	0.01	Urban areas/water bodies	2,712.42	0.01	Vertisol	6,868.44	0.01
Nitisol	1,167.96	0.00	Gleysol	1,303.55	0.01	Plinthosol	6,343.42	0.01
Plinthosol	778.09	0.00	Chernozem	993.16	0.00	Chernozem	3,906.10	0.00
Fluvisol	616.51	0.00	Regosol	558.91	0.00	Nitisol	3,186.08	0.00
Gleysol	30.30	0.00	Nitisol	487.69	0.00	Gleysol	1,704.18	0.00
Rock Outcrops	22.57	0.00	Rock Outcrops	239.11	0.00	Dunes	938.76	0.00
Dunes	9.83	0.00	Dunes	185.46	0.00	Rock Outcrops	674.43	0.00
Histosol	0.00	0.00	Histosol	19.19	0.00	Histosol	34.68	0.00
Total area	349,873.26	1.00	Total area	245,515.58	1.00	Total area	862,639.53	1.00

Supplementary Table S1.2: Reference soil groups (RSGs) coverages in each geologic province encompassed in Caatinga. Total area and fraction cover refer to the proportion of the Caatinga land covered by each RSG. Colours represent relative coverage proportions of each RSG within geologic provinces, whereby warmer colours means relatively higher coverages whereas cooler colours represent relatively lower coverages. Calculations based on BDIA/IBGE. Coverage values in km².

WRB classification	Borborema	Cenozoic Coverage	C. Province and C. Margin	Mantiqueira	Parnaíba	R. Tucano-Jatobá	São Francisco	Total area	Fraction cover
Ferralsol	12,350.05	98,551.00	1,201.75	441.21	15,864.23	2,195.81	75,011.55	205,647.32	0.24
Leptosol	78,519.67	5,719.00	90.68	706.89	20,240.34	4,468.07	43,073.32	152,867.40	0.18
Acrisol	69,544.96	20,003.01	2,474.27	407.31	4,769.38	2,675.64	42,412.80	142,421.72	0.17
Luvisol	83,339.88	1,575.37	17.31	21.56	477.40	1,223.68	7,380.09	94,072.47	0.11
Planosol	42,696.66	8,116.65	183.04	-	1,075.19	3,078.87	33,098.64	88,355.41	0.10
Arenosol	2,596.76	32,333.33	1,331.99	-	10,776.74	14,651.57	3,189.43	64,910.93	0.08
Cambisol	1,508.56	8,636.46	5,591.30	134.85	8.03	337.09	34,186.91	50,435.09	0.06
Regosol	12,864.50	170.40	28.57	-	-	477.13	3,996.33	17,538.71	0.02
Water bodies	777.21	708.68	55.84	-	21.70	1.58	159.22	10,700.23	0.01
Fluvisol	872.60	7,468.71	170.11	-	993.25	28.68	1,033.51	10,620.31	0.01
Vertisol	2,077.64	2,024.92	616.79	-	84.35	431.32	1,639.43	6,876.77	0.01
Plinthosol	189.47	1,480.92	41.21	-	3,989.63	-	647.09	6,349.31	0.01
Chernosol	2,515.19	30.62	991.67	-	-	-	368.56	3,906.11	0.00
Nitisol	954.37	129.11	-	0.85	60.45	-	2,041.34	3,186.14	0.00
Gleysol	15.09	619.07	1,125.84	-	85.61	-	1.82	1,856.67	0.00
Urban area	68.50	193.26	92.68	0.13	34.12	-	85.86	1,193.71	0.00
Dunes	12.35	78.64	886.61	-	-	-	-	991.31	0.00
Rock outcrops	96.78	11.75	-	-	-	-	565.90	674.43	0.00
Histosol	-	32.67	2.80	-	-	-	-	35.47	0.00
Total	311,000.23	187,883.61	14,902.46	1,712.80	58,480.41	29,569.45	248,891.82	862,639.53	1.00

Chapter 2

Chemical and physical properties of geologically
distinct Caatinga soils

Chapter 2 – Chemical and physical properties of geologically distinct Caatinga soils

2.1. Introduction

The semiarid Caatinga soils have a marked spatial variability (Figure 1.3, Chapter 1), which makes it common to be referred to as ‘soil mosaic’ (e.g., SAMPAIO, 1995; OLIVEIRA, 2011; MEIADO et al., 2012). Such a patchy soil pattern can be considered an interactive product of the prevailing semiarid climate and considerable geodiversity, the latter corresponding to both landforms and geologically-determined soil parent materials. In this respect, several schemes of geological compartmentalisation have been proposed in Brazil, with the seminal work of Almeida et al. (1977) being the main basis for the scheme currently adopted by the IBGE. Basically, this scheme separates the territory into discrete structural provinces, i.e., extensive continuous domains with particular rock composition and shared geotectonic history, which is different from the surrounding provinces (ALMEIDA et al., 1977). The structural provinces comprised in the Caatinga borders are shown in Figure 1.2, Chapter 1.

In an attempt to compartmentalise the Northeast Brazil region into discrete units sharing biotic and abiotic features, Veloso et al. (2002) proposed the Ecoregions for the Caatinga biome. This work was mostly based on the Northeast Agroecological Zoning (ZANE) (SILVA et al., 1993) and separated the Caatinga region into eight distinct ecoregions, each of them showing particular biotic and abiotic characteristics, including typically associated soil types. Despite these existing schemes, Caatinga has traditionally been divided into (i) Precambrian lowland crystalline rock depressions; (ii) ancient sedimentary basins and dunes; (iii) karst deposits (FERNANDES et al., 2022). The most typical landscape and ecological conditions are, however, associated with Precambrian crystalline terrains [‘the Caatinga core’ (AB SABER, 1974)]. Indeed, most of the Caatinga soils are derived from crystalline areas (Chapter 1, Section 1.5; DA SILVA; LEAL; TABARELLI, 2017).

From the pedological standpoint, soil types (hereafter RSGs; Reference Soil Groups) associated with (i), (ii) and (iii) are expected to show more or less predictable properties. For example, Leptosols, Planosols and Luvisols are expected to occur in crystalline terrains (i) to a large extent. These RSGs have low to intermediary pedogenetic stages, being commonly shallow but with reasonably fertility conditions. On the other hand, soils developed from sedimentary parent materials (ii) are, in general, deeper but

with less favourable soil fertility conditions (e.g. Ferralsols, Arenosols, Acrisols). Karst environments can potentially give rise to distinct RSGs, including Leptosols, Chernozems and Cambisols, with the latter usually predominating (ARAÚJO FILHO, 2011; ARAÚJO FILHO et al., 2017; OLIVEIRA et al., 2018). Due to their original base-rich parent materials, these soils usually show high base saturation levels and high soil pH, which is particularly important for several biogeochemical processes.

These geological categories have been extensively considered in ecological and botanical studies (KENZO et al., 2017; QUEIROZ, 2006, QUEIROZ et al., 2017, FERNANDES et al., 2020; 2022), sometimes to reflect the influence of nutritional and hydrological soil properties upon vegetation stands (e.g. MORO et al., 2015). But in any case, it seems reasonable to expect that geological features and associated discrete units may reflect soil type distribution across Caatinga. In turn, RSGs are, to a large degree, associated with soil chemical and physical properties since they should reflect soil-forming processes (Section 1.4, Chapter 1).

In this respect, the general idea of *a priori* marked differences among soils derived from different rock types categories, direct qualitative and quantitative comparisons have been rarely been made. Moreover, although some global relationships among soil properties are well-established, studies exploring these relationships are required to improve our general understanding of the pedogenetic process in semiarid environments, especially as regards the underlying biogeochemical processes. For example, if parent material largely determines soil texture and associated biological-mediated processes such as the decomposition of organic matter and nutrient cycling (PALM et al., 2007; SANCHEZ, 2019), then soil geologic affiliation can potentially influence soil organic carbon and nitrogen dynamics. This may more often be the case in semiarid environments, where the influence of parent material on soil properties is expected to be more pronounced than in wetter environments (ARAÚJO et al., 2017). As weathering forces are of smaller relevance compared to humid tropics, levels of exchangeable and total chemical species of macro and micronutrients are mostly driven by the composition of soil parent materials. In addition, under these conditions, leaching and losses of soil bases take place at low rates giving rise to the formation of 2: 1 silicate clay minerals (or expansive clays) through partial hydrolysis reactions (RIGHI; MEUNIER, 1995; FONTES, 2012). Expansive clays are thought to considerably present Caatinga soils (ARAÚJO et al., 2017). Along with soil organic matter (SOM), clay mineralogy and soil

texture are considered soil core properties (PALM et al., 2007; WEIL; BRADY, 2016). These properties covary but interplay with many other soil properties such as pH, and effective cation exchange capacity (I_E).

For instance, the size of the soil sorptive complex reflected by I_E is influenced by both soil particle size distribution and soil mineral assemblage, including silicate clay minerals and species of Al and Fe (oxy)hydroxides. Thus, differences in the relative proportion of these constituents, which are thought to reflect geologic affiliations, are expected to influence soil properties such as soil surface charge density and associated I_E . Effective cation exchange capacity is also sensitive to soil pH, i.e., through hydrolysis, H^+ ions replace cations in the silicate lattice, which can be leached out of the system or form clay minerals (QUESADA et al., 2010). Since hydrolysis-induced soil weathering should occur at a prevailing low rate in Caatinga, the quality of soil parent materials will strongly affect I_E and its interactions with other soil properties. Indeed, I_E seems to be primarily influenced by pedogenic stages, whereas the relative proportions of bases and aluminium seem to be associated with soil parent material and its mineral assemblage (QUESADA et al., 2010).

Similarly, apatite-bearing minerals concentrations in soil parent materials should reflect soil total phosphorus concentrations $[P]_T$, which have already been reported to be three to five-fold higher in soils derived from crystalline terrains compared to soils derived from sediments in Caatinga (SALCEDO, 2006). Nevertheless, manifold factors should influence phosphorus availability in soils. For instance, soil pH ultimately governs the predominance of (by decreasing solubility): (Ca)-bonded > (Al)-bonded > (Fe)-bonded phosphates (SMECK, 1985; GUO et al., 2000). Moreover, parent materials quality and mineral assemblage are expected to influence these associations. In addition, if an ecosystem has evolved so a relatively high amount of P circulates through the organic pathway (P_O), it might be expected that $[P]_T$ correlate to soil total organic carbon (SOC), as reported in Menezes et al. (2012). Nevertheless, it has been also suggested that the build-up of P_O in soils depends on high inorganic P supplies (MCGILL; COLE, 1981). Soil texture, general fertility, and mineral assemblage are also known to influence processes related to SOC dynamics and accumulation in soils (SMECK, 1985; BRUUN; ELBERLING; CHRISTENSEN, 2010; SINGH et al., 2018). Therefore, the interrelationships among geologically-determined soil parent materials, RSGs and soil properties are also expected to relate to SOC concentrations and dynamics.

Several potential causes of variation in soil N isotopic signature in (seasonally) dry environments were described in Chapter 1, Section 1.7.3. The literature shows that soil ^{15}N enrichment can be driven by both edaphic and climatic factors, with the latter usually prevailing in arid or semiarid regions (e.g. SWAP et al., 2004; ARANIBAR et al. 2004; SANTOS et al. 2022). Edaphic effects, however, cannot be disregarded, but the potential mechanisms involved are not fully understood. For example, Aranibar et al (2004) report higher soil and plant $\delta^{15}\text{N}$ values associated with sandy soils. In contrast, clay contents were found to positively influence $\delta^{15}\text{N}$ values in Caatinga soils (SANTOS et al., 2022). Alternative pathways were suggested accounting for the clay effects. For instance, Houlton et al. (2015) pointed out that, in addition to potential higher N fractionating in clayey soils, the latter can also contain stabilised N^{15} -enriched complexes. Importantly, if geologically-determined soil properties (e.g. texture and mineral assemblage) account for variation in isotopic discrimination patterns, then variations in soil ^{15}N values might be reflected by geological origins and associated RSGs.

Spatial information concerning soil $\delta^{15}\text{N}$ values for the Caatinga region is still lacking, with only the work of Santos et al. (2022) reporting on $\delta^{15}\text{N}$ values in Alisols of Pernambuco state under different land uses and varying climatological conditions. Information over a biome-wide scale can be useful to provide insights into N dynamics on a subcontinental scale.

Regarding weathering relationships explored in this work, weatherable primary minerals are known to be associated with sand and silt particles, whereas secondary minerals are known to be mostly associated with clay particles (SANCHEZ, 2019). Thus, given the prevailing quartz (SiO_2) composition of most sand (i.e., negligible weatherable minerals), nutrient capital reserves can be markedly influenced by weatherable primary minerals present in the soil silt fraction, likely reflecting the contents of other chemical species (e.g. Fe, Zn, Mn).

Potential environmental drivers that control effective root depth across soil profiles are also explored in this chapter. Effective rooting depth is thought to reflect a balance between benefits acquired with deeper rooting relative to carbon costs associated with root tissue construction and autotrophic respiration (GUSWA, 2010). Considering the typical negative water balances of the Caatinga, lower mean annual climatic water deficits (CWD) translate into potential evapotranspiration rates closer to mean annual precipitation (P_A) year-round, which in turn might advantage deeper root systems.

An intensive sampling effort spanning a wide latitudinal and longitudinal range across the Brazilian Caatinga territory gave rise to the unique opportunity to study the variability of several soil properties across geologically distinct soil groups. Sites sampled here also encompassed both rainfall and temperature gradients, allowing for the investigation of potential systematic relationships between soil parent materials, current climate conditions and selected soil properties.

Specifically, in this chapter, the following questions:

- 1) How does geology (as a determinant of the types of soil parent material) influence a suite of soil chemical and physical properties of the soil?
- 2) How do soil core properties, i.e., texture, mineralogy, and soil total carbon $[C]_T$ relate to other soil properties considering different soil geological affiliations?
- 3) Do climate [represented by mean annual precipitation (P_A), mean annual temperature (T_A) and climatic water deficit (CWD) and Aridity Index (AI)] exert significant influence on specific soil properties, that is, total carbon $[C]_T$, total nitrogen $[N]_T$, C/N ratio, $\delta^{15}N$ values, and effective rooting depth (R_{EF})?

This study is by no means intended to generalise soil properties for all Caatinga soils belonging to broad geological affiliations. As already mentioned, the astounding environmental heterogeneity of the Caatinga would make this task impossible. Instead, this study is intended to evaluate the above-mentioned questions and serve as a baseline soil survey for current and future research in the established permanent plots achieved by the Nordeste Project (FAPESP Grant 2015/50488-5 / NERC Grant NE/N012488/1).

2.2 Material and methods

2.2.1 Study sites

Data analysed here come from 29 study plots spanning latitudinal and longitudinal ranges, encompassing much of the geographic extent of the Caatinga region (Table 2.2.1). The study sites encompassed a wide range of edaphic conditions with P_A varying from 0.512 m a⁻¹ at CND-01, Bahia to 1.363 m a⁻¹ at PSC-02, Piauí. Soil sampling was undertaken over three intensive fieldwork campaigns (2017, 2018, and 2019). Despite other vegetation types being common throughout the Caatinga domain, only soils under drought-deciduous Seasonally Dry Tropical Forests (herein SDTFs) were analysed in this work. The geographical location of the study sites is shown in Figure 1.2 (Chapter 1), and additional information on the sites are available in Table 2.2.1 and Table 2.2.2 below.

2.2.2 Soil sampling

Taking into account the morphological particularities of individual soils, soil sampling was carried out according to a standard protocol (available at <https://rainfor.org/wp-content/uploads/sites/129/2022/07/soilandfoliarsampling.pdf>) as has been widely used in former field sampling in tropical biomes research such as the RAINFOR and TROBIT Projects (e.g. QUESADA et al., 2010; 2011; LLOYD et al., 2015). Typically, 4–7 soil cores were taken in each 100 x 50 m (0.5 ha). Specifically, four auger cores were established as baseline sampling, with one to three additional cores drilled in cases of within-plot marked spatial variability (e.g. irregular topography, rock outcrops, vegetation changes, etc). In addition, a soil pit was dug just outside each plot to allow for soil profile description, also serving as an additional sampling location for soil physical and chemical analysis (in the same depth as for auger samplings). The maximum sampling depth was set to 2 m. It should, however, be noted that shallower soils are quite common in the region, with bedrock or other hardpans commonly found within the upper 1 m or shallower.

Soil collection at specific depths was undertaken with the aid of an auger set (VanWalt Ltd), with proper drills for different soil types, i.e., sandy, loamy, clayey, stony and rocky. Samples were separated at the depths: 0.00 – 0.05; 0.05 – 0.10; 0.10 – 0.20; 0.20 – 0.30; 0.30 – 0.50; 0.50 – 1.00; 1.00 – 1.50; 1.50 – 2.00 m (according to the maximum depth reached). Soil pits were described following the Guidelines for Soil

Description (JAHN et al., 2006). Important properties such as horizons width, diagnostic horizons and materials, soil structure, colour, roots depth and distribution, soil total depth and the presence (or absence) of any hardened impervious layer were always recorded. After collection, all samples were air-dried as soon as practical and sent to the Soil and Plant Thematic Laboratory (LTSP) of the National Institute for Research in the Amazon (INPA, Manaus, Brazil).

2.2.3 Laboratory analysis

Samples were loosened, sieved in 2 mm (10 mesh), and had residues removed (i.e. stones, vegetation or faunal debris, etc). Most soil chemical and physical analyses were performed in the facilities of the LTSP-INPA, usually starting a few days after the fieldwork campaigns or as soon as practical. All analyses were carried out following specific protocols described in "Procedures for Soil Analysis" (REEUWIJK, 2002). Calibration procedures and standard samples were routinely used to ensure the results. The X-ray fluorescence (XRF; μ -EDX 1300, Shimadzu, Kyoto, Japan) analysis was undertaken by Prof. PhD. José J. L. Leal de Souza, at the Soil Department of the Federal University of Viçosa (UFV), Minas Gerais, Brazil.

2.2.3.1 Soil pH

Soil pH was determined both in water and in 1 M KCl. This method consists of measuring the pH in the supernatant suspension of a 1:2.5 soil-deionised water (or 1 M KCl). Samples were shaken for one hour in a reciprocating shaking machine, and the measurements were undertaken with the aid of a glass electrode. pH in 1 M KCl was also determined as the Δ pH (Δ pH = $\text{pH}_{\text{H}_2\text{O}} - \text{pH}_{\text{KCl}}$) is, in some instances, required for classification purposes. This measure is also used as an indicator of the predominance of soil charges. That is, the lower the Δ pH, the more electronegative the soil is.

Table 2.1: Plot codes, site names/states, latitude, longitude, mean annual precipitation (P_A), mean annual temperature (T_A), altitude, average plot slope, geologic provinces and broad geological classes. Study plots were grouped according to their respective geologic provinces. Note: F = flat; SS = slightly slope.

Plot Code	Site Name/States	Lat	Long	P_A (m)	T_A (°C)	Alt (m a.s.l.)	Average Plot Slope	Geologic Province	Geologic Class
LGE-01	Embrapa Semiárido - PE	-9.048	-40.320	0.59	25.1	384	F	Borborema	Metamorphic
ARI-03	Araripe 3 - CE	-7.271	-39.453	1.08	22.0	680	SS	Borborema	Sedimentary
SJO-01	São João - PE	-8.81	-36.405	0.79	21.4	495	F	Borborema	Metamorphic
SET-01	Serra Talhada - PE	-7.97	-38.385	0.75	23.7	275	F	Borborema	Metamorphic
CGR-01	INSA/Campina Grande - PB	-7.28	-35.976	0.60	22.8	256	F	Borborema	Metamorphic
PAT-01	Patos 1 - PB	-7.007	-37.396	0.79	26.2	311	F	Borborema	Metamorphic
PAT-02	Patos 2 - PB	-7.023	-37.403	0.81	26.2	460	F	Borborema	Metamorphic
SDA-03	R. N. Serra das Almas - CE	-5.117	-40.873	0.82	25.5	760	F	Borborema	Metamorphic
ARI-04	Araripe 4 - CE	-7.36	-39.477	1.01	21.4	901	F	Cenozoic Coverage	Sedimentary
IBD-01	Ibiraba Dunes 1- BA	-10.787	-42.819	0.70	25.5	425	SS	Cenozoic Coverage	Sedimentary
IBD-02	Ibiraba Dunes 2 - BA	-10.785	-42.776	0.68	25.6	421	F	Cenozoic Coverage	Sedimentary
PFF-01	Furna Feia National Park - RN	-5.041	-37.521	0.86	26.8	106	F	Coastal Province	Karst
SCP-02	Serra da Capivara N. Park - PI	-8.862	-42.676	0.77	25.6	500	F	Parnaíba	Sedimentary
SDA-01	R. N. Serra das Almas - CE	-5.147	-40.928	0.97	23.0	620	F	Parnaíba	Sedimentary
PSC-02	Sete Cidades National Park - PI	-4.134	-41.684	1.36	26.0	98	F	Parnaíba	Sedimentary
SCP-01	Serra da Capivara N. Park - PI	-8.865	-42.702	0.79	25.4	620	F	Parnaíba	Sedimentary
BTI-01	Buriti dos Lopes - PI	-3.362	-41.743	1.22	26.6	237	SS	Parnaíba	Sedimentary
SDA-02	R. N. Serra das Almas - CE	-5.141	-40.915	0.97	23.3	510	F	Parnaíba	Sedimentary
CND-01	Canudos - BA	-9.971	-39.006	0.51	22.7	533	F	R. Tucano-Jabobá	Sedimentary
BVT-01	Fazenda Boa Esperança - BA	-12.725	-40.711	0.72	22.2	489	SS	São Francisco	Metamorphic
CJU-01	Lagoa do Cajueiro S. Park - MG	-14.965	-43.916	0.83	24.2	459	F	São Francisco	Sedimentary
MCS-02	Macaúbas 2 - BA	-13.061	-42.517	0.78	24.4	545	F	São Francisco	Metamorphic
MOR-01	Morro do Chapéu 1 - BA	-11.493	-41.331	0.60	20.5	926	F	São Francisco	Sedimentary
CTI-01	Caetité - BA	-14.225	-42.530	0.94	20.9	638	SS	São Francisco	Metamorphic
GBR-01	Gruta dos Brejões - BA	-11.014	-41.439	0.52	23.3	791	F	São Francisco	Karst
GBR-02	Gruta dos Brejões - BA	-11.021	-41.411	0.52	22.9	880	F	São Francisco	Karst
MCS-01	Macaúbas 1 - BA	-13.002	-42.707	0.79	23.1	524	SS	São Francisco	Metamorphic
MOR-02	Morro do Chapéu 2 - BA	-11.495	-41.346	0.59	20.8	857	SS	São Francisco	Sedimentary
JUV-01	Juvenília - MG	-14.425	-44.157	0.90	24.2	593	SS	São Francisco	Sedimentary

Table 2.1 (continued): soil classification (WRB/FAO System), clay activity and main regional parent materials. Notes: Within each soil classification, Reference Soil Groups (RSGs) are shown in bold; HAC = high-activity clays; LAC = low-activity clays; ARE = arenic.

Plot Code	WRB Soil Classification	Clay Activity	Main Regional Parent Materials
LGE-01	Skeletal Abruptic Luvisol (Clayic, Hypereutric, Ochric)	HAC	Phyllite, Marble, Mica Schist
ARI-03	Haplic Alisol (Arenic - ARE, Ochric)	LAC	Sandstone, Siltite
SJO-01	Eutric Protic Arenosol (Ochric)	ARE	Orthogneiss, Migmatite, Metadiorite
SET-01	Rhodic Leptic Luvisol (Arenic, Hypereutric, Ochric, Profondic)	HAC	Metabasalt, Metagabbro, Paragneiss
CGR-01	Leptic Abruptic Luvisol (Clayic, Differentic, Hypereutric, Ochric, Magnesian)	HAC	Metabasalt, Metagabbro, Paragneiss
PAT-01	Rhodic Stagnic Leptic Abruptic Luvisol (Loamic, Hypereutric, Humic)	HAC	Schist, Marble, Paragneiss
PAT-02	Rhodic Stagnic Leptic Luvisol (Loamic, Densic, Hypereutric, Ochric)	HAC	Schist, Marble, Paragneiss
SDA-03	Chromic Abruptic Luvisol (Loamic, Differentic, Hypereutric, Ochric)	HAC	Schist, Paragneiss
ARI-04	Haplic Acrisol (Loamic, Ochric, Vetic)	LAC	Sandstone, Siltite
IBD-01	Hypereutric Protic Arenosol (Aeolic)	ARE	Aeolian Sediment
IBD-02	Hypereutric Protic Arenosol (Aeolic)	ARE	Aeolian Sediment
PFF-01	Skeletal Calcisol (Clayic)	HAC	Calcarenite, Calcilitite, Shale
SCP-02	Xanthic Leptic Acrisol (Loamic, Differentic, Ochric, Profondic, Vetic)	LAC	Sandstone, Shale, Sandy Siltite, Conglomerate
SDA-01	Orthodystric Rhodic Arenosol (Humic)	ARE	Sandstone, Shale, Sandy Siltite, Conglomerate
PSC-02	Orthodystric Regosol (Ochric)	LAC	Sandstone
SCP-01	Orthodystric Skeletic Sideralic Pisoplinthic Cambisol (Loamic, Ochric)	LAC	Sandstone, Shale, Siltite
BTI-01	Orthodystric Hyperskeletal Leptosol (Loamic, Profundihumic)	HAC	Sandstone, Shale
SDA-02	Hyperdystric Leptic Leptosol (Loamic, Ochric)	HAC	Sandstone, Shale, Sandy siltite, Conglomerate
CND-01	Orthodystric Chromic Sideralic Arenosol (Aridic)	ARE	Sandstone, Argillite, Shale, Siltite
BVT-01	Xanthic Acrisol (Loamic, Hyperdystric, Humic, Vetic)	LAC	Orthogneiss
CJU-01	Hyperdystric Arenosol (Ochric)	ARE	Sandstone, Arkose, Calcarenite, Dolomite, Shale
MCS-02	Hypereutric Arenosol (Ochric)	ARE	Gneiss, Migamatite, Orthogneiss
MOR-01	Orthodystric Sideralic Arenosol (Humic)	ARE	Quartz-sandstone
CTI-01	Hyperdystric Regosol (Loamic, Profundihumic, Magnesian)	LAC	Phyllite, Metaconglomerate
GBR-01	Calcaric Chromic Eutric Cambisol (Loamic, Humic)	HAC	Calcarenite, Calcilitite
GBR-02	Hypereutric Calcaric Lithic Leptosol (Loamic, Profundihumic)	HAC	Calcarenite, Calcilitite
MCS-01	Hyperdystric Hyperskeletal Leptosol (Loamic, Ochric)	LAC	Mica-quartzite, Quartzite-feldspar, Metaconglomerate
MOR-02	Hyperdystric Hyperskeletal Leptosol (Loamic, Humic)	LAC	Arkose arenite, Pelite
JUV-01	Rhodic Luvisol (Loamic, Hypereutric, Humic, Profondic)	HAC	Arkose, Argillite, Calcarenite, Dolomite, Shale

2.2.3.2 Soil exchangeable cations

Soil exchangeable cations were determined by the Silver-Tiourea (AgTU) method (PLEYSIER; JUO, 1980). This is a rapid and efficient cations extraction based on the affinity of the AgTU complex with the negatively charged soil colloids. It allows a complete cations extraction (including aluminium) in a single-step centrifuge extraction with an unbuffered 0.01 M AgTU solution (PLEYSIER; JUO, 1980). The concentration of each cation in the samples was then determined using an Atomic Absorption Spectrophotometer (AAS, Model 100b, Perkin Elmer, Norwalk, CT, USA). Subsequently, the soil sum of bases (\sum_B), effective cation exchange capacity (I_E), base (BS%) and aluminium (m%) saturation were calculated as follows:

$$\sum_B = [\text{Ca}]_{\text{ex}} + [\text{Mg}]_{\text{ex}} + [\text{K}]_{\text{ex}} + [\text{Na}]_{\text{ex}}, \quad \text{Eqn. (2.1)}$$

$$I_E = \sum_B + [\text{Al}]_{\text{ex}}, \quad \text{Eqn. (2.2)}$$

where $[\text{X}]_{\text{ex}}$ represents the respective exchangeable cation content.

The effective base saturation is:

$$\text{BS}\% = \frac{[\text{Ca}] + [\text{Mg}] + [\text{K}] + [\text{Na}]}{[\text{Ca}] + [\text{Mg}] + [\text{K}] + [\text{Na}] + [\text{Al}]} \times 100. \quad \text{Eqn. (2.3)}$$

Where BS% = effective soil sum of bases (%). Effective aluminium saturation (m%) was calculated as $\text{m}\% = 100 - \text{BS}\%$.

2.2.3.3 Soil carbon and nitrogen

Total soil carbon and nitrogen were determined using an automated analyser (Vario Max CN, Element Analyzer; PELLA, 1990; NELSON; SOMMERS, 1996).

2.2.3.4 Isotopic composition ($\delta^{15}\text{N}$)

Soil $\delta^{15}\text{N}$ was analysed from composite air-dried samples from the upper 0.00 - 0.05; 0.05 - 0.10; 0.10 - 0.20; 0.20 - 0.30 m soil layers (to be consistent with the other analyses) at the Isotopic Ecology Laboratory of the Center of Nuclear Energy in Agriculture (CENA-USP). Measurements were undertaken with an elemental analyser (Carlo Erba, 1100 model, Milan, Italy), along with a coupled isotopic mass spectrometer (Thermo Quest-Finnigan Delta Plus). The abundance of ^{15}N compared to the lighter ^{14}N was expressed as thousand deviations (‰) relatively to the atmospheric standard through the equation:

$$\delta^{15}\text{N} (\text{‰}) = (\text{R}_{\text{sample}} / \text{R}_{\text{standard}} - 1) \times 1000, \quad \text{Eqn. (2.4)}$$

where $\delta^{15}\text{N}$ is the stable isotopic composition in deviations per thousand and R_{sample} and $\text{R}_{\text{standard}}$ are the respective $^{15}\text{N}:^{14}\text{N}$ ratios of the samples and standard, the latter being internationally adopted as the atmospheric N.

2.2.3.5 Phosphorus

Total soil phosphorus (P) was determined using composite samples from the upper 0.00 - 0.05; 0.05 - 0.10; 0.10 - 0.20; 0.20 - 0.30 m soil layers. Samples were digested with concentrated sulfuric acid, followed by peroxide hydrogen additions (TIESSSEN; MOIR, 1993). After this process, the total P contents were determined by colourimetry using molybdenum blue colour development as described by Olsen and Sommers (1982), using a spectrometer (Model 1240, Shimadzu, Kyoto, Japan).

2.2.3.6 Total reserve Bases (\sum_{RB}) and soil elemental ratios

Soil total cations concentrations were obtained through concentrated sulfuric acid digestion, followed by peroxide hydrogen additions (TIESSSEN; MOIR, 1993). Extract concentrations were determined using an Atomic Absorption Spectrophotometer (AAS, Model 100b, Perkin Elmer, Norwalk, CT, USA), with the sum of total Ca, Mg, K, and Na (\sum_{RB}) was calculated as an indicator of soil chemical weathering (DELVAUX; HERBILLON; VIELVOYE, 1989). The TRB index was calculated as:

$$\sum_{\text{RB}} = [\text{Ca}_T] + [\text{Mg}_T] + [\text{K}_T] + [\text{Na}_T], \quad \text{Eqn. (2.5)}$$

where \sum_{RB} = Total reserve bases, and $[\text{X}_T]$ is the total content of a given base (usually in $\text{mmol}_c \text{ kg}^{-1}$ or $\text{cmol}_c \text{ kg}^{-1}$).

Soil total elemental composition was also obtained using an automated analyser (μ -EDX-1300, Shimadzu, Kyoto, Japan). To help understand weathering status across the studied soils, elemental ratios were calculated from oxides concentrations, these being iron to zircon ($\text{Fe}_2\text{O}_3/\text{ZrO}_2$), potassium to zircon ($\text{K}_2\text{O}/\text{ZrO}_2$) and silicon to aluminium ($\text{SiO}_2/\text{Al}_2\text{O}_3$). The rationale for using zircon (Zr) as a denominator in the ratios is that this element is highly resistant to weathering and immobile in the soil (SHAHID et al., 2013). Using [Zr] as a common

denominator provides a straightforward way to compare groups of soils derived from relatively close parent materials.

2.2.3.7 Soil texture

Soil texture was determined using the pipette method (GEE; BAUDER, 1986). Ten grams of soils were treated with 20 mL of sodium pyrophosphate 5% (a dispersant) and completed to ca. 200 ml in Erlenmeyer flasks. After 18 hours, samples were shaken for 15 minutes and had the sand fraction (sand_f) separated with a 212 μm sieve. The remaining water, soil and dispersant were, subsequently, transferred to a measuring cylinder and completed to 1 L, agitated and left to rest for a pre-established period according to the mixture temperature. After that, the clay fraction (clay_f) of each sample was obtained by pipetting 20 mL from the upper part of the cylinder and the silt fraction (silt_f) was obtained by subtracting sand_f and silt_f from the initial sample weight.

2.2.3.8 Soil bulk density

Soil bulk density was determined through the volumetric ring method (Eijkelkamp Agrisearch Equipment BV, Giesbeek, Netherlands). For this purpose, samples were collected from the trench walls at specific depths, i.e. 0.00 – 0.10, 0.10 – 0.20, 0.20 – 0.30, 0.30 – 0.50, 0.50 – 1.00, 1.00 – 1.50, 1.50 – 2.00 m. In the laboratory, the samples were oven-dried at 105°C until constant weight, and the bulk density was obtained by the division of dried soil mass by the ring of known volume.

2.2.4 Soil classification

The soil classification was attained through the WRB/FAO System 2014 (updated in 2015). The classification procedure is mainly based on the characterisation of diagnostic horizons, properties both observed in the field and determined in the laboratory. These attributes relate to soil-forming processes (e.g. clay illuviation giving rise to *argic* horizons). Initially, the Reference Soil Groups (RSGs) were determined, followed by principal and complementary qualifiers. This system was designed to accommodate national systems instead of substituting them and serving as an international denominator for soil science (IUSS Working Group WRB, 2015). Effective base saturation (BS%) was then calculated to differentiate clay-enriched subsurface diagnostic horizons (i.e. Acrisols, Alisols, Luvisols and Nitisols) and Eutric to

Dystric qualifiers (rather than the previously employed base saturation at pH 7). BS% combines exchangeable bases ($\text{Ca}_{[\text{ex}]} + \text{Mg}_{[\text{ex}]} + \text{K}_{[\text{ex}]} + \text{Na}_{[\text{ex}]}$) extracted by 1 M NH_4OAc (ammonium acetate) at buffer pH 7 and exchangeable aluminium ($\text{Al}_{[\text{ex}]}$) extracted by 1 M KCl. The addition of 1 M KCl was also undertaken in some samples to detect the eventual presence of calcic horizons (i.e. calcium carbonate equivalent in the fine earth fraction $\geq 15\%$). The soil classification was performed with the aid of the WRB Tool 1.1.2.0 for Windows (OrlovDO, 2017; <https://apps.microsoft.com/store/detail/wrb-tool/>), which follows the WRB key in a structured way.

2.2.5 Geological surveying

The geoscience system (GeoSGB) of the Geological Survey of Brazil (CPRM) was used as a reference to achieve proper geological characterisations. In brief, the surveying consisted of identifying the sheets of the International Map of the World (IMW) comprised in the RADAMBRASIL Project (viz. SA.24 – Fortaleza; SB.24 – Jaguaribe; SB.25 – Natal; SC.24 – Aracaju; SC.23 - Rio São Francisco; SD.24 – Salvador; SD.23 – Brasília). Thus, the respective geological charts (available as shapefiles) were thoroughly analysed, and relevant attributes were extracted, such as geological units, initial and final geologic formation times, and predominant rock types (soil parent materials). When feasible, soil parent materials were identified and documented in the field. In addition, local publications, larger-scale geological charts, and personal communication with a few experts (Prof. Dr. José J. L. Leal de Souza, Prof. Dr. Vanda Claudino Sales and Dr. Tony J. F. Cunha) also helped in the sense of adding any relevant information to attain appropriate geologic characterisations.

2.2.6 Soil depth and plant water availability

Because direct soil water availability measurements in the field were impractical, a pedotransfer function (PTF) was used, which indirectly allowed for obtaining soil available water contents (AWC) as given in HODNETT AND TOMASELLA (2002). Volumetric soil water (θ_v) content associated with specific soil textural classes (following USDA soil textural classes) was calculated assuming plant-available soil water as the range between field capacity (-10 kPa) and the permanent wilting point (-1500 kPa). In addition, texture-associated volumetric soil water contents were weighted across each soil profile ($W\theta_v$) according to sampling depths. In Hodnett and Tomasella's work, 771 horizons were included encompassing

several reference soil groups (RSGs) and distinct clay mineralogies, i.e. kaolinite and montmorillonite clays. The calculations were attained according to the widely used Van Genuchten model (VAN GENUCHTEN, 1980) as given in Eqn 2.6.

$$\theta_v = \theta_r \frac{\theta_s - \theta_r}{[1 + (\alpha|\psi|)^n]^m}, \quad \text{Eqn. (2.6)}$$

where θ_v = volumetric soil water content ($\text{m}^3 \text{m}^{-3}$); θ_s and θ_r = the saturated and residual water content, respectively; ψ = a given absolute matric potential; α , n and m stand for shape parameters (m generally assumed as $1 - 1/n$). After that, volumetric soil water content θ_v was calculated for each sample to the maximum measured profile depth (m), thus providing the plant-available water storage capacity (θ_p) in $\text{m}^3 \text{m}^{-2}$ (or m) integrated across the soil profile.

2.2.7 Climatological data

Climatological data were extracted from WorldClim Version 2.1 (released in January 2020). Initially, 19 bioclimatic variables (BIO1-BIO19) were obtained for each site (each variable's meaning can be seen at <https://www.worldclim.org/data/bioclim.html>). These variables represent the historical averages for the 1970 – 2000 period with 30 arc-seconds ($\sim 1 \text{ km}^2$) resolution (FICK; HIJMANS, 2017), with the current version providing a refined version of the previous WorldClim Version 1 database due to the increased number of meteorological stations over the past decade (FICK; HIJMANS, 2017). In this chapter, I use mean annual precipitation (BIO12, P_A) and mean annual temperature (BIO1, T_A).

An estimate of the long-term climatic water deficit (CWD) was also extracted from raster files for each study site. CWD represents the net balance between precipitation and evapotranspiration in the driest months (i.e. months where evapotranspiration exceeds rainfall, usually in mm a^{-1} (CWD is negative by definition) and was obtained from http://chave.ups-tlse.fr/pantropical_allometry.htm with 2.5 arc-minute resolution. For easier interpretation, I here use CWD with opposite positive signs (CWD_{adj}), where CWD_{adj} serves as a measure of the water deficit to which the vegetation is subjected. In addition, potential evapotranspiration (ETP_0) and the Global Aridity Index (AI) Version 3 were obtained from <https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/> with 30 arc-seconds resolution. The index represents the ratio between precipitation and potential evapotranspiration, with higher values representing more humid

conditions (ZOMER; TRABUCCO, 2022). Site elevation was obtained from the Shuttle Radar Topography Mission (SRTM) data.

2.2.8 Data analysis

Data were first grouped into geologic affiliations (i.e. sedimentary - S_{SED} , metamorphic - S_{MET} and karst - S_{KAR}) and according to clay mineralogy [i.e. Low-activity (S_{LAC}), High-activity (S_{HAC}) and Arenic - (S_{ARE})]. As detailed in Section 1.6, Chapter 1, S_{HAC} soils are dominated by 2: 1 silicate clay minerals, with low to moderate weathering status, whereas S_{LAC} soils are dominated by 1: 1 silicate clay minerals, with more advanced weathering. Thus, soils with CEC ammonium acetate pH 7 > 24 $cmol_c kg^{-1}$ were considered S_{HAC} (typically Luvisols; most developing on the metamorphic/crystalline terrains of Caatinga), whereas values below this threshold were considered S_{LAC} soils (typically Acrisols; most commonly found in sedimentary terrains of Caatinga). Soils with predominant loamy sand texture or coarser were classified as S_{ARE} (typically Arenosols; most commonly found in sedimentary terrains of Caatinga). Subsequently, selected soil properties belonging to the above-mentioned geologic affiliations were compared through a non-parametric robust Kruskal-Wallis test (χ^2), followed by the Wilcoxon-Mann-Whitney rank-sum test with Benjamin and Hochberg (BH) correction for multiple comparisons.

Bivariate relationships amongst the studied soil properties were evaluated using Kendall's rank correlation coefficient (τ), with ordinary least squares (OLS) linear models used to evaluate potentially meaningful relationships at the entire dataset level, as well as within the three geologically clustered soils (as detailed above). In a few cases, some data points were not considered in the regression analyses based on justifications as explained throughout the results session. Regression assumptions, i.e. normality of residuals and homoscedasticity, with logarithmical transformations applied when necessary. The spatial independence of the residuals was also checked. For such, the function *listw.candidates* function of the *adespatial* R package (DRAY et al., 2021) was used to generate spatial weighting matrices (SWC). When spatial structures were detected in model residuals, spatial filtering techniques were undertaken using Moran's Eigenvectors Maps (MEMs), which were introduced into the models to correct for spatial autocorrelations.

Additionally, soil $\delta^{15}N$ values were modelled using an OLS multiple linear regression approach. Initially, a series of climatic and edaphic candidate variables that could potentially account for variations in soil $\delta^{15}N$ were selected, *viz.* mean annual precipitation (P_A), aridity

index (AI), potential evapotranspiration (ETP₀), precipitation seasonality (ψ), mean annual temperature (T_A), soil sand fraction (sand_f), soil clay fraction (clay_f), soil effective cation exchange capacity (I_E) and all associated exchangeable cations (i.e. Ca, Mg, K, Na, Σ_B and Al), soil pH_{H2O}, soil total phosphorus - [P]_T, soil total carbon - [C]_T and soil C/N ratio. Aiming to facilitate the model's coefficients interpretation, predictor variables were standardised, i.e. the means of each variable were subtracted from individual observations and then divided by its standard deviation, thus providing comparative scores ('effect size') among predictors using the *caret* package (MAX et al., 2020). Subsequently, a global model expressed in Eqn. (2.7) was constructed for the subsequent steps:

$$\delta^{15}\text{N} = \beta_0 + \beta_1\text{AI} + \beta_2\text{ETP}_0 + \beta_3\psi + \beta_4T_A + \beta_5\text{sand}_f + \beta_6I_E + \beta_7[\text{P}]_T + \beta_8[\text{C}]_T + \beta_9\text{pH}_{\text{H}_2\text{O}} + \beta_{10}\text{C/N} + \beta_{11}\text{AI} \times \psi + \beta_{12}\text{AI} \times \text{sand}_f \quad \text{Eqn. (2.7)}$$

From the global model of Eqn. (2.7), all possible combinations among candidate variables (including interaction terms) were tested using the *dredge* function of the *MuMIn* package (BARTON; BARTON, 2021), with this process generating 121 unique models. Subsequently, an information-theoretic (I-T) approach was used to select those models with $\Delta\text{AICc} < 4$, which retained only five models. Note that, despite some relatively high correlations existing between variables included in the global model of Eqn. (2.7), only variables with Pearson's ($|r| \leq 0.6$) were allowed to be included simultaneously in the same models, with variance inflation factor (VIF) also being posteriorly checked. Moreover, the maximum number of predictor variables included simultaneously in each model was set to three, thus controlling potential overfitting issues. Moreover, since P_A and AI showed a nearly perfect correlation ($r = 0.97$, $p < 0.000$), they were evaluated by replacing one for the other and comparing their performance in the model. Similarly, the replacement of I_E for alternative cations (or Σ_B) and sand_f by clay_f was undertaken, with these attempts not justifying the inclusion of any of these alternative terms in the global model. Subsequently, the potential presence of spatial structures in the model's residuals (represented by the Global Moran's I) was checked in the selected models, with spatial filters (MEMs) being incorporated in those models showing spatially structured residuals. These procedures were comprehensively described in BAUMAN et al., (2018a) and (BAUMAN et al., 2018b). After corrections, models were re-ranked according to their ΔAICc and Akaike weights (W). Subsequently, the model's predictions were extrapolated for the entire Caatinga region with the best-ranked model including only spatially explicit

variables (i.e. AI and ψ). Finally, attempting to identify additional sources of noise in predictions provided by Model 1, $\delta^{15}\text{N}$ data were categorised in terms of mean annual precipitation levels (i.e. high $P_A > 0.8 \text{ m a}^{-1}$ and low $P_A < 0.8 \text{ m}^{-1}$), with a non-parametric robust Kruskal-Wallis test (χ^2) being undertaken to verify potential differences among these P_A categories. In addition, OLS linear regression models were used to investigate the influence of nutrient availability (expressed by I_E) on soil $\delta^{15}\text{N}$ considering different P_A levels. The Caatinga Soil $\delta^{15}\text{N}$ Isoscape Map' was produced using functionalities of the *plyr*, *tidyverse*, *sf*, *geobr*, *ggplot2*, and *ggspatial* R packages. All graphs were produced with the *ggplot2* package (WICKHAM et al., 2021) and all analyses were performed in the environment R version 4.1.1 (R CORE TEAM, 2021). The QGIS 3.16.10-Hannover was also used for geoprocessing and map tools.

2.3 Results

2.3.1 Cations availability and soil texture

The Kruskal-Wallis test revealed consistent differences in some of the studied soil properties associated with the three distinct geologic affiliations. Median values, interquartile ranges (IQR), and statistical comparisons of medians for all variables are shown in Table 2.2. For example, medians for $[\text{Ca}]_{\text{ex}}$ decreased following $S_{\text{KAR}} \geq S_{\text{MET}} \geq S_{\text{SED}}$ ($p = 0.001$); medians for $[\text{Mg}]_{\text{ex}}$ decreased following $S_{\text{KAR}} = S_{\text{MET}} \geq S_{\text{SED}}$ ($p = 0.005$); differences in the medians of $[\text{K}]_{\text{ex}}$ and $[\text{Na}]_{\text{ex}}$ were not significant at $p \leq 0.05$; medians for $[\text{Al}]_{\text{ex}}$ decreased following $S_{\text{KAR}} \geq S_{\text{SED}}$, $S_{\text{SED}} = S_{\text{MET}}$, $S_{\text{MET}} = S_{\text{KAR}}$, ($p = 0.028$). Proportions of soil bases in the sorptive complex typically followed $[\text{Ca}]_{\text{ex}} \geq [\text{Mg}]_{\text{ex}} \geq [\text{K}]_{\text{ex}} \geq [\text{Na}]_{\text{ex}}$, with a few exceptions (Figure 2.1). Median values for $[\text{Na}]_{\text{ex}}$ were comparably low ($\leq 1.0 \text{ mmol}_c \text{ kg}^{-1}$) for all geologic affiliations.

Regardless of geologic affiliation, bases and aluminium concentrations, in general, showed opposite trends, i.e. when base concentrations were high, aluminium concentrations tended to be lower. However, there were a few cases where both bases and aluminium appeared in relatively high concentrations. Soil $\text{pH}_{\text{H}_2\text{O}}$ was strongly associated with both $[\text{Al}]_{\text{ex}}$ and \sum_{B} [Figure 2.2; Kendall's $\tau = -0.63$ ($p = 0.000$) for $[\text{Al}]_{\text{ex}}$, and $\tau = 0.57$; ($p = 0.000$) for \sum_{B}], with soil $\text{pH}_{\text{H}_2\text{O}}$ decreasing markedly from $S_{\text{KAR}} \geq S_{\text{MET}} \geq S_{\text{SED}}$ (Table 2.2, $p = 0.004$). Exchangeable aluminium concentrations in S_{KAR} sites and some S_{MET} sites were virtually negligible and were found to be more pronounced in S_{SED} sites, with S_{MET} sites showing relatively high values only

in a few cases. Figure 2.1-b shows that, in general, effective base saturation was proportionately higher than aluminium saturation, even for soils with relatively higher [Al]_{ex} contents.

Table 2.2: Selected soil properties compared among distinct geological affiliations (i.e. S_{SED}; S_{MET}; S_{KAR}). Letters within lines represent significant differences at $p \leq 0.05$ detected through the Wilcoxon-Mann-Whitney rank-sum test with Benjamin & Hochberg (BH) correction for multiple comparisons. The absence of letters within lines indicates that there were no statistical differences. Kruskal-Wallis chi-squared (χ^2), p -values, median values and interquartile ranges (IQR) for each group are shown.

Variable	χ^2	p	S _{SED} (n=15)		S _{MET} (n=11)		S _{KAR} (n=3)	
			Median	IQR	Median	IQR	Median	IQR
Cations availability and soil reaction								
[Ca] _{ex} (mmol _c kg ⁻¹)	14.49	0.001	2.54 c	3.86	12.35 b	20.57	55.78 a	4.96
[Mg] _{ex} (mmol _c kg ⁻¹)	10.71	0.005	1.15 b	1.81	5.83 a	5.06	9.59 a	1.42
[K] _{ex} (mmol _c kg ⁻¹)	6.95	0.031	0.7	1.34	1.82	1.1	2.58	1.21
[Na] _{ex} (mmol _c kg ⁻¹)	4.79	0.091	0.25	0.27	0.47	0.49	0.27	0.36
[Al] _{ex} (mmol _c kg ⁻¹)	7.17	0.028	4.75 a	7.39	2.02 ab	5.62	0.09 b	0.4
Σ _B (mmol _c kg ⁻¹)	14.99	0.001	5.37 c	3.51	18.46 b	26.15	68.54 a	7.67
I _E (mmol _c kg ⁻¹)	13.34	0.001	11.72 c	9.59	21.97 b	21.3	68.64 a	8.07
pH _{H2O}	11.19	0.004	4.51 c	0.43	5.47 b	1.29	7.77 a	0.2
BS %	10.6	0.005	53.94 b	30.03	87.6 a	33.37	99.86 a	0.48
m%	10.6	0.005	46.06 a	30.03	12.4 b	33.37	0.14 b	0.48
Carbon and nitrogen								
[C] _T (mg g ⁻¹)	4.09	0.129	11.38	9.01	9.55	4.84	16.75	4.01
[N] _T (mg g ⁻¹)	6.17	0.046	0.92 ab	0.51	0.87 b	0.38	1.55 a	0.22
C/N ratio	2.45	0.293	12.13	3.10	11.44	1.95	9.38	2.64
Soil δ ¹⁵ N (‰)	1.27	0.539	8.82	7.38	8.27	2.98	11.11	1.25
Phosphorus								
[P] _T	7.8	0.020	101.3 b	104.22	148.38 b	86.05	468.56 a	416.79
Weathering metrics								
Σ _{RB} (mmol _c kg ⁻¹)	12.81	0.002	60.66 c	74.73	176.27 b	51.17	377.76 a	1043.73
[Fe] _T (g kg ⁻¹)	4.66	0.097	42.64	63.44	44.56	30.26	105.4	62.06
[Zn] _T (mg kg ⁻¹)	9.28	0.010	60 b	68	128 b	48	268 a	78
[Mn] _T (mg kg ⁻¹)	9.22	0.010	412 b	234	912 b	932	2684 a	226
XRF K/Zr	19.94	0.000	6.18 b	10.65	40.77 a	35.82	73.19 a	21.19
XRF Ca/K	3.80	0.149	0.28	0.47	0.23	0.20	0.32	0.44
Water availability								
Wθ _v (m ³ m ⁻³)	5.26	0.072	0.10	0.06	0.12	0.03	0.20	0.05
θ _P (m ³ m ⁻²)	0.37	0.832	0.13	0.11	0.12	0.01	0.11	0.01

Figure 2.1-b also shows that slight increases in soil $\text{pH}_{\text{H}_2\text{O}}$ are associated with marked changes in the dominance of bases or aluminium in the soil sorptive complex and, when soil $\text{pH}_{\text{H}_2\text{O}}$ approaches 6.0, $[\text{Al}]_{\text{ex}}$ levels are negligible.

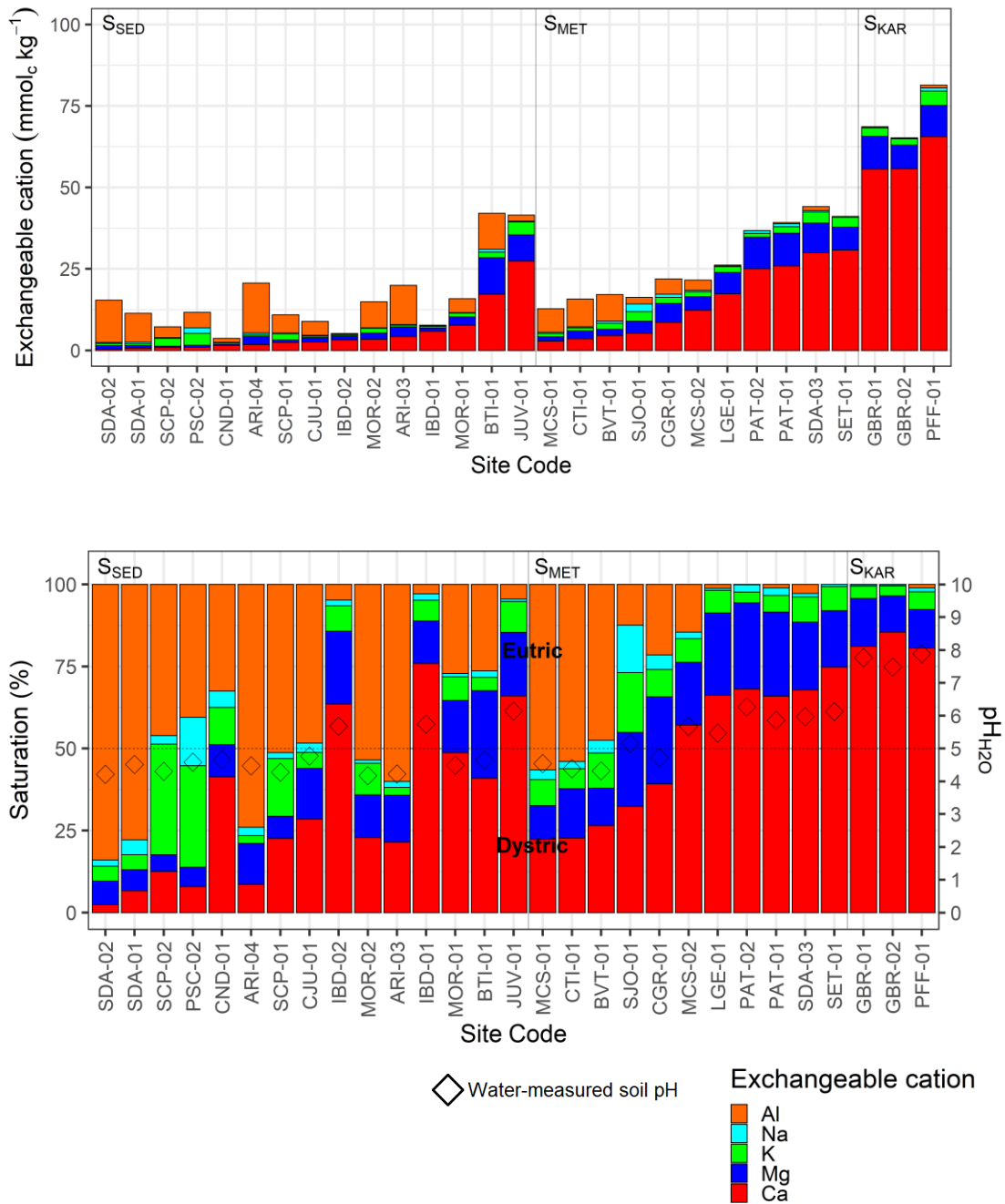


Figure 2.1. a) Contents of main exchangeable cations according to soil geological affiliations [sedimentary (S_{SED}); metamorphic (S_{MET}) and karst (S_{KAR})]; b) AgTU measured soil bases and aluminium saturation and soil pH. In both cases, study sites are ordered according to increasing exchangeable calcium levels. In Figure 2.1-b, soils with BS% greater than 50% relate to the “Eutric” qualifier, whereas soils with BS% lower than 50% relate to the “Dystric” qualifier. Note: “Eutric” and “Dystric” qualifiers are usually used for diagnostic subsurface horizons and here were used for the soil upper 0.3 m layer only for differentiation purposes.

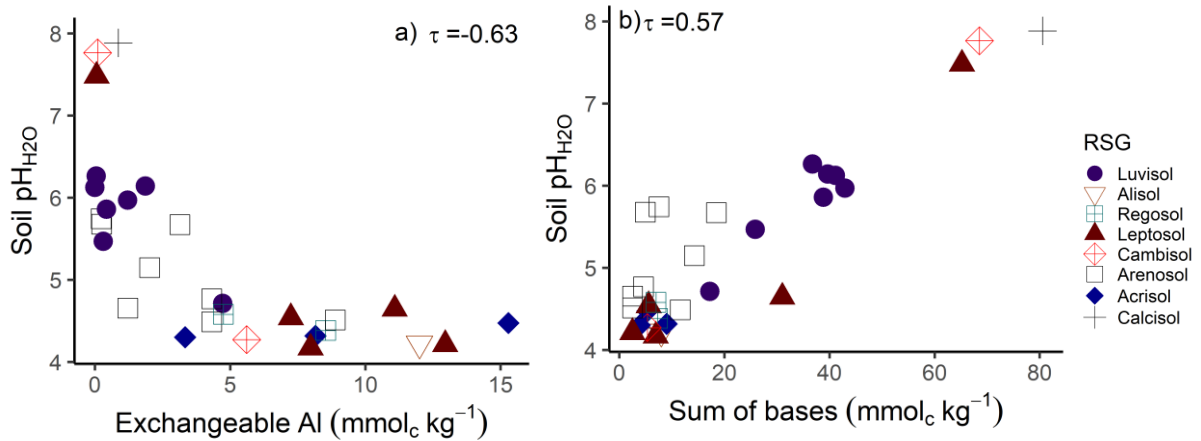


Figure 2.2. a) Water-measured soil pH and exchangeable aluminium – $[Al]_{ex}$; b) Water-measured soil pH and soil sum of bases (Σ_B). RSGs are shown.

Table 2.3 shows Pearson's correlation coefficients (r) for all bivariate relationships among the main soil cations and associated indices. As expected, base cations were in general positively correlated to each other, Σ_B and I_E . Exceptionally, $[Na]_{ex}$ was correlated only with potassium. Correlations levels varied from moderate to nearly perfect.

Table 2.3: Pearson correlation coefficients (r) for all possible combinations among main soil exchangeable cations and associated composite indexes (Σ_B and I_E). Significant correlations at $p \leq 0.05$ are shown in bold below dashes and associated probabilities are shown above dashes.

	$[Ca]_{ex}$	$[Mg]_{ex}$	$[K]_{ex}$	$[Na]_{ex}$	$[Al]_{ex}$	Σ_B	I_E
$[Ca]_{ex}$	–	0.000	0.001	0.961	0.004	0.000	0.000
$[Mg]_{ex}$	0.80	–	0.004	0.383	0.048	0.000	0.000
$[K]_{ex}$	0.59	0.52	–	0.018	0.023	0.000	0.001
$[Na]_{ex}$	0.01	0.17	0.44	–	0.938	0.673	0.656
$[Al]_{ex}$	-0.52	-0.37	-0.42	-0.02	–	0.004	0.068
Σ_B	0.99	0.86	0.64	0.08	-0.52	–	0.000
I_E	0.97	0.86	0.61	0.09	-0.34	0.98	–

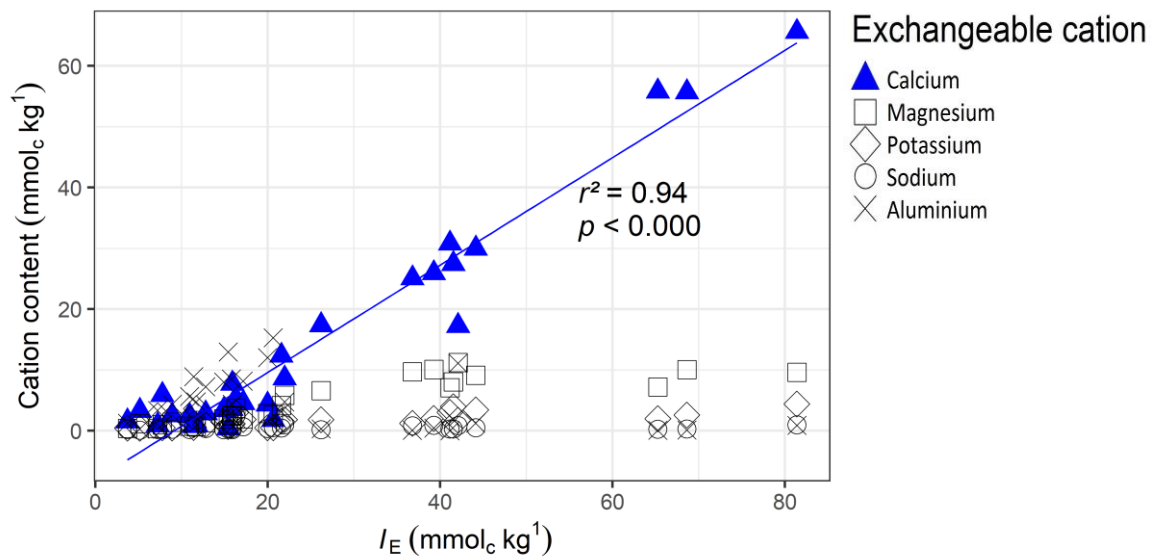


Figure 2.3: Relationship between soil effective cation exchange capacity (I_E) and individual soil exchangeable cations. The blue line represents a linear model fit for I_E and $[Ca]_{ex}$ relationship.

The relative proportion of individual soil cations is further illustrated in Figure 2.3, where $[Ca]_{ex}$ appears as the bulk of I_E for most study soils. Although $[Al]_{ex}$ accounts for the higher proportion of I_E in a few soils, neither $[Mg]_{ex}$ nor $[K]_{ex}$ and even less $[Na]_{ex}$ correlates with I_E so well as $[Ca]_{ex}$ does, with a simple linear regression showing that $[Ca]_{ex}$ accounts for ($r^2 = 0.94$; $p < 0.000$) of the variance in I_E (Figure 2.3). As regards the composite indexes Σ_B and I_E , median values decreased in both cases from $S_{KAR} \geq S_{MET} \geq S_{SED}$ (Table 2.2, $p = 0.001$ and $p = 0.001$, respectively), with S_{KAR} values being ca. three-fold higher than S_{MET} sites and even higher relative to S_{SED} sites. Two S_{SED} sites (BTI-01 and JUV-01) had significantly higher cation contents compared to other S_{SED} sites. Base saturation was close to 100% for S_{KAR} sites but high for S_{MET} sites (median = 88%) and significantly lower for S_{SED} sites (median = 54%, $p = 0.005$). Conversely, aluminium saturation decreased from $S_{SED} \geq S_{MET} = S_{KAR}$ ($p = 0.005$), with S_{KAR} showing negligible values.

Regarding soil texture, and except for S_{KAR} sites, the majority of soil samples analysed for particle size distribution fell into the “Sand Loam” class or coarser, as shown in the USDA textural triangle of Figure 2.4.

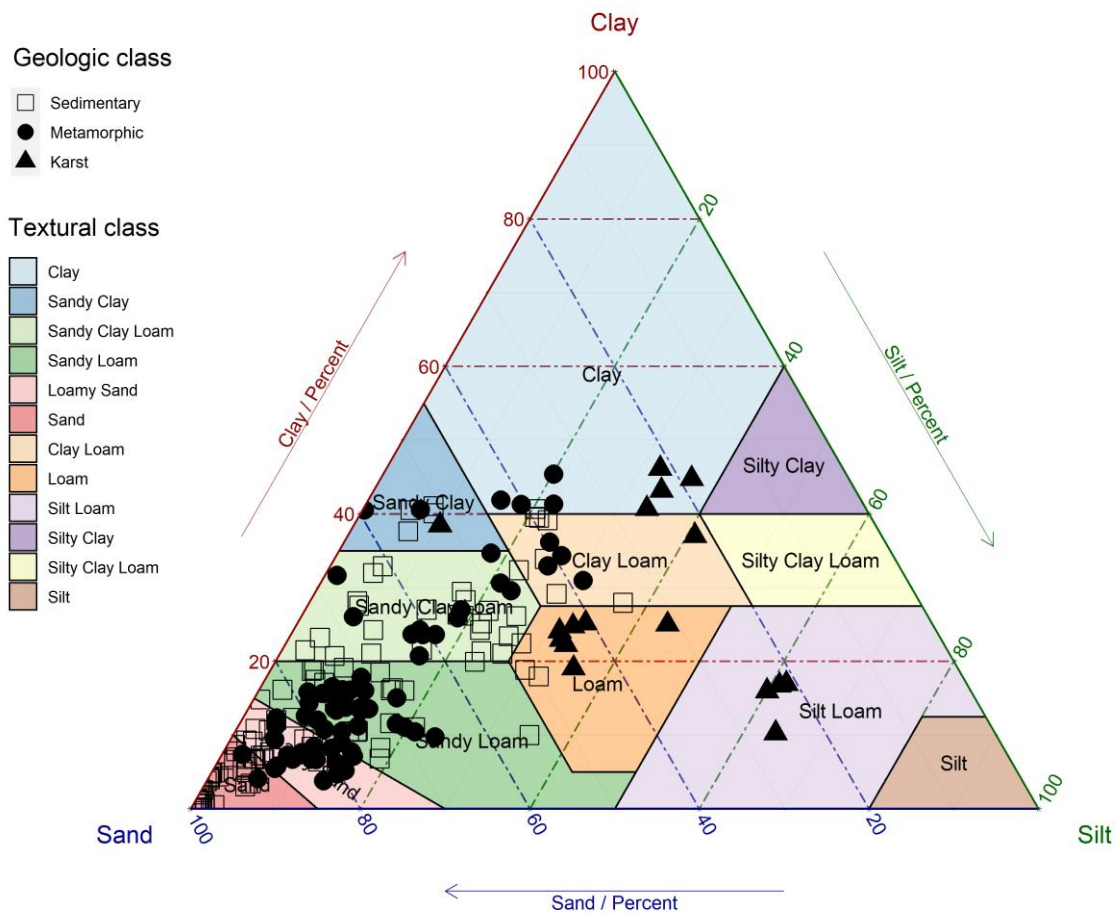


Figure 2.4: Textural classes of soil samples from 29 profiles distributed in the Caatinga region. Samples were discriminated according to their geological affiliations.

Regarding the tested bivariate relationships, all three textural fractions (that is, sand_f , silt_f , and clay_f) accounted for variations in I_E at the whole data set level and at the S_{SED} sites, while only silt_f was associated with I_E at the S_{MET} sites (Table 2.4, Figure 2.5). In addition, XRF measured Fe_2O_3 and Al_2O_3 also appeared as reasonable predictors of I_E in the entire dataset (Table 2.4-a) as well as both S_{MET} and S_{SED} separately (Figure 2.5). For the lowest AICc model (Al_2O_3 only), when Al_2O_3 is equal to its dataset average (8.03%), the model predicts that $I_E = 19.49 \text{ mmol}_c \text{ kg}^{-1}$ (geometric mean) calculated by $I_E = \exp(\beta_0 = 2.970)$. The model also predicts that I_E increases by ca. 19% for every 1% increase in Al_2O_3 since $\exp(\beta_1 = 0.172)$. Considering the second-best AICc-ranked predictor, for each 10% increase in sand_f , I_E should increase by 27% in a proportional sense since $\exp(\beta_1 \times 10 = -0.31)$. A similar interpretation can be taken for all I_E predictors in Table 2.4.

Table 2.4: Pairwise relationships between selected soil properties at the full sampling level. Predictors have been centred so that intercept (β_0) reflects predicted response variables when predictors are at their means and slope (β_1) represents increases in response variables as predictors increases by one unit. Units: sand_f, silt_f and clay_f, Fe₂O₃ and AlO₃ in %; Mean annual temperature (T_A) in °C; Mean annual precipitation (P_A) in m; [C]_T in mg g⁻¹; [N]_T in dag kg⁻¹; [P]_T in mg kg⁻¹; I_E and \sum_{RB} in mmol_c kg⁻¹; [Fe]_T in g kg⁻¹; total zinc and manganese, [Zn]_T and [Mn]_T in mg kg⁻¹, C/N; K/Zr and Ca/K unitless.

<i>x</i>	<i>y</i>	$S_{SED} + S_{MET} + S_{KAR}$					
		β_0	β_1	r^2_{adj}	<i>p</i>	AICc	
a)	sand _f	ln(I_E)	2.970	-0.031	0.60	0.000	45.74
	silt _f	ln(I_E)	2.970	0.045	0.56	0.000	48.54
	clay _f	ln(I_E)	2.970	0.048	0.29	0.001	62.19
	Fe ₂ O ₃	ln(I_E)	2.970	0.382	0.48	0.000	53.38
	Al ₂ O ₃	ln(I_E)	2.970	0.172	0.60	0.000	45.63
b)	Fe ₂ O ₃	[P] _T	142.606	61.094	0.83	0.000	288.9
	Al ₂ O ₃	[P] _T	142.606	17.521	0.43	0.000	315.5
	CaO	ln[P] _T	4.723	1.003	0.12	0.040	-
	SOC	ln[P] _T	4.723	0.034	0.03	0.191	-
	sand _f	[P] _T	142.607	-4.859	0.63	0.000	305.6
	silt _f	[P] _T	142.606	8.552	0.75	0.000	301.8
	clay _f	[P] _T	142.606	6.990	0.39	0.002	319.0
c)	sand _f	ln[C] _T	2.270	-0.019	0.32	0.001	39.6
	silt _f	ln[C] _T	2.270	0.020	0.19	0.011	44.2
	clay _f	ln[C] _T	2.270	0.038	0.25	0.004	42.2
	T_A	ln[C] _T	2.270	-0.052	-0.01	0.370	50.4
	P_A	ln[C] _T	2.270	0.533	0.00	0.302	50.1
	Fe ₂ O ₃	ln[C] _T	2.270	0.188	0.16	0.019	45.2
	Al ₂ O ₃	ln[C] _T	2.270	0.060	0.11	0.051	47.1
d)	T_A	ln[N] _T	2.153	-0.025	-0.03	0.652	48.2
	P_A	ln[N] _T	2.153	0.371	-0.02	0.452	47.8
	I_E	ln[N] _T	2.153	0.014	0.20	0.010	41.2
	[P] _T	ln[N] _T	2.153	0.001	0.15	0.024	42.9
	SOC	ln[N] _T	2.153	0.080	0.77	0.000	6.3
e)	T_A	ln(C/N)	2.432	-0.028	0.05	0.141	-12.8
	P_A	ln(C/N)	2.432	0.169	0.00	0.325	-11.5
f)	silt _f	ln(TRB)	4.794	0.061	0.71	0.000	-
	\sum_{RB}	ln[Fe] _T	3.805	0.001	0.19	0.010	-
	\sum_{RB}	ln[Zn] _T	4.628	0.001	0.24	0.004	-
	\sum_{RB}	ln[Mn] _T	6.358	0.001	0.20	0.009	-
	\sum_{RB}	ln(K/Zr)	2.837	0.001	0.08	0.070	-
	\sum_{RB}	ln(Ca/K)	1.103	0.001	0.06	0.099	-
	\sum_{RB}	[P] _T	142.607	0.688	0.57	0.000	-
	I_E	[P] _T	142.607	4.614	0.69	0.000	-

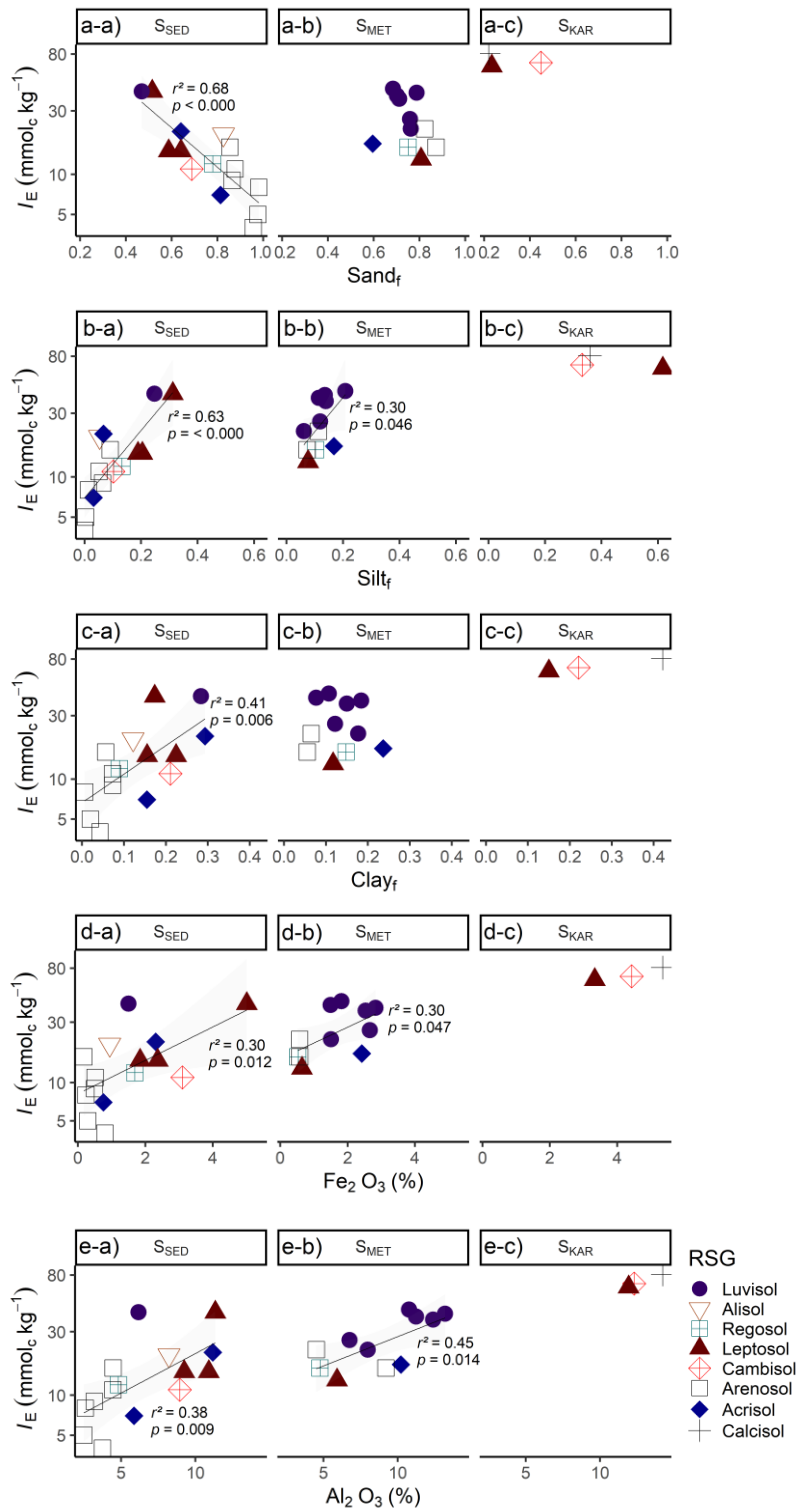


Figure 2.5: Soil effective cation exchange capacity (I_E), soil texture (sand_f, silt_f and clay_f) and total XRF measured Fe₂O₃ and Al₂O₃ relationships (a, b, c, d and e, respectively). Study soils have been discriminated according to their respective geological affiliation (i.e. S_{SED}, S_{MET} and S_{KAR}) across panels. Note that y-axis is in log₁₀ scale.

Main soil base cations availability was considered as a function of the total reservoir of bases (Σ_{RB}) and soil pH_{H_2O} (Figure 2.6 and Table 2.5). It is noteworthy that considering Σ_{RB} and pH_{H_2O} individually, the predictive power was relatively high ($r^2 = 0.60$; $p < 0.001$ for pH_{H_2O} and $r^2 = 0.70$; $p < 0.001$ for Σ_{RB}). However, when Σ_{RB} and pH_{H_2O} were included interactively in the model, the model accounted for 94% of the variation in the sum of bases. As predictors were centred at their means and scaled by their standard deviations (SD), Table 2.5 shows that holding all predictors at their dataset averages, modelled $\Sigma_B = 17.62 \text{ mmol}_c \text{ kg}^{-1}$ and increasing

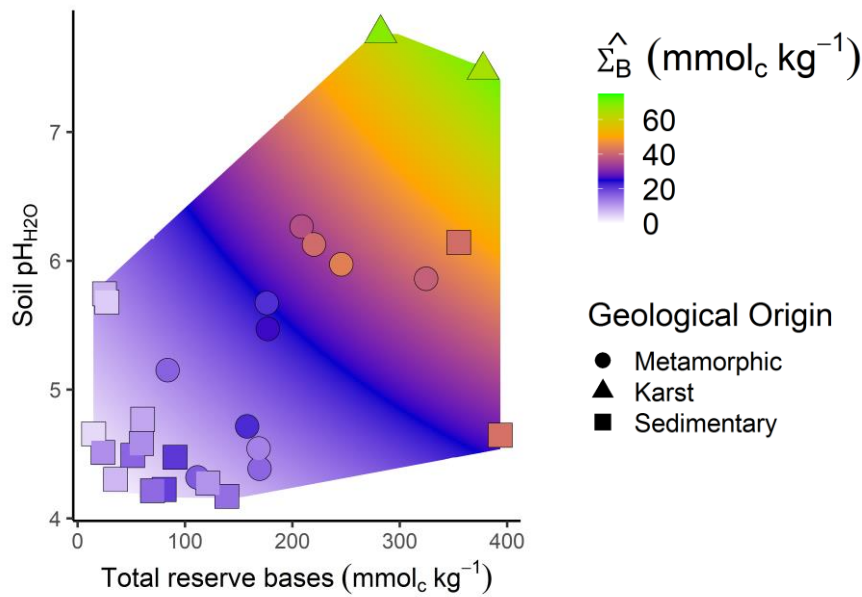


Figure 2.6: Predicted soil sum of bases (Σ_B) as a function of total reserve bases (Σ_{RB}) and soil pH_{H_2O} . Field measured Σ_B overlain their respective $\Sigma_{RB} \times pH_{H_2O}$ environment. Geological affiliation is represented.

Table 2.5: Regression metrics relating soil sum of bases (Σ_B) to soil total reserve bases (Σ_{RB}) and water-measured soil pH. Predictor variables have been centred at their means and scaled by their SD so as intercept reflects Σ_B values when all variables are at their means and predictors β coefficients represent changes in Σ_B values as predictors increase one SD. Regression residues were free of spatial structure issues. Variance inflation factor (VIF) and corrected Akaike Information Criterion (AICc) are also shown.

Σ_B : $r^2 = 0.94$; $p < 0.000$; AICc = 175.73					
Standardised coefficients					
	β	t	p	SD	VIF
Intercept	17.63	16.0	< 0.000	1.10	-
pH_{H_2O}	9.88	7.6	< 0.000	1.16	1.56
Σ_{RB}	8.81	7.3	< 0.000	1.35	2.14
$pH_{H_2O} \times \Sigma_{RB}$	2.54	2.4	0.027	1.08	1.69

1 SD \sum_{RB} (i.e. 113.72 mmol_c kg⁻¹), \sum_B increases by 8.81 mmol_c kg⁻¹. As regards the modelled effects of changes in soil pH_{H2O}, the model predicts that an increase of 0.98 in soil pH_{H2O} leads to an increase of 9.88 mmol_c kg⁻¹ in \sum_B . Regarding the interactive effect of $\sum_{RB} \times \text{pH}_{H2O}$, it can be seen in the “heatmap” of Figure 2.6 that, at similar soil bases reservoir concentration. For example, when $\sum_{RB} \approx 300$ mmol_c kg⁻¹, the model predicts $\sum_B = 20.85$ mmol_c kg⁻¹ when soil pH_{H2O} 4.91, whereas, at the same $\sum_{RB} \approx 300$ mmol_c kg⁻¹, the model predicts $\sum_B = 52.68$ mmol_c kg⁻¹ when soil pH_{H2O} = 6.91. The field measured values largely correspond to the modelled responses, and a clear distinction can be seen in the $\sum_{RB} \times \text{pH}_{H2O}$ environmental space of S_{SED}, S_{MET} and S_{KAR} sites.

2.3.2 Phosphorus

Soil [P]_T contents ranged from 15 mg kg⁻¹ in CJU-01 (Hyperdystric Arenosol) to 1194 mg kg⁻¹ in GBR-02 (Hypereutric Calcaric Lithic Leptosol) (Figure 2.7), with median values decreasing from S_{KAR} \geq S_{MET} = S_{SED} ($p = 0.02$; Table 2.2). Regarding OLS relationships exploring the associations between selected soil attributes and soil [P]_T (Table 2.4-d), there was a strong association between [P]_T and Fe₂O₃ (XRF-measured), with an increase of 1% in Fe₂O₃ accounting for an increase of 61.1 mg kg⁻¹ in soil [P]_T. To a lower degree, Al₂O₃ and (even lower) CaO were also related to soil [P]_T at the entire dataset level (Table 2.4-b). These relationships were partially maintained across soil geologic affiliations (Figure 2.8), with Al₂O₃ predicting [P]_T in both S_{SED} and S_{MET} with similar predictive ability, but with Fe₂O₃ only significant in predicting [P]_T of S_{SED} soils ($r^2 = 0.71$; $p = 0.000$). The XRF CaO was associated with [P]_T only for the S_{MET} sites ($r^2 = 0.55$; $p = 0.005$). All S_{SED} had virtually negligible Ca whereas unusual high CaO content (2.50%) was found in a Calcisol in PFF-01 (S_{KAR}).

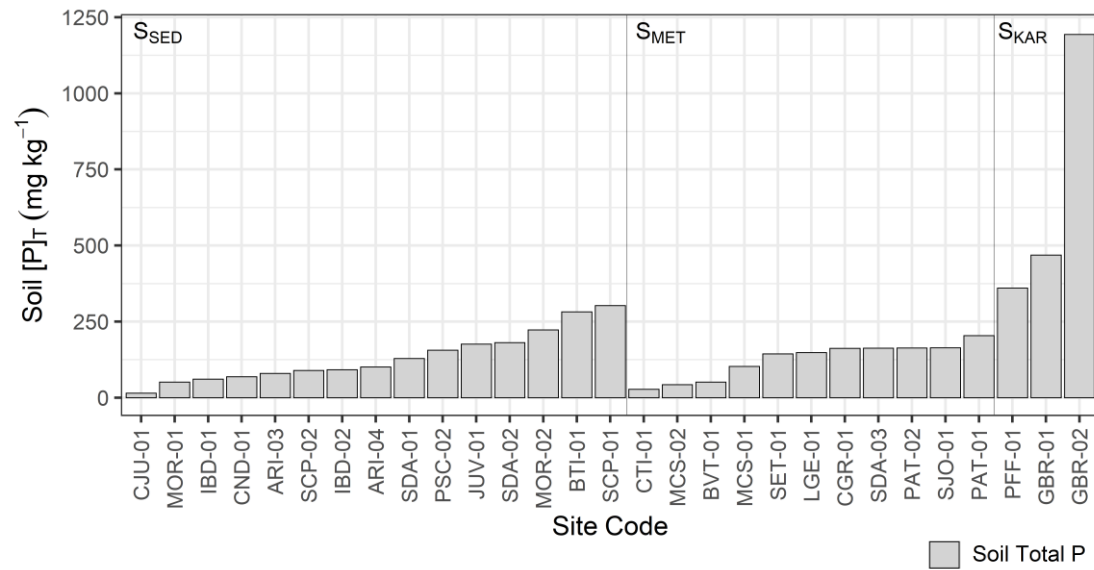


Figure 2.7: Soil total phosphorus $[P]_T$ concentrations. Sites were ordered according to increasing $[P]_T$ within each geologic affiliation.

Regarding soil texture effects, sand_f , clay_f and silt_f were all related to soil $[P]_T$ at the entire dataset level, with silt_f showing the strongest relationship with $[P]_T$ ($r^2 = 0.75$; $p < 0.001$) and the model predicts an increase of 85 mg kg^{-1} for every 10% increase in the silt_f content. Relationships between soil texture and $[P]_T$, however, were maintained only for S_{SED} sites (Figure 2.8-e, f, g).

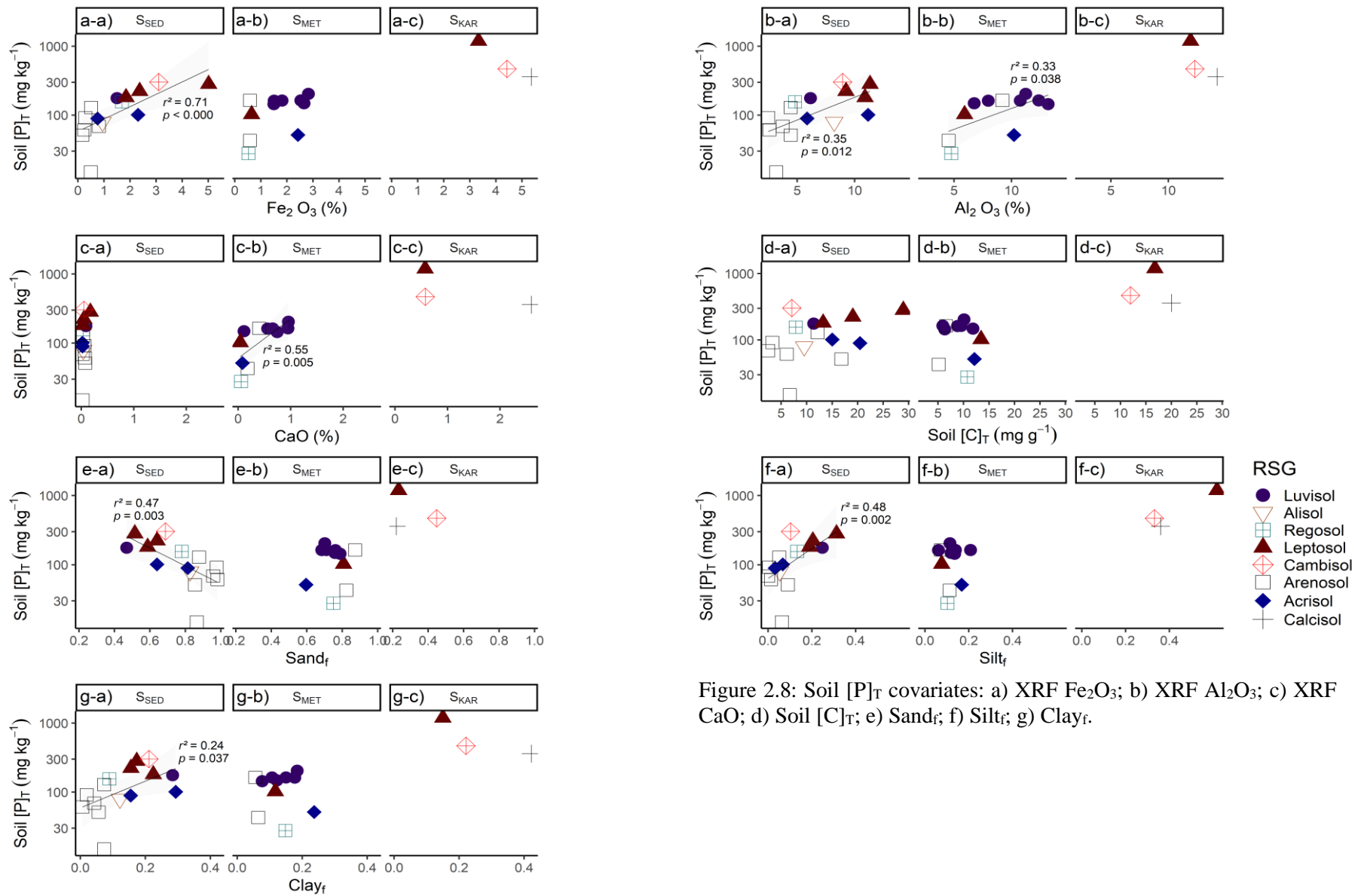


Figure 2.8: Soil $[P]_T$ covariates: a) XRF Fe_2O_3 ; b) XRF Al_2O_3 ; c) XRF CaO; d) Soil $[C]_T$; e) Sand_f; f) Silt_f; g) Clay_f.

2.3.3 Carbon, nitrogen and soil $\delta^{15}\text{N}$

Differences in $[\text{C}]_{\text{T}}$ contents among geologically distinct soils were not significant at $p \leq 0.05$ (Table 2.2), with the median values of 16.75 mg g^{-1} ; 11.38 mg g^{-1} and 9.01 mg g^{-1} for S_{KAR} , S_{SED} and S_{MET} , respectively (Table 2.2; Figure 2.9). Soil $[\text{N}]_{\text{T}}$ contents were, however, significantly higher for S_{KAR} than for S_{MET} sites, but equal to S_{SED} sites, with median values were 1.55 mg g^{-1} ; 0.87 mg g^{-1} and 0.92 mg g^{-1} for S_{KAR} , S_{MET} and S_{SED} , respectively (Table 2.2). Differences in soil C/N were not significant at $p \leq 0.05$ among the studied groups, with median values equal to 12, 11, and 9 for S_{SED} , S_{MET} , S_{KAR} , respectively (Table 2.2). With regards to soil nitrogen isotopic composition, $\delta^{15}\text{N}$ tended to be slightly higher for S_{KAR} sites than for S_{MET} and S_{SED} sites (median values were 11.11‰ , 8.82‰ and 8.27‰ for S_{KAR} , S_{SED} and S_{MET} , respectively), but these differences were not significant at $p \leq 0.05$ (Table 2.2).

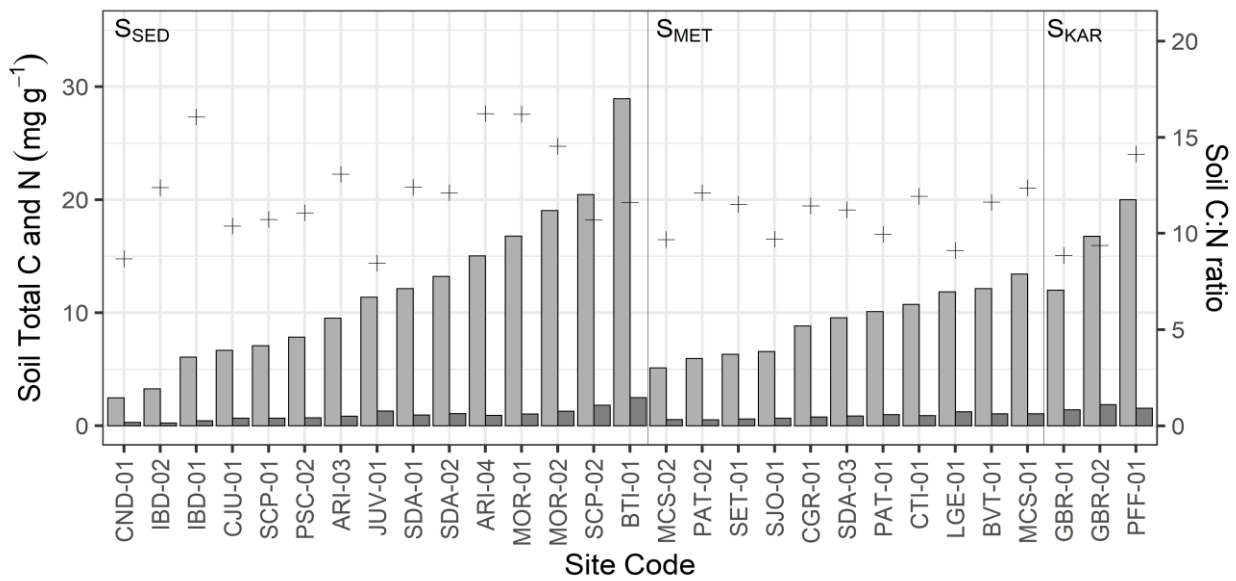


Figure 2.9: Total soil carbon, total soil nitrogen and C/N ratio according to geological affiliations. Sites are ordered by increasing total C contents in each group.

Element
 ■ Carbon
 ■ Nitrogen
 + C:N ratio

Across the entire dataset level, sand_f showed the best ability to predict $[\text{C}]_{\text{T}}$ ($r^2 = 0.32$; $p = 0.001$; $\text{AICc} = 39.6$; Table 2.4-c). As $\exp(\beta_1 \times 10) = (-0.019 \times 10) = 0.83$, the model predicts a proportional reduction of 17% every 10% increase in sand_f . According to AICc values, better $[\text{C}]_{\text{T}}$ predictions can be achieved in the following order: $\text{sand}_f > \text{clay}_f > \text{silt}_f > \text{Fe}_2\text{O}_3 > \text{Al}_2\text{O}_3$. All these relationships were maintained for S_{SED} sites, where sand_f was again the best predictor ($r^2 = 0.37$; $p = 0.00$; Figure 2.10).

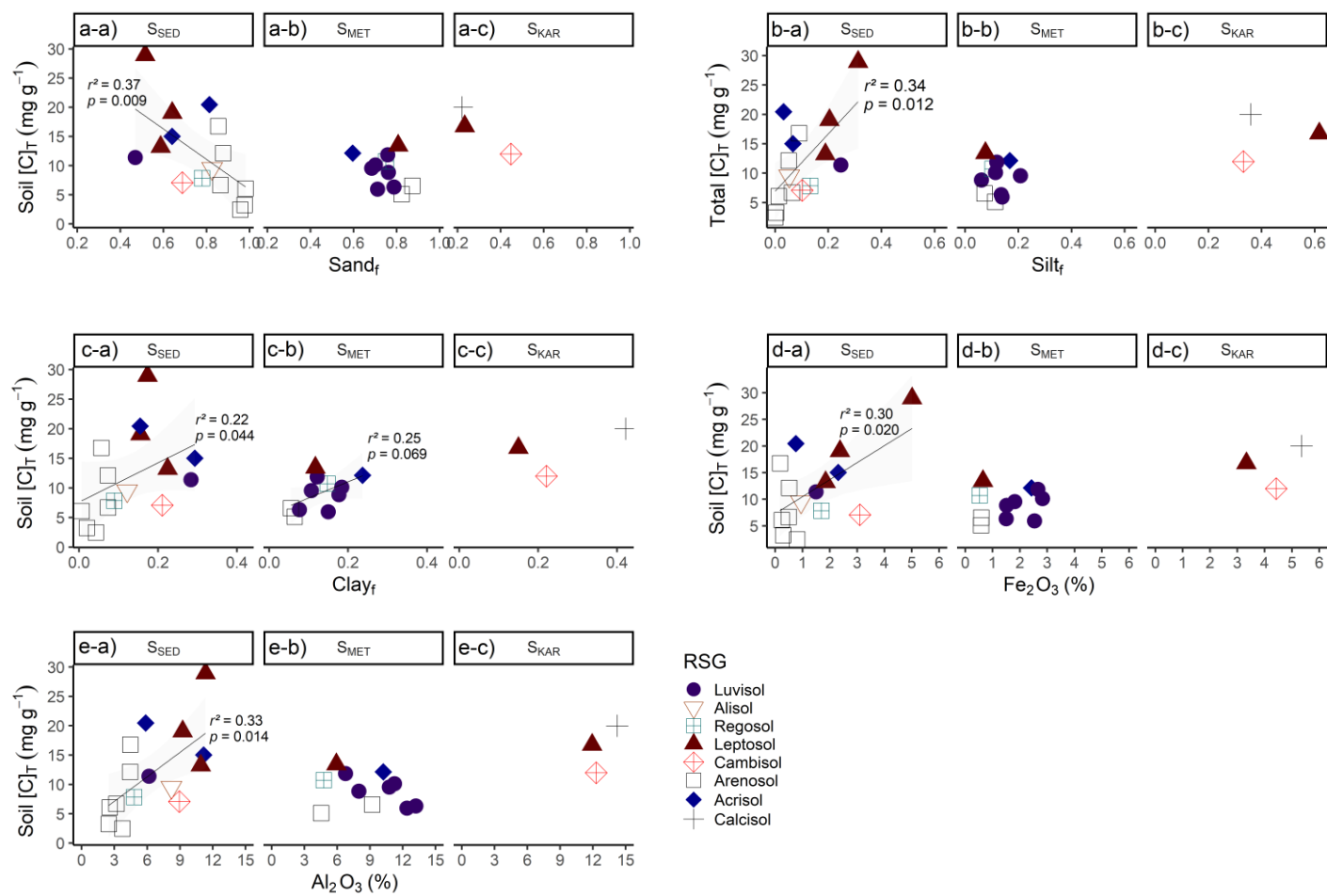


Figure 2.10: Total soil carbon covariates: a) sand fraction; b) silt fraction; c) clay fraction; d) XRF Fe₂O₃ and e) XRF Al₂O₃.

Both soil $[P]_T$ and I_E were associated with $[N]_T$ concentrations when the full dataset was analysed (Table 2.4-d). The relationship was slightly stronger for I_E ($r^2 = 0.20$; $p = 0.010$) compared to $[P]_T$ ($r^2 = 0.15$; $p = 0.024$). Both relationships remained present considering only S_{SED} sites (Figure 2.11). Also for the S_{SED} sites case, the relationship was stronger for I_E ($r^2 = 0.40$; $p = 0.007$) compared to $[P]_T$ ($r^2 = 0.16$; $p = 0.074$).

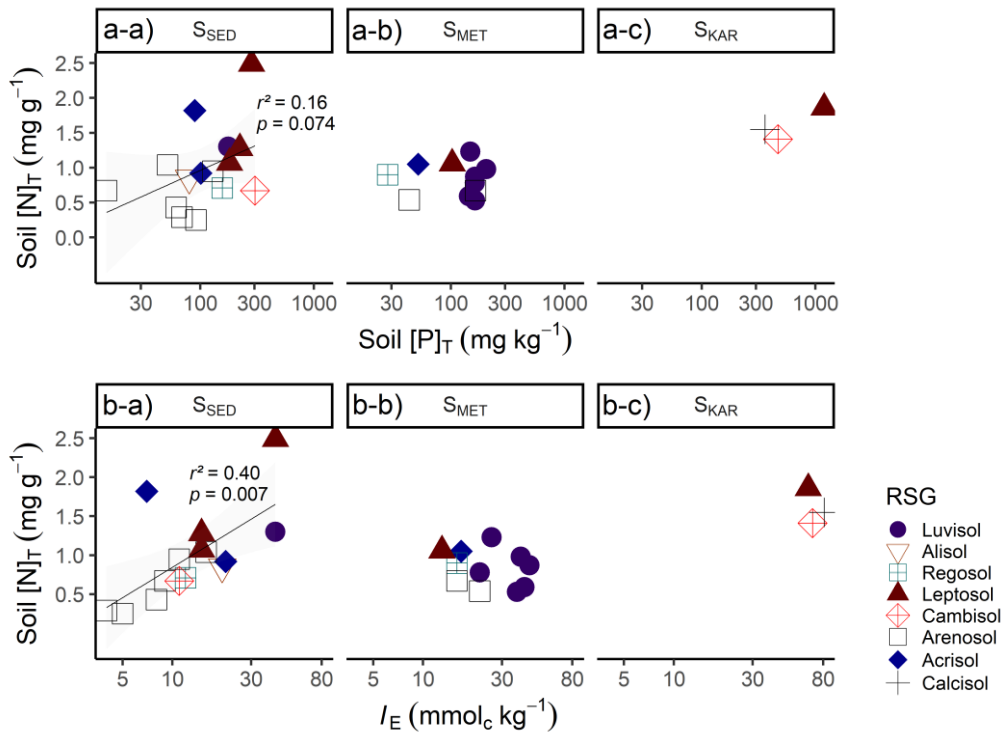


Figure 2.11: a) Relationship between soil total nitrogen and soil total phosphorus; b) relationship between soil total nitrogen and soil effective cation exchange capacity (I_E).

Climatic parameters (i.e. P_A and T_A) were not related to $[C]_T$, $[N]_T$ and soil C/N ratio at the entire dataset level (Table 2.4-c,d,e). Nevertheless, an additional analysis considering the 0.9 percentile showed a negative relationship between T_A and $[C]_T$ ($r^2 = 0.26$; $p = 0.005$; Figure 2.12). Such exclusion of the upper 0.9 quantile omitted PFF-01, SCP-02 and BTI-01 from the analysis, which is justified by the likely confounding presence of pedogenic carbon ($CaCO_3$) in PFF-01 soil as well as the unusually high values of $[C]_T$ measured in BTI-01 and SCP-02 (28.94 and 20.46 $mg\ g^{-1}$, respectively). The 0.9 percentile filtered data set was also used to test the same relationships across the soil geological classes, with T_A showing a negative influence on both $[C]_T$ and $[N]_T$. The relationship was stronger for $[C]_T$ ($r^2 = 0.49$; $p = 0.004$) compared to $[N]_T$ ($r^2 = 0.23$; $p = 0.055$) (Figure 2.12). Climatic parameters (i.e. P_A and T_A) were not significantly related to C/N ratios at $p \leq 0.05$ (Table 2.4-e).

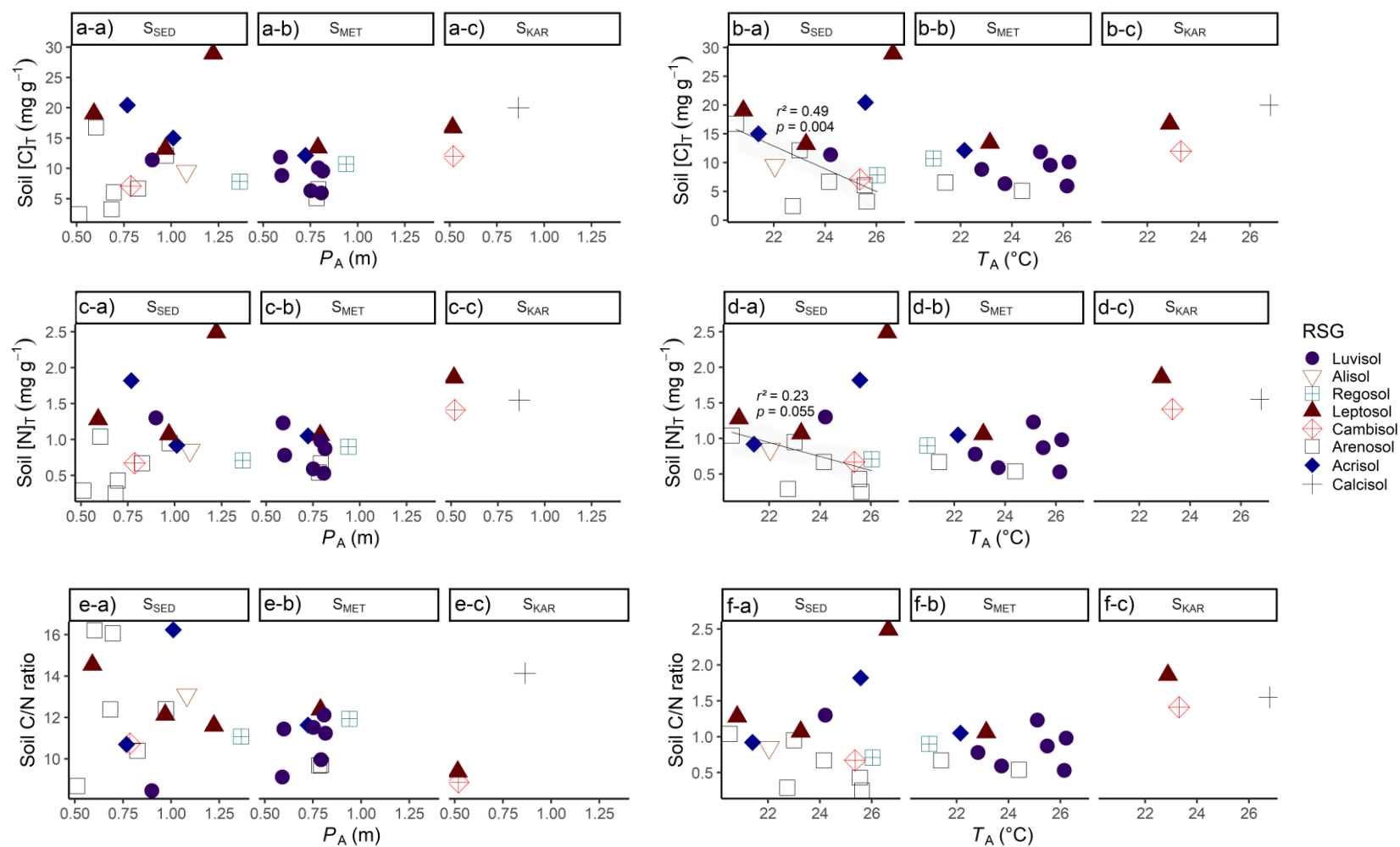


Figure 2.12: Effects of P_A and T_A on $[C]_T$ (a-b), $[N]_T$ (c-d) and soil C/N ratio (e-f). Regression lines refer to 0.9 quantile OLS linear regressions.

Regarding the relationships between soil $\delta^{15}\text{N}$ and selected climatic and edaphic predictors, only climatic predictors had significant relationships with soil $\delta^{15}\text{N}$ at the entire data set levels. After required spatial correction for models' residuals, the predictive power decreased following ψ ($r^2 = 0.74$; $p < 0.000$; $\text{AICc} = 128.80$) $> P_A$ ($r^2 = 0.72$; $p < 0.000$; $\text{AICc} = 131.51$) $> \text{AI}$ ($r^2 = 0.69$; $p < 0.000$; $\text{AICc} = 133.83$). No edaphic variables, even after spatial correction, were significant at $p \leq 0.05$. A similar trend was found for S_{SED} and S_{MET} evaluated separately (Figure 2.13).

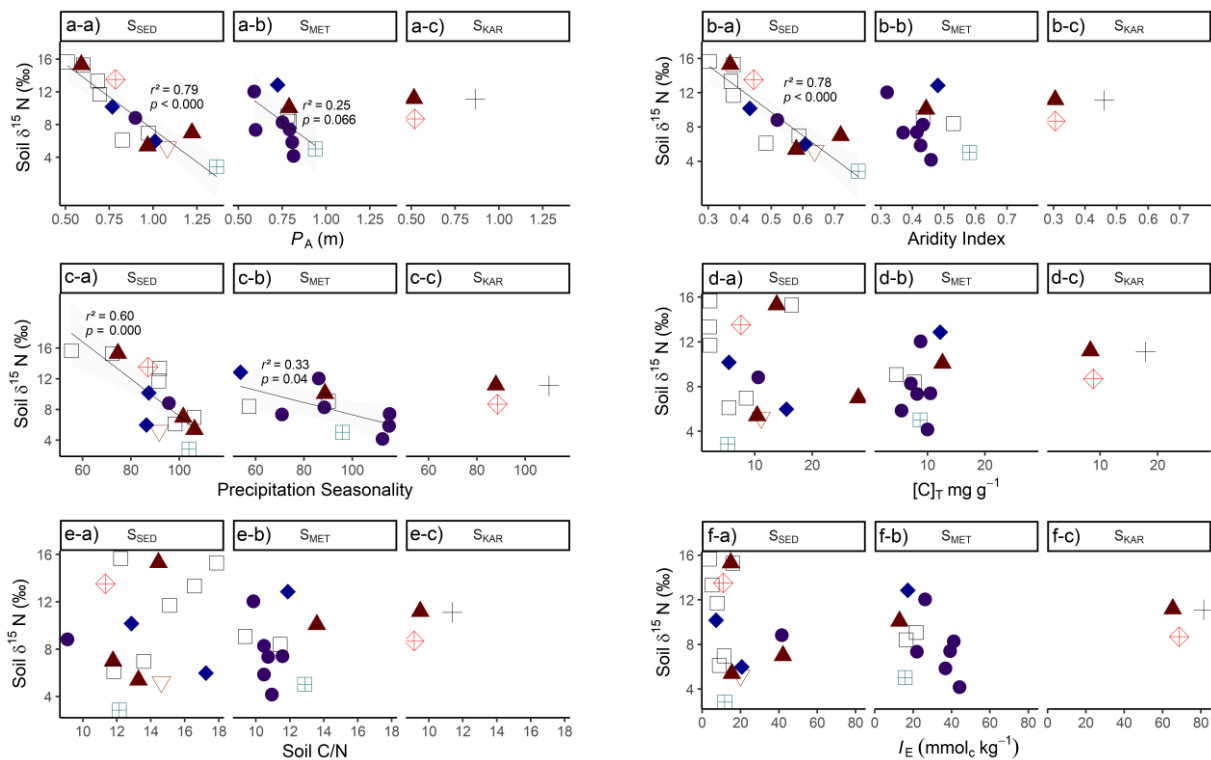


Figure 2.13: Potential edaphic and climatic soil $\delta^{15}\text{N}$ potential covariates. a) Mean annual precipitation (P_A); b) aridity index (AI); c) precipitation seasonality (ψ); d) Soil total carbon

RSG
 ● Luvisol
 ▼ Alisol
 ▲ Regosol
 ▲ Leptosol
 ◇ Cambisol
 □ Arenosol
 ◆ Acrisol
 + Calcisol

Results from the OLS multiple linear regression modelling (Table 2.6), however, suggest a slightly different picture, with some edaphic variables (i.e. $[\text{C}]_T$, C/N ratio and I_E) also included in the $\Delta\text{AICc} < 4$ range. A purely climatic model was better ranked in terms of AICc , i.e., after spatial correction for models' residuals, the best-ranked model retained only AI and ψ ($r^2 = 0.81$; $p < 0.000$; $\text{AICc} = 122.0$). Standardised coefficients were -1.882 and -1.657 for ψ and AI, respectively. Additional information and model metrics are provided in Table 2.6.

Table 2.6: Best AICc-ranked models accounting for variations in soil $\delta^{15}\text{N}$ values of Caatinga. β_0 = model intercept and standardised predictors coefficients are shown: AI = aridity index; P_A = mean annual precipitation; ψ = precipitation seasonality; $[C]_T$ = soil total carbon; C/N = soil C/N ratio; I_E = effective cation exchange capacity; $\text{pH}_{\text{H}_2\text{O}}$ = water-measured soil pH. Selected spatial filters, i.e. Moran Eigenvector Maps (MEM) were incorporated into models with spatially structured residues. Predictor variables have been centred at their means and scaled by their SD so that the intercept reflects soil $\delta^{15}\text{N}$ values when all variables are at their means and predictors coefficients represent changes in units of soil $\delta^{15}\text{N}$ values as predictors variables increase by one SD. Note that models 1,2 and 4 correspond to corrected versions (for residual spatial structures) of models 8, 7 and 9, respectively. AICc = Corrected Akaike Information Criterion; W = Akaike weights; I = Global Moran's I. Letter "a)" includes models with $\Delta\text{AICc} < 4$, whereas "b)" includes models with $\Delta\text{AICc} > 4$. Significant Moran's I at $p \leq 0.05$ are shown in bold.

Model	β_0	AI	P_A	ψ	$[C]_T$	C/N	I_E	AI x ψ	MEM11	MEM7	MEM1	MEM12	R^2_{adj}	p	AICc	ΔAICc	W	I
a) 1	9.133	-1.657	-	-1.882	-	-	-	-	1.290	-0.752	-0.686	-0.670	0.81	< 0.000	122.0	0	0.42	-0.06
2	9.133	-1.983	-	-1.978	0.707	-	-	-	1.317	-0.694	-0.687	-	0.81	< 0.000	122.2	0.28	0.37	0.15
3	9.133	-	-1.749	-1.557	-	-	-	-	1.329	-0.818	-0.668	-0.748	0.80	< 0.000	124.1	2.09	0.15	0.04
4	8.954	-1.854	-	-1.862	-	-	-	0.566	1.298	-0.783	-0.673	-	0.79	< 0.000	125.8	3.86	0.06	-0.06
b) 5	9.133	-2.106	-	-1.306	-	0.896	-	-	-	-	-	-	0.63	< 0.000	135.5	13.50	0.00	0.37
6	9.133	-3.257	-	-	1.673	-	-1.633	-	-	-	-	-	0.61	< 0.000	136.5	14.57	0.00	-0.06
7	9.133	-2.188	-	-1.474	0.795	-	-	-	-	-	-	-	0.61	< 0.000	136.8	14.87	0.00	0.58
8	9.133	-1.887	-	-1.492	-	-	-	-	-	-	-	-	0.58	< 0.000	137.3	15.31	0.00	0.56
9	8.947	-2.008	-	1.385	-	-	-	0.589	-	-	-	-	0.58	< 0.000	139.0	17.04	0.00	0.48

Nevertheless, the second-best model takes into account ψ , AI and $[C]_T$ ($r^2 = 0.81$; $p < 0.000$; AICc 122.2), also showing a low ΔAICc (0.28 in the scale of information). This provides evidence that $[C]_T$ is likely to account for variations in soil $\delta^{15}\text{N}$ values of the studied soils. Any other models including alternative edaphic variables (i.e. I_E and C/N ratio) had $\Delta\text{AICc} > 2$ units relative to the first two best-ranked models, thus being considered less likely to reflect the reality. Also of note is that a version of the best-ranked model replacing AI for P_A yielded a worse model in terms of AICc (124.1), supporting the inclusion of the former rather than the latter. Figure 2.14 shows measured soil $\delta^{15}\text{N}$ versus model simulated $\delta^{15}\text{N}$ values using the parameters of Model 1 ($r^2 = 0.81$; $p < 0.000$; AICc = 122.0).

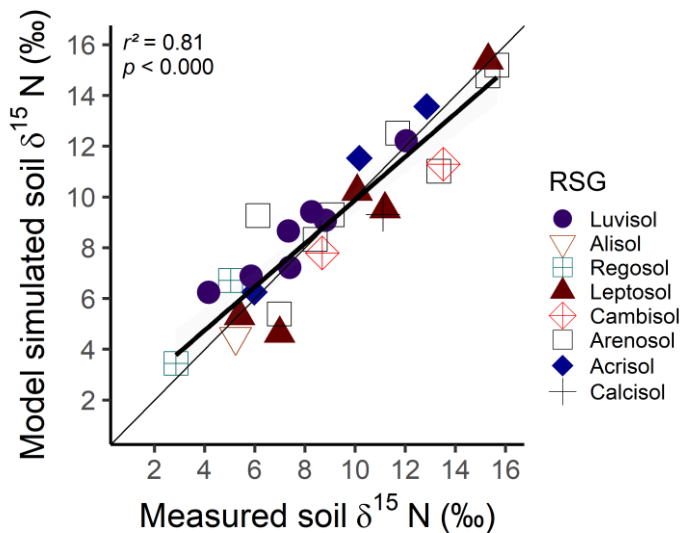


Figure 2.14: Measured soil $\delta^{15}\text{N}$ values *versus* model simulated soil $\delta^{15}\text{N}$ values. The coarser line represents the model fit and the thinner line is the 1: 1 line.

Subsequently, coefficients of Model 1 (Table 2.6) were used to produce map-modelled responses. Figure 2.15, therefore, shows soil $\delta^{15}\text{N}$ map modelled responses extrapolated for the entire Caatinga region, the “The Caatinga Soil $\delta^{15}\text{N}$ Isoscape”. In Figure 2.15, field-measured $\delta^{15}\text{N}$ values overlain modelled responses values with reasonable accuracy.

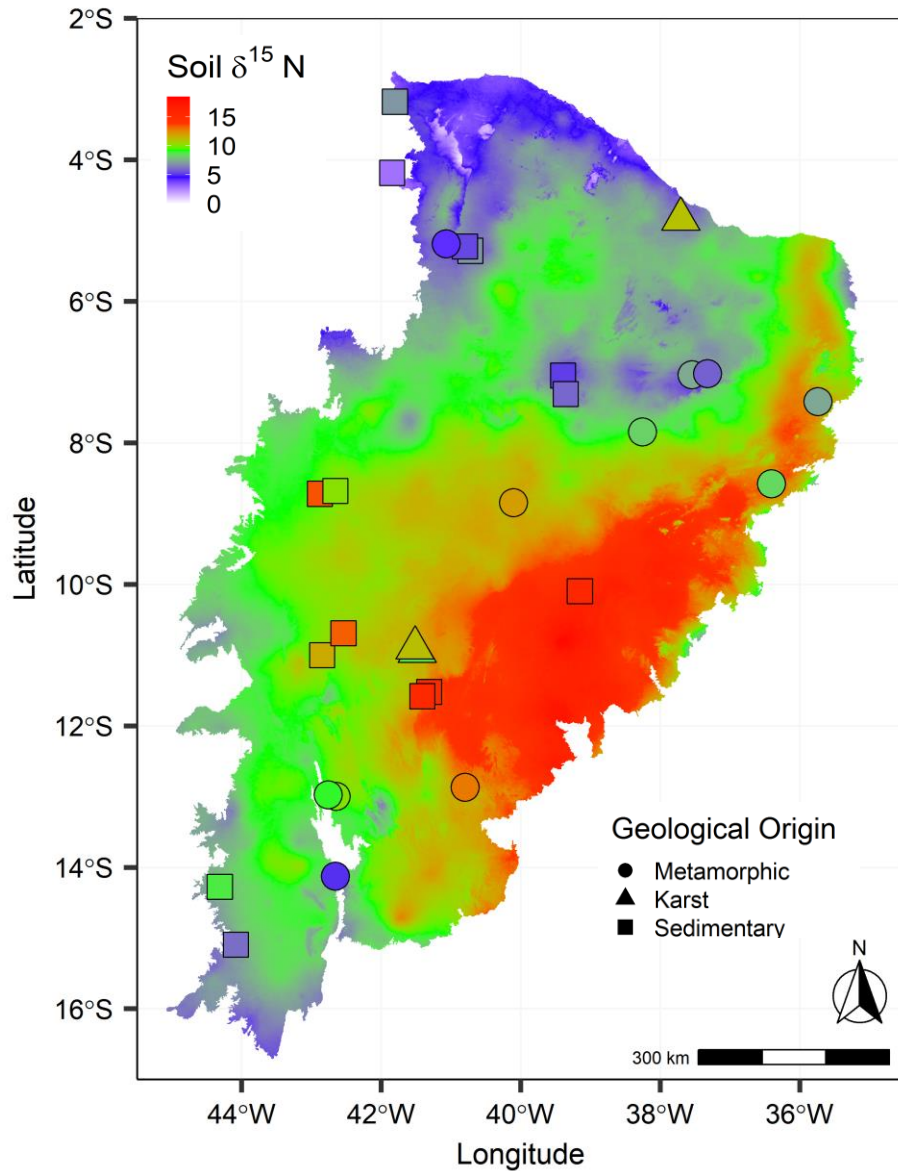


Figure 2.15: Model simulated soil $\delta^{15}\text{N}$ values across the Caatinga region. Soil measured $\delta^{15}\text{N}$ values overlain their respective geographical space. Modelled responses obtained with spatially explicit variables included in the Model 1 (Table 2.6): Soil $\delta^{15}\text{N} = 9.133 - 1.657 \cdot \text{AI} - 1.882 \cdot \psi$. Model metrics: $R^2_{adj} = 0.81$; $p < 0.001$; $\text{AICc} = 122.00$; $W = 0.42$; Global Moran's $I = -0.06$ after residual spatial correction.

Finally, a comparison between $\delta^{15}\text{N}$ values in soils associated with high and low P_A (i.e. $> 0.8 \text{ m a}^{-1}$ and $< 0.8 \text{ m a}^{-1}$) showed that soil $\delta^{15}\text{N}$ values were lower in the former category (Figure 2.16-a; $\chi^2 = 15.53$; $p < 0.000$). An OLS linear regression model showed that, within the high- P_A category, effective cation exchange capacity (I_E) explained 44% of the variance in soil $\delta^{15}\text{N}$ values (Figure 2.16-b; $r^2 = 0.44$; $p < 0.000$), whereas in the drier category, I_E was not associated with soil $\delta^{15}\text{N}$ values. In Figure 2.16, labels correspond to S_{KAR} sites (PFF-01, GBR-01 and GBR-02).

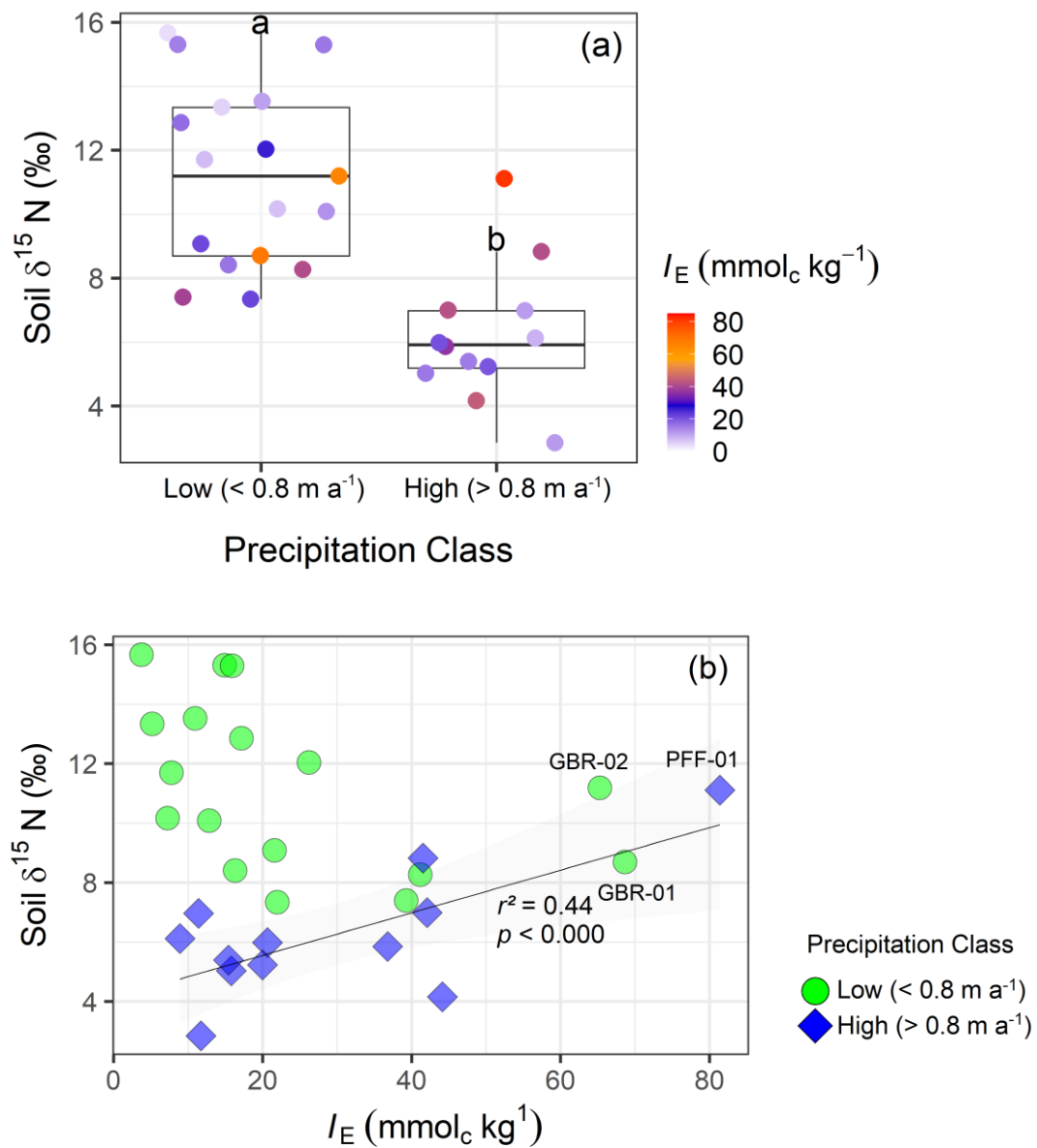


Figure 2.16: a) Soil $\delta^{15}\text{N}$ values according to low ($< 0.8 \text{ m a}^{-1}$) and high ($> 0.8 \text{ m a}^{-1}$) precipitation classes and effective cation exchange capacity (I_E). Letters associated with boxplots represent significant differences (at $p \leq 0.05$) detected through a Kruskal-Wallis test (χ^2); b) Soil $\delta^{15}\text{N}$ values according to I_E under high and low precipitation levels. Regression line represents an OLS linear model fit where $\delta^{15}\text{N} = 4.120 + I_E \cdot 0.813$. Regression's residuals met normality at $p \leq 0.05$ and were free of spatial structures (Moran's $I = -0.06$; $p = 0.55$). Labels indicate S_{KAR} sites.

2.3.4 Weathering metrics

Significant differences in soil total reserve bases (\sum_{RB}) were evident among soils of different geologic affiliations, with \sum_{RB} sharply decreasing for $S_{KAR} \geq S_{MET} \geq S_{SED}$ ($p = 0.002$), with median values of 377.76, 176.27 and 60.66 mmol_c kg⁻¹, respectively (Table 2.2). Both $[Zn]_T$ and $[Mn]_T$ median values decreased following $S_{KAR} \geq S_{MET} = S_{SED}$ ($p = 0.01$ for both cases). Median values for $[Zn]_T$ were 268, 128 and 60 mg kg⁻¹ for S_{KAR} , S_{MET} and S_{SED} , respectively (Table 2.2). Median values for $[Mn]_T$ were 2684, 912 and 412 mg kg⁻¹ for S_{KAR} , S_{MET} and S_{SED} , respectively (Table 2.2). Differences in $[Fe]_T$ were not significant at $p \leq 0.05$, with median values of 42.64, 44.56 and 105.4 g kg⁻¹ for S_{SED} , S_{MET} and S_{KAR} , respectively (Table 2.2). Median values for the K/Zr elemental ratio decreased from $S_{KAR} = S_{MET} \geq S_{SED}$, ($p = 0.000$), with median values of 6.18, 40.77 and 73.19 for S_{SED} , S_{MET} and S_{KAR} , respectively (Table 2.2). Finally, differences in the Ca/K ratio, taken here as an indication of the current proportion of weathering products of plagioclases to K-feldspars primary mineral were not significant at $p \leq 0.05$, with median values of 0.28, 0.23 and 0.32 for S_{SED} , S_{MET} and S_{KAR} , respectively (Table 2.2).

Similarly to previous soil properties, differences in weathering-associated key properties among soils of distinct geologic affiliations were verified with potentially meaningful OLS models investigated for both the entire dataset level as well S_{SED} , S_{MET} and S_{KAR} separately. For example, OLS fits have shown that $silt_f$ was strongly associated with \sum_{RB} levels at the entire dataset level ($r^2 = 0.71$; $p = 0.000$), with an increase of 10% in $silt_f$, representing a proportional increase of 84% \sum_{RB} . This relationship was even stronger for S_{SED} sites ($r^2 = 0.91$; $p < 0.000$; Figure 2.17-a), where the model predicts that an increase of 10% in $silt_f$ is associated with a proportional increase of 141% in \sum_{RB} levels. Increases in \sum_{RB} levels represented relatively small but significant increases in $[Fe]_T$, $[Zn]_T$, $[Mn]_T$ levels (regression metrics Table 2.4-f), but these relationships were maintained only for S_{SED} for $[Fe]_T$ and $[Zn]_T$ cases and only for S_{MET} soils for the $[Mn]_T$ case (Figure 2.17-d). Total reserve base levels were not associated with XRF-analysed K/Zr and Ca/K elemental ratios, despite being marginally significant (Table 2.4-f). Considering only S_{SED} , however, K/Zr increased reasonably with increasing \sum_{RB} ($r^2 = 0.28$; $p = 0.024$; Figure 2.18-e; function not shown). Finally, $[P]_T$ was associated with both \sum_{RB} ($r^2 = 0.69$; $p = 0.000$) and I_E ($r^2 = 0.57$; $p = 0.000$). Relationships involving weathering metrics were more evident at the entire dataset level than considering geological affiliations separately.

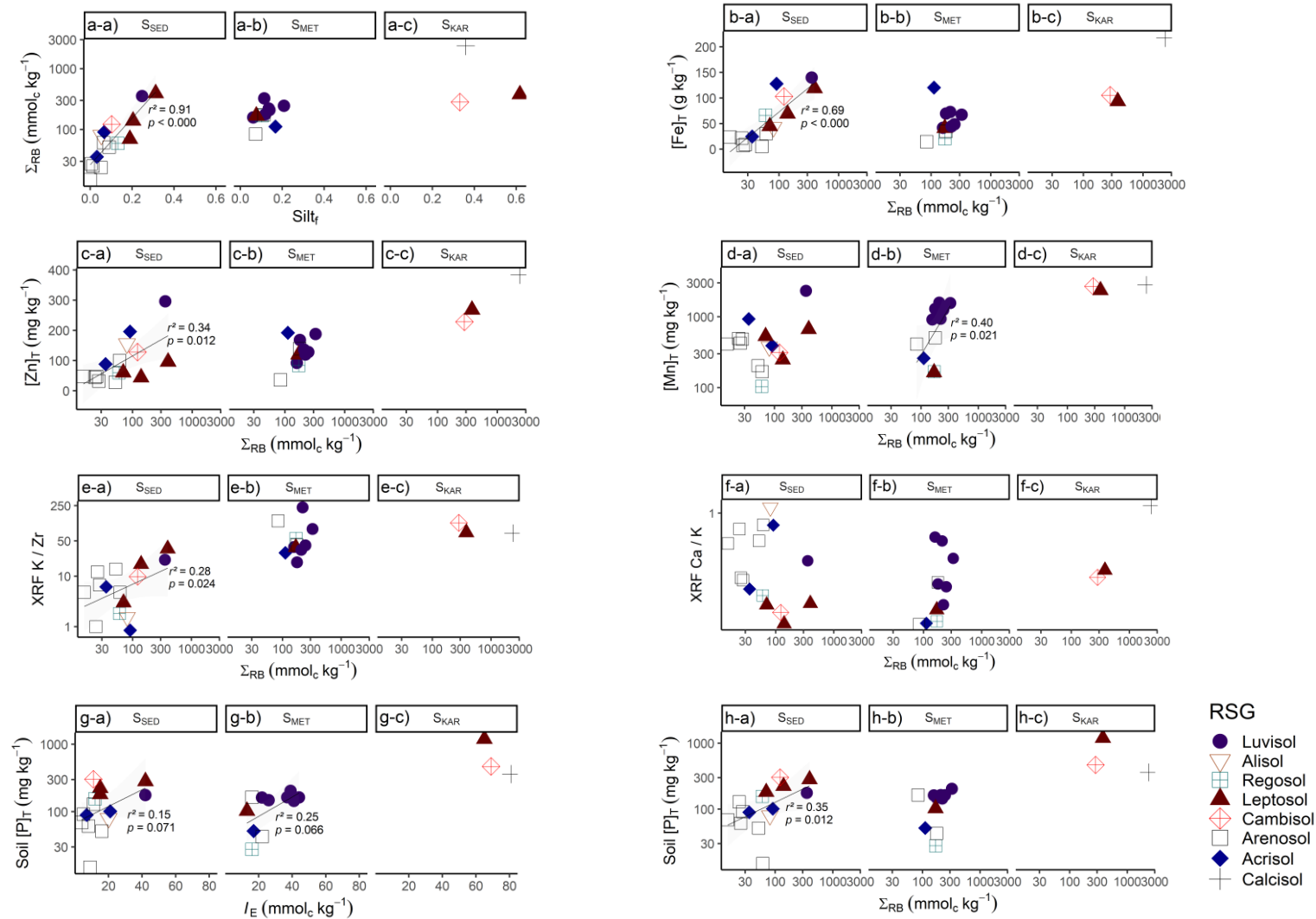


Figure 2.17: Selected weathering-associated relationships. a) Soil silt_f and total reserve bases (Σ_{RB}); b) Σ_{RB} and $[\text{Fe}]_T$; c) Σ_{RB} and $[\text{Zn}]_T$; d) Σ_{RB} and $[\text{Mn}]_T$; e) Σ_{RB} and XRF K/Zr; f) Σ_{RB} and XRF Ca/K; g) Σ_{RB} and I_E ; h) Σ_{RB} and $[\text{P}]_T$. R-squared, p -values and regression lines are shown for significant relationships at $p \leq 0.05$, along with 0.95 confidence interval bands.

2.3.5 Soil morphology, effective rooting depth (R_{EF}) and water availability

Maximum measured soil and effective rooting depths are shown in Figure 2.18. As expected, there was a marked tendency for deeper soils at the S_{SED} sites rather than their S_{MET} and S_{KAR} counterparts. The effective rooting depth, however, was markedly variable in both the S_{MET} , S_{SED} and S_{KAR} sites, i.e., in some cases, roots generally occupied all exploitable profiles and, in other cases, it was concentrated in the upper soil layers (regardless of the soil total depth). Moreover, R_{EF} did not show systematic variations among RSGs, suggesting that soil types are not a sensible surrogate to predict predicting R_{EF} in Caatinga soils, at least for the profiles studied.

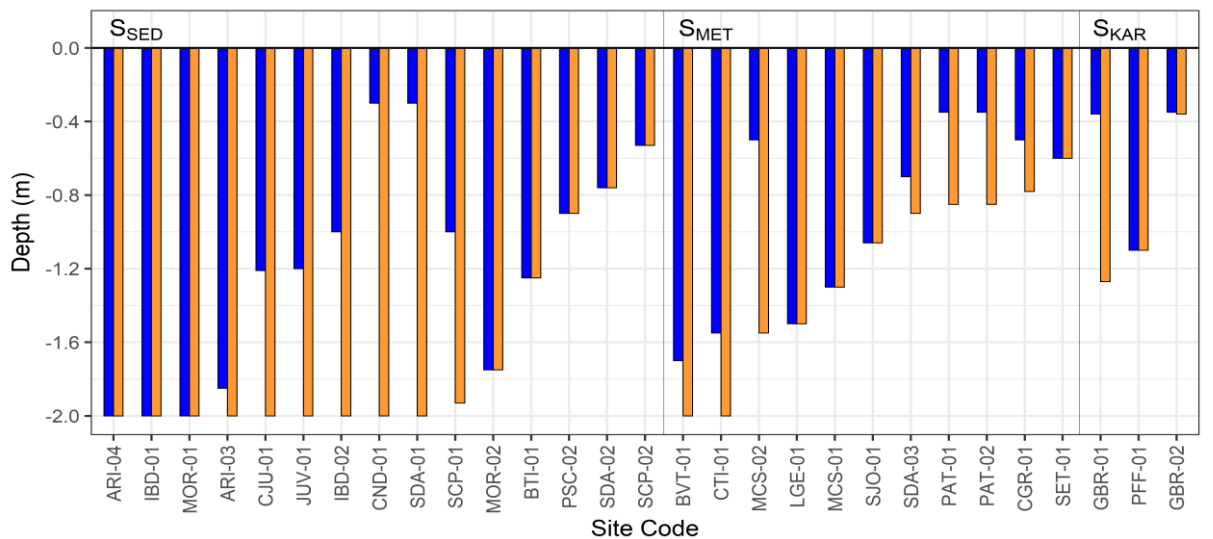


Figure 2.18: Maximum measured soil depth and maximum measured effective rooting depth (R_{EF}) for each studied site. Study sites are ordered according to maximum measured soil depth within each geologic category [Sedimentary (S_{SED}); Metamorphic (S_{MET}) and Karst (S_{KAR})]. The “0.0 horizontal line” correspond to the soil surface.

Variable

■ Rooting depth
■ Soil depth

Furthermore, R_{EF} did not appear to be related to soil bases or aluminium, soil bulk density or soil texture. Rather, Figure 2.19, suggests a climatic control on R_{EF} . Here, data have been categorised into “restrictive” soil profiles for root growth, i.e. presence of impervious layers (e.g. bedrock; saprolites) within the 2 m from the soil surface and “non-restrictive”, i.e. absence of impervious layers within the upper 2 m from the soil surface. For the latter, a simple linear regression model showed that the mean annual climatic water deficit (CWD_{adj}) accounted for a substantial component of the variation in R_{EF} ($r^2 = 0.25$; $p = 0.065$) in the non-restrictive group. Considering the 0.9 quantile data [i.e. excluding two semideciduous forests (ARI-03 and

ARI-04), and IBD-01, a loose sand dune], the predictive power of CWD_{adj} to account for differences R_{EF} increased significantly ($r^2 = 0.56$; $p = 0.020$; Figure 2.19).

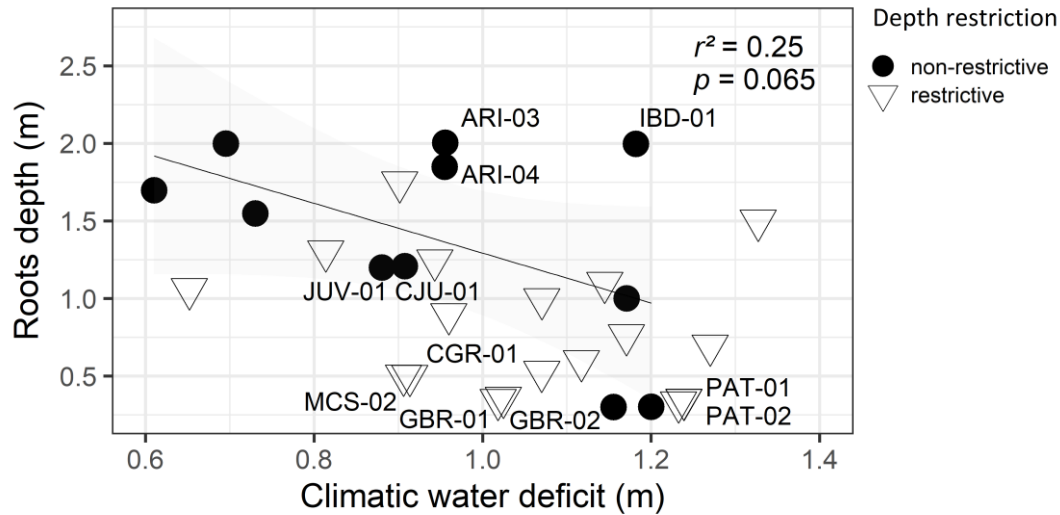


Figure 2.19: Relationship between roots depth and climatic water deficit (the higher CWD, the higher the water stress). Regression line stands for a simple linear regression considering the non-restrictive soils [i.e., absence of shallow impeditive layers (< 2.0 m) for root growth]. Confidence interval bands at 0.95 of probability is shown. A 0.9 quantile regression for the “non-restrictive” group yielded $r^2 = 0.56$; $p = 0.020$ (function not shown).

Differences in texture-associated volumetric soil water storage capacity weighted across soil profiles ($W\theta_v$) were, however, marginally significant among the studied categories, with medians decreasing from $S_{KAR} \geq S_{MET} \geq S_{SED}$ ($p = 0.072$; Table 2.2). Median values of $W\theta_v$ were 0.20 , 0.12 and $0.10 \text{ m}^3 \text{ m}^{-3}$ for S_{KAR} , S_{MET} and S_{SED} , respectively (Table 2.2). Moreover, differences in maximum plant-available soil water (θ_p) were not significant at $p \leq 0.05$ across S_{SED} , S_{MET} and S_{KAR} , with median values of 0.13 , 0.12 and $0.11 \text{ m}^3 \text{ m}^{-2}$ for S_{SED} , S_{MET} and S_{KAR} , respectively (Table 2.2). Figure 2.20 illustrates the relative importance of texture-associated volumetric soil water and soil depth in accounting for the total plant-available soil water. It is of note that these results involve calculations only to the maximum sampled soil depth of 2.0 m. If deeper profiles are considered, then likely larger maximum plant-available soil water reservoirs may be found, especially in S_{SED} terrains.

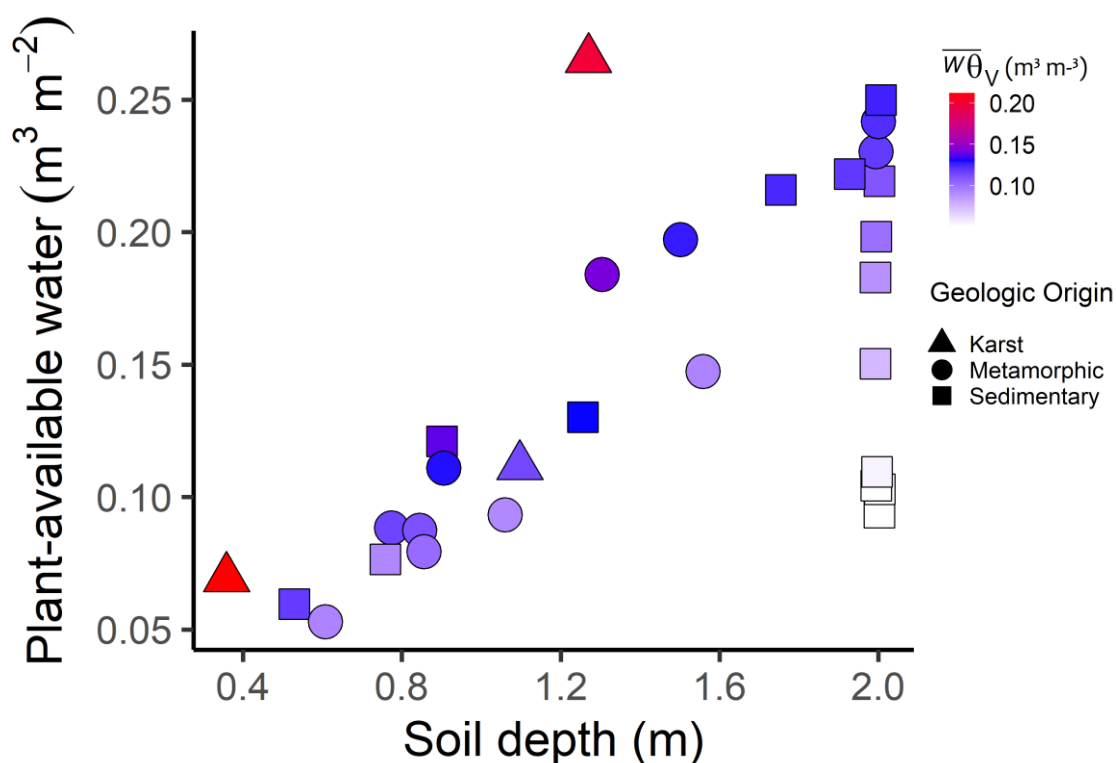


Figure 2.20: Maximum plant-available soil water content (θ_p) as a function of soil depth and volumetric soil water content (θ_v) calculated from across-profile textural volumetric soil water. Symbols representing distinct geological affiliations were coloured according to the textural volumetric soil water weighted across each soil profile ($W\theta_v$).

2.4 Discussion

In this chapter, I aimed to investigate to which extent geology (as reflected by soil parent materials) accounts for differences in soil properties of geologically distinct groups. In addition, a series of bivariate relationships were employed amongst soil core properties (i.e. soil texture, mineralogy and $[\text{C}]_T$; PALM et al., 2007) and a suite of soil properties to evaluate pedogenetic aspects and weathering products. Potential drivers of variations in soil $\delta^{15}\text{N}$ values were evaluated through a multiple linear regression approach and a model with spatially explicit predictors was proposed for Caatinga. Finally, the potential influence of climatological parameters (i.e. mean annual rainfall, mean annual temperature and long-term climatic water deficit) on selected soil properties (i.e. soil pH, $[\text{C}]_T$, $[\text{N}]_T$, $\delta^{15}\text{N}$ values, soil C/N ratio and R_{EF}) were evaluated in the context of soil geological affiliations.

2.4.1 The influence of geology on soil properties

2.4.1.1 Cations availability and soil reaction

Across the study sites, RSGs occurrence and their properties largely mirrored the geological origin, though some of the studied properties varied more than others. For example, except for $[K]_{\text{ex}}$ and $[Na]_{\text{ex}}$, most main exchangeable soil cations, effective cations exchange capacity and associated base and aluminium saturation varied systematically across geological classes (Figures 2.1-a and 2.1-b). These results are aligned with the expected variability of soil cations levels according to typical strata of distinct geological classes pointed out in several works reporting on Caatinga soils (e.g. SAMPAIO, 1995; SAMPAIO, 2010; ARAÚJO, 2011; ARAÚJO et al., 2017; 2019).

Regarding the exceptions, both $[K]_{\text{ex}}$ and $[Na]_{\text{ex}}$ were, in general, present in proportionately lower concentrations compared to other base cations. The largest part of K in soils is known to present in primary and secondary minerals (Structural K), with only a small fraction present in both the soil solution (Solution K) and electrostatically bonded as an outer-sphere complex on the negatively charged soil particles (Exchangeable K) (SPARKS, 2002). The latter is considered to be readily available for plants, replenishing K to the soils when it is lost by leaching or taken up by plants (ERNANI; ALMEIDA; SANTOS, 2007). This is considered a dynamical chemical equilibrium (NAJAFI-GHIRI et al., 2019), where weatherable K-bearing minerals should constitute a major factor in determining K availability in the long term. Higher concentrations of K are reported in igneous (e.g. granites and sianites), intermediate in pelitic sedimentary rocks such as (e.g. shales, argillites and siltites) and lower in calcareous rocks (ERNANI; ALMEIDA; SANTOS, 2007). Therefore, the prevailing quartz-rich composition of many soils in this study helps explain the relatively low potassium contents.

Similarly, $[Na]_{\text{ex}}$ was present only in small concentrations (except for PSC-02 and SJO-01, all soils had $[Na]_{\text{ex}} \leq 1 \text{ mmol}_c \text{ kg}^{-1}$). Despite losses through leaching are expected to occur at a relatively low pace in Caatinga, the electrostatically bonded Na may be more prone to be lost from the soil system compared to divalent cations (i.e. Ca^{2+} and Mg^{2+}), the latter more strongly adsorbed on soil particles. Coarse-textured soils, largely represented in this study, are unlikely to exhibit salt accumulation issues (FREIRE; FREIRE, 2007). Sodium is found in a wide range of both felsic and mafic igneous rocks, as well as in their metamorphic counterparts (SMITH et al., 2019). The latter may also contain silicate Na-bearing minerals, such as Na-Plagioclases, a major source of Na in soils (SMITH et al., 2019). Regardless of the mineralogical aspects, Na is expected to be easily weathered (QUESADA et al. 2010) and

leached through the soil profiles, though this process should be relatively slower in Caatinga compared to soils of wetter regions.

Contrary to most S_{SED} sites, JUV-01 and BTI-01 have shown relatively higher exchangeable cations concentrations. The likely reason is that the former is situated in the Bambuí Group geologic formation (in the Minas Gerais side) where, along with limestones and dolomites, arkose – a detrital sedimentary rock rich in feldspar also occurs to a large extent. Regarding BTI-01, the study plot is situated nearby the limits of Cabeças and Pimenteiras Formations (Piauí State), soil parent materials such as siltites, conglomerates and shales widely occur (CPRM, 2004), with the latter recorded in the BTI-01 soil. Both JUV-01 and BTI-01 had comparable I_E , with BTI-01, however, holding a relatively higher content of $[Al]_{ex}$. These results reinforce that, despite the predominance of certain soil characteristics in sedimentary areas, several exceptions may occur across Caatinga. It has been asserted that “crystalline soils” have more varying properties than “sedimentary soils” (SAMPAIO, 2010). Nevertheless, marked variability in soil properties of S_{SED} sampled in this study is also evident. Moreover, regardless of the geological affiliations, a marked predominance of coarse-textured soils was noted (see the textural triangle in Figure S2.1). The tendency of coarse-textured soils in Caatinga has been previously observed (JARAMILLO; MURRAY-TORTAROLO, 2019), which is of great importance for several biogeochemical processes as soil texture largely influences the surface charge density, adsorption capacity as well as elemental fluxes between organic and inorganic pools (WEIL; BRADY, 2016; SANCHEZ, 2019).

As pointed out in the Amazon forest study of QUESADA et al. (2010), high I_E levels usually reflect mineral weathering still taking place, with the dominance of the soil sortive complex by either bases or aluminium reflecting the current product of the active weathering. Clay activity is known to influence the overall soil sortive complex's size and composition, but contrary to findings in Western Amazon soils (MARQUES et al., 2002), the high-activity clay soils identified in this work had relatively much lower (often negligible) aluminium contents compared to their low-activity clay counterparts. Of note in this respect, is that most soil pH_{H_2O} in Marques and coworkers' study occupied the 4.4 to 4.7 range, with an increase of 0.3 pH_{H_2O} being associated with a doubling of exchangeable aluminium concentration (from 91 to 181 $mmol_c kg^{-1}$). In this study, soil pH_{H_2O} values were often around 5.0, reflecting the influence of soil pH on the solubility of Al-bearing compounds. Figure 2.1-b shows that small changes in soil pH may lead to abrupt changes in aluminium or base dominance in the soil sortive complex.

In addition to the chemical nature and composition of parent materials, soil pH is a major determinant of cation availability. Figure 2.6 shows measured values of soil bases (Σ_B) along with modelled responses of Σ_B as a function of Σ_{RB} and soil pH_{H_2O} . Considering a few exceptions, the geochemical environments of S_{SED} , S_{MET} and S_{KAR} were found to be reasonably delimited.

2.4.1.2 Phosphorus

Despite a wide range of observed $[P]_T$ contents, the majority of both S_{MET} and S_{SED} soils had relatively low contents of $[P]_T$ (ranging from 100 to 200 mg kg⁻¹). These values are in agreement with other studies in the region considering the upper soil layer or horizons A (e.g. TIESSEN; SAMPAIO; SALCEDO, 1992; FRAGA; SALCEDO, 2004; ARAÚJO; SCHAEFER; SAMPAIO, 2004; SILVEIRA; ARAÚJO; SAMPAIO, 2006). Soil $[P]_T$ contents were, however, markedly higher for the S_{KAR} sites [median of 469 mg kg⁻¹ and high 1194 mg kg⁻¹ measured in GBR-02 soil (Hypereutric Calcaric Lithic Leptosol)]. Karst-derived soils can be considered a special case since the high $[P]_T$ levels commonly found in these soils usually do not reflect P availability (FERREIRA, 2013). If parent material (geology) P concentration reflects soil $[P]_T$ concentration (PORDER; RAMACHANDRAN, 2013), this probably is not applicable for karst-derived soils, in which original limestone and dolomite P levels were shown to be comparable to P-depleted sandstone contents (PORDER; RAMACHANDRAN, 2013). Assuming a generic rock classification, Jackson (1969) encountered, on average, 1300 mg kg⁻¹ of P in igneous and metamorphic rocks, 750 mg kg⁻¹ in schists, 350 mg kg⁻¹ in sandstones and a comparably scanty 180 mg kg⁻¹ in calcareous rocks (JACKSON, 1969, *apud* SALCEDO, 2006). The most likely underlying reason is the tendency of accumulation of calcium phosphates (Ca-P) of low solubility (PANSU; GAUTHEYROU, 2006). Former pedological studies have shown that typical high P of tropical karst soils were, in fact, the product of secondary accumulation in insoluble compounds originally present in the limestones strata (SCHROO, 1963). A comprehensive assessment of bioavailable P-forms as well as P distribution across organic (P_o) and inorganic (P_i) pools would, however, require specific methods such as Olsen-P (OLSEN; SOMMERS, 1982) and Hedley's fractionation (HEDLEY et al., 1982).

Indeed, despite the very high $[P]_T$ levels of S_{KAR} , the availability of this nutrient might be a concern in these soils, which is likely to be counteracted by biological players. For

example, phosphorus-bearing minerals (i.e. apatites) are dissolved by soil natural acidity as well as by enzymatic activity (i.e. phosphatases) of both roots, mycorrhizae and microorganisms (SANCHEZ, 2019). In addition, “biocrusts” (BELNAP, 2013; SZYJA et al., 2019) have been observed in several semiarid areas. These are communities of non-photosynthetic and photosynthetic organisms that, in contrast to wetter ecosystems, often thrive in arid and semiarid soils because of the presence of spaced canopy covers. Specifically, discontinuous canopy coverages leave sun-exposed soil surfaces available for biocrusts colonisation (BELNAP, 2013), and these communities are involved in several ecological processes, including carbon and nitrogen fixation as well as promoting increases in phosphorus availability (ZHANG et al., 2016; BELNAP et al., 2016). The latter takes place at least through two pathways: (1) Some microorganisms can secrete phosphatases so that P-availability in soils underlying biocrusts sheets might be higher than surrounding soils as well as the associated higher P concentration on overlying plant tissues (ZHANG et al., 2016); (2) Intricate symbiotic mechanisms have been proposed among biocrusts species such as the possibility of free-living fungi delivering P to immobile lichen and bryophyte (comparable to mycorrhiza delivering P to plants at the expense of plant-derived carbon) or the fungi-produced phosphatases enhancing P availability across the biocrust but also likely improving the soil general fertility (BELNAP et al., 2016). These processes could be of great importance in karst-derived soils of Caatinga, potentially participating in weathering processes as shown for karst exposed to wetting-drying cycles (CHEN et al., 2014). Furthermore, biocrusts might be considerably important across the entire region, potentially catalysing fluxes from both organic and inorganic unavailable P into available pools. Biocrusts were found to be conspicuous in the Caatinga, including several taxa and potentially covering about 10% of old-growth and secondary-growth topsoil total surfaces (SZYJA et al., 2019).

2.4.1.3 Carbon and nitrogen

In this study, neither geological clustered soils nor their associated RSGs showed marked differences in $[C]_T$ contents, a result in broad agreement with the results of MENEZES et al. (2021), who did not find differences in soil carbon storage among the main soil groups of Caatinga. Calcareous soils are known to enhance the stability of carbon, potentially causing nutrient limitation in karst ecosystems (HU et al., 2012). Despite a tendency for higher $[C]_T$ values in S_{KAR} sites, the current results suggest that carbon dynamics and storage should not show marked differences in a reasonable range of soils in Caatinga. Total nitrogen levels did

not differ between S_{MET} and S_{SED} sites. However, $[N]_T$ contents in S_{KAR} sites were 68% and 78% greater than S_{SED} and S_{MET} , respectively. Soil N is often considered a limiting nutrient in karst ecosystems this being attributable to $CaCO_3$ enhancing the stability of soil organic matter (PAN et al., 2016). Measures of N availability such as potential mineralisation rates were not included in this study, but the high contents of $[N]_T$ measured in S_{KAR} are potentially present in stable recalcitrant soil organic compounds. Studies have shown that nitrogen availability in these ecosystems may be improved through the exudation of oxalic acid from hyphae and roots, potentially playing a crucial role in N (and other nutrients) acquisition in calcareous soils (CLARHOLM; SKYLLBERG; ROSLING, 2015; PAN et al., 2016). This is believed to be an important mechanism to buffer potential N limitations, especially in the S_{KAR} study sites.

2.4.2 Causes of isotopic discrimination in Caatinga soils

Soil $\delta^{15}N$ values were, in general, similar across geological soil affiliations with no clear patterns across pedogenetic conditions reflected by RSGs. Most measured soil $\delta^{15}N$ values were higher than values commonly measured in soils of wetter tropical regions such as those reported by Martinelli et al. (1999) and Quesada et al. 2010). Soil $\delta^{15}N$ values varied from $\delta^{15}N = 2.85$ (‰) at PSC-02 (Orthodystric Regosol) to 15.66 (‰) at CND-01 (Orthodystric Chromic Sideralic Arenosol). Interestingly, the lowest and the highest measured soil $\delta^{15}N$ values in the dataset were found at the sites with the highest and lowest P_A levels, respectively.

Here of note is that high $\delta^{15}N$ values do not necessarily translate into high N availability. High $\delta^{15}N$ values indicate an open N cycle (MARTINELLI et al., 1999). The low N fixation rates by legumes commonly found in Caatinga may be due to the high stress by other factors under which these plants are held making N fixation too costly to bring any advantage.

The values presented in this study were also consistent with those reported by Santos et al. (2022), who measured a maximum soil $\delta^{15}N$ value of 17.3 (‰) in an Alisol in the *Sertão Pernambucano* under native Caatinga and $P_A = 0.71 \text{ m a}^{-1}$. Freitas et al. (2015) also reported soil $\delta^{15}N$ values ranging from 4 (‰) to 16 (‰) along a rainfall gradient encompassing a vegetation transition in Northeast Brazil. It is of note that both Freitas et al. (2015) and Santos et al. (2022) adopted soil $\delta^{15}N$ mean values relative to the upper 0.20 m layers, whereas, in this study, I used data from the upper 0.3 m layer. The association between mean soil $\delta^{15}N$ values from the 0.20 and the 0.30 m layers in this study, however, was very high ($r^2 = 0.99$; $p < 0.000$), with potential implications for the interpretation of the results being considered negligible.

Similarly to this study, Santos et al. (2022) have found a marked influence of climatic variables on soil $\delta^{15}\text{N}$ values. This pattern has already been noticed in several studies in arid and semiarid regions over the past years (e.g. SHEARER et al., 1993; SWAP et al., 2004; ARANIBAR et al., 2004; FREITAS et al., 2015; SANTOS et al., 2022), and also for a wide range of environmental conditions at global and subcontinental scales (e.g. HANDLEY et al., 1999; NARDOTO et al., 2008), the latter study reporting on foliar $\delta^{15}\text{N}$. Also using foliar $\delta^{15}\text{N}$ data, Martinelli et al. (2021) found the highest $\delta^{15}\text{N}$ values for Caatinga leaves compared to other Brazilian biomes, which was attributed to longer N residence time in soil associated with lower leaching rates and plant uptake. It is worthy to mention that, with no exception, all Caatinga sites included in the study of Martinelli and coworkers' (2021) are also part of this study, which is thought to largely explain the similarities found between the $\delta^{15}\text{N}$ range in both studies.

The aridity index (AI) and precipitation seasonality (ψ) were significantly related to soil $\delta^{15}\text{N}$ values. The former is a quantification of the precipitation availability over the atmosphere demand (ZOMER; TRABUCCO, 2022), where higher values translate into more humid conditions, whereas low values represent higher aridity. On the other hand, precipitation seasonality is a measure of the long-term rainfall variability throughout the year, where greater values represent greater precipitation variability (O'DONNELL; IGNIZIO, 2012), and lower values mean that precipitation is more concentrated over a part of the year. The AI was strongly associated with P_A ($r^2 = 0.95$; $p < 0.000$), therefore was not allowed to be included simultaneously in models attempting to account for variations in soil $\delta^{15}\text{N}$. These variables are thought to contain redundant information as the index is simply the mean annual precipitation divided by mean annual reference evapotranspiration (ETP_0). The latter was found to be more or less constant across the dataset, with minimum and maximum values reaching 1.49 and 1.91 m a^{-1} , respectively. Anyway, both variables are expected to influence N processing in soils as well as the biologically-mediated soil organic nitrogen (SON) mineralisation. Indeed, in addition to total annual rainfall amounts, precipitation temporal variability has been suggested as a key driver influencing N processing in dry regions (ARANIBAR et al., 2004; SANTOS et al., 2022). Swap et al. (2004) suggest that the gradual increase of soil $\delta^{15}\text{N}$ in dry regions is the result of intense episodic microbial activity during the onset of the wetter season after long-lasting dry spells in southern Africa. However, under extreme seasonal conditions, the rainy period can be not long enough to process all available N in the soils, thus causing isotopic signatures toward higher $\delta^{15}\text{N}$ values. (SWAP et al., 2004).

The mechanisms underlying soil $\delta^{15}\text{N}$ -enrichment conditioned by climatic forces remain somewhat enigmatic, but the main line of thought suggests that such enrichment is influenced by complex bio geophysical controls, whereby rainfall (or aridity) affects N pools processing and the openness of the N cycle (SWAP et al., 2004). In this regard, it has been proposed that either decrease in the overall fluxes of N into organic pools or a greater flux of N from organic to minerals pools can induce changes in isotopic signatures, with N mineral forms susceptible to being lost as leachate or gaseous emissions (HÖGBERG, 1997; HANDLEY et al., 1999; MARTINELLI et al., 1999). Thus, whenever N loss rates surpass N incoming in a given ecosystem, then internal cycling tends to discriminate against ^{15}N , causing its enrichment in the soil (QUESADA et al., 2010).

The map modelled $\delta^{15}\text{N}$ values for the Caatinga region presented in Figure 2.15 were produced with a purely climatic model that includes AI and ψ variables (Model 1; Table 2.6; $r^2 = 0.81$; $p < 0.000$; AICc = 122.0). Because the ΔAICc of the second best-ranked model was only 0.28 (scale of information), this model could be also considered feasible in explaining variations in soil $\delta^{15}\text{N}$ if information theory is strictly considered. Similarly to Model 1, the Model 2 (Table 2.6; $r^2 = 0.81$; $p < 0.000$; AICc = 122.2) includes the AI and ψ variables, but also soil total carbon - $[\text{C}]_{\text{T}}$. Some lines of evidence may help explain such an influence. Higher levels of $[\text{C}]_{\text{T}}$ in soils are likely to reflect the presence of more stable/recalcitrant organic compounds for a longer period. In turn, soil organic carbon stability can be conditioned by a variety of factors, including chemical recalcitrance, physical protection and interaction with soil mineral surfaces (LÜTZOW et al., 2006). In this study, clay contents accounted for a considerable proportion of the variation in $[\text{C}]_{\text{T}}$ ($r^2 = 0.35$; $p = 0.000$). The positive influence of $[\text{C}]_{\text{T}}$ on $\delta^{15}\text{N}$ values, therefore, can potentially be associated with direct and indirect effects. On the one hand, old recalcitrant N pools tend to become more ^{15}N enriched. On the other hand, higher clay contents, beyond promoting greater N gaseous losses during fractionating processes (CRAINE et al., 2015), are suggested to influence the persistence of stable long-lasting ^{15}N -enriched organic compounds (BAISDEN et al., 2002; MARIN-SPIOTTA et al., 2009; CRAINE et al., 2015). Santos et al. (2022) reported an effect for clay in increasing $\delta^{15}\text{N}$ values in Caatinga, but also highlight that it may be due to the greater stability of organic matter in clayey soils. The higher $\delta^{15}\text{N}$ in this study, however, was found in an Arenosol (> 90% of sand). Alternative explanations for sandy soils also giving rise to ^{15}N -enriched soils are provided in Aranibar et al. (2004). In summary, SOM compounds are, in general, less physically protected

in coarse-textured soils. Thus, the easier biological attack (i.e. SOM mineralisation) can also potentially give rise to higher $\delta^{15}\text{N}$ values in the remaining N pools of these soils.

The model simulated soil $\delta^{15}\text{N}$ values for the Caatinga Domain presented in Figure 2.15 provides the first approximation of the isotopic behaviour across the region. Modelled $\delta^{15}\text{N}$ values over the region were made possible due to the inclusion of only spatially explicit predictors variables in the lowest-AIC model (i.e. AI and ψ). Field-measured $\delta^{15}\text{N}$ values overlying modelled responses indicate that the model can reasonably predict $\delta^{15}\text{N}$ values in Caatinga, with measured soil ^{15}N *versus* model simulated soil $\delta^{15}\text{N}$ shown in Figure 2.14 providing additional support for the model accuracy.

The spatial representation of $\delta^{15}\text{N}$ for the Pernambuco state of SANTOS et al. (2022) provided a clear picture of the climatic control on isotopic discrimination in semiarid places. In their work, this control remained even under distinct land uses and over three physiographic domains. However, soil isotopic composition is thought to be the result of a multitude of processes (BAUMGARTNER et al., 2021). For instance, geomorphological features are also likely to control soil isotopic discrimination processes. Despite the prevailing apparent regional climatic control on soil $\delta^{15}\text{N}$ values on regional scales, the topography may be important at a local scale (BAUMGARTNER et al., 2021). Erosive forces may operate at different rates across slope gradients, therefore influencing soil rejuvenation processes (AMUNDSON et al., 2003). Furthermore, relief dictates orographic rainfall, therefore exerting indirect control on isotopic composition.

The results of SANTOS et al. (2022) provide further insights into potential differences in soil $\delta^{15}\text{N}$ values arising from geomorphological characteristics. For example, the Zona da Mata Physiographic Domain has a warm and humid climate and showed the lowest soil $\delta^{15}\text{N}$ value. In contrast, the Sertão Physiographic Domain has a hot and dry semiarid climate and showed the highest soil $\delta^{15}\text{N}$ value. The Agreste Domain is the transition zone between Zona da Mata and Sertão covering much of the Planalto da Borborema mountain range (SANTOS et al., 2022). Accordingly, regions surrounding higher terrains areas are susceptible to experiencing orographic rainfall, potentially influencing isotopic signatures. In addition, influence from erosive processes is thought to potentially influence isotopic signatures in these sloping/rough terrain areas.

Finally, despite the somewhat expected variations in soil $\delta^{15}\text{N}$ values between the two P_A categories (Figure 2.16-a; $\chi^2 = 15.53$; $p < 0.000$), subsequent evaluation of the nutrient availability (expressed by effective cation exchange capacity; I_E) considering these two levels

of P_A may provide further insights into isotopic discrimination processes in Caatinga. For instance, the considering the ‘high-rainfall’ category (i.e. $P_A > 0.8$), effective cation exchange capacity appeared to explain 44% of the variation in soil $\delta^{15}\text{N}$ values ($r^2 = 0.44$; $p < 0.000$; Figure 2.16-b). Indeed, it has been suggested that nutrient availability may become more important in ecosystems where water is not (or less limiting) factor (SWAP et al., 2004). Nutrient-rich ecosystems were shown to be associated with more open “leaky” N cycles (VITOUSEK et al., 1989; MARTINELLI et al., 1999, QUESADA et al., 2010). Interestingly, soil $\delta^{15}\text{N}$ values were relatively high for both S_{KAR} sites under different precipitation conditions, potentially reflecting the influence of nutritional status on the isotopic discrimination. Collectively, evidence from the literature and the results presented here suggest that differences in nutrient availability and geomorphologic-environmental variation may account for unexplained variances when attempting to predict $\delta^{15}\text{N}$ values using purely climatic models.

2.4.3 Weathering and total nutrient capital reserves (NCR_T)

Within the weathering metrics evaluated in this study, \sum_{RB} , $[\text{Zn}]_T$, $[\text{Mn}]_T$ and the K/Zr elemental ratio were higher for S_{KAR} sites, with S_{MET} sites also showing higher \sum_{RB} and K/Zr than the S_{SED} sites. These metrics clearly show the influence of parent materials on nutrient capital reserves. Importantly, the weathering course in semiarid regions is likely substantially distinct from warm humid places. Specific conditions such as very high potential evapotranspiration rates (E_p) to relatively low annual P_A , barriers to water drainage and typical soil reactions range (moderately acid to moderately alkaline) are all geochemical processes that favour the persistence of bases in the soils, thus controlling the formation of 2: 1 (expansive) silicate clay minerals such as smectite (SCHULZE, 2005), a representative group found in many Caatinga soils. (ARAÚJO et al., 2017).

2.4.4 Interrelationships between soil properties

Figure 2.5 shows that soil texture across soils derived from metamorphic rocks (S_{MET}) had much less variation in the contents of sand, clay and silt, not surprisingly then soil texture accounted more strongly for variations in I_E of S_{SED} sites. Soil texture is known to widely account for the surface charge density of soils. Specifically, sand and silt particles hold relatively much lower specific surface area (SSA) than clay particles, but might store considerable amounts of weatherable minerals, potentially releasing essential nutrients for plant

growth into the soil solution over time (PALM et al., 2007). Conversely, clay particles are not constituted of weatherable minerals but have a large SSA and plenty of charged edges, thus allowing clay-rich soils to hold relatively large amounts of exchangeable cations (SANCHEZ, 2019).

Figure 2.8 provides a picture of how soil $[P]_T$ relates to several soil constituents, namely soil total iron, aluminium and calcium oxides percentages (XRF-measured), soil sand_f, silt_f and clay_f and $[C]_T$. Such constituents reflect a wealth of potential P-associations. Nevertheless, $[C]_T$ and soil $[P]_T$ were not related considering the full dataset together neither S_{SED} nor S_{MET} separately. These results are contrary to results reported by Menezes et al. (2012; *apud* Menezes et al., 2005), who reported a strong significant positive relationship between soil carbon and soil P_T ($r = 0.89^{**}$) calculated from several soil surveys covering the main soil orders of Caatinga. This relationship could indicate proportional increases in P contents as soil SOC increases, presumably in organic P-forms (P_o). Such discordant results probably are associated with differences in texture and mineral assemblages of the soils included in the Menezes and coworkers' compilation. As shown in Figure 2.4, the soils sampled in this work were mostly coarse-textured, which influences SOC storage and most likely also P_o forms. The importance of P_o for tropical soils has been widely considered (NZIGUHEBA AND BÜNEMANN, 2005; QUESADA et al., 2010) with P_o often considered to be the major pool in advanced weathered soils (SANCHEZ, 2019).

The current literature concerning P_o and P_i pools, however, most reports on soils of humid tropics and cannot be simply extrapolated for semiarid regions such as the Caatinga (SILVEIRA; ARAÚJO; SAMPAIO, 2006). In general, the P_o fractions of Caatinga soils are lower than P_i . For example, Araújo, Schaefer and Sampaio (2004), in a toposequence study, found relatively low proportions of P_o in pedogenically distant Ferralsols and Luvisols (25% and 28% of the total P, respectively), despite P_o levels increasing downslope. It has been suggested that unlike $[P]_T$, P_o is not closely associated with the degree of weathering (SANCHEZ, 2019). Rather, biologically-produced P_o should be related to soil organic matter build-up processes. For example, Silveira, Araújo, Sampaio (2006) reported soils of relatively high $[P]_T$ but with only 13% and 17% of P_o and soils with relatively low $[P]_T$ with 26% and 33% of P_o . The above-mentioned studies help explain the lack of relationship encountered between $[C]_T$ and $[P]_T$, which seems to be primarily associated with soil mineral constituents.

All measured soil textural fractions (i.e. sand_f, silt_f and clay_f) were associated with $[P]_T$ at the level of the full dataset. However, considering geologic the classes separately, the

association existed only for S_{SED} sites. A likely underlying reason is that the S_{MET} group had a less varying texture, whereas the S_{SED} group had a larger textural spectrum, allowing for a more easy evaluation of textural influence on $[P]_T$ levels. The highest predictive power was assigned to $silt_f$, followed by $sand_f$ and $clay_f$ at both the entire sampling level as well as only for S_{SED} . This “silt signal” is interpreted as follows: primary minerals are those whose mineral compositions have not changed significantly since their extrusion as molten lava (WEIL; BRADY, 2016; NANZYU; KANNO, 2018). Then, considering that weatherable primary minerals are assumed to be only present in the physically-weathered $sand_f$ and $silt_f$, phosphate-bearing primary accessory minerals such as fluorapatite must be predominantly present in the $silt_f$, which can be interpreted as an indicator of low pedogenic development (ARAÚJO-FILHO et al., 2017). For example, the presence of accessory minerals in the silt and sand fractions was assigned to low weathering levels in Planosols of Pernambuco state (PARAHYBA et al., 2010). In addition, $silt_f$ holds a relatively high surface charge density which may, partially, account for the $silt_f \times [P]_T$ association. On the other hand, $[P]_T$ contents decrease proportionately as $sand_f$ increases, which seems fairly logical as sandy soils hold a low charge density along with a low adsorption capability (QUESADA et al., 2010).

In addition, the essentially quartzose nature of the $sand_f$ implies negligible weatherable minerals presence (PALM et al., 2007). Quesada et al. (2010) compared Amazonian sandy soils with the “terminal steady state” of the seminal conceptual Walker and Syers’ model (WALKER; SYERS, 1976), whereby the continuous cycling of P_o is hypothesised to sustain the vegetation P demand, and this may also be the case for several Caatinga soils. Although manifold environmental differences exist between the Amazon and Caatinga, some geochemical relationships should be valid for both regions. As regards the modest relationship between $[P]_T$ and $clay_f$, it should reflect different proportions of clay-sized particles with descending SSA from allophane to aluminium and iron oxy(hydroxides) (PALM ET AL., 2007; (SINGH et al., 2017). In general, $clay_f$ is expected to determine phosphorus sorption capacity for soils of similar mineralogy. In addition, this association is maintained through the formation of secondary phosphorus clay minerals, namely (Ca)-bonded, (Al)-bonded and (Fe)-bonded phosphates (SANCHEZ, 2019). The proportional occurrence of these forms is known to be conditioned by soil pH, where acid reactions allow for (Ca)-phosphate hydrolysis, giving rise to (Al)-bonded and (Fe)-bonded phosphates (GUO et al., 2000; SALCEDO, 2006), the latter usually being of lowest solubility (SANCHEZ, 2019). Considering that the soils of this study were collected in Caatinga, measured soil pH_{H_2O} values were somewhat low, which may help

explain the higher predictive ability of Fe_2O_3 to account for $[\text{P}]_{\text{T}}$ rather than the Al_2O_3 and CaO (Table 2.4). In addition, a compilation of P contents in several common rock types has shown that median P contents were marked higher in Fe-rich rocks as opposed to Si-rich rocks (PORDER; RAMACHANDRAN, 2013), which suggests proportional abundances of $[\text{P}]_{\text{T}}$ and $[\text{Fe}]_{\text{T}}$, thus giving rise to (Fe)-P compounds.

The $[\text{P}]_{\text{T}} \times \text{CaO}$ relationship was, however, weak at the overall sampling level ($r^2 = 0.12$; $p = 0.04$), but was relatively high considering S_{MET} sites only (Figure 2.8-c; $r^2 = 0.53$; $p = 0.005$). But CaO at all S_{SED} sites was negligible, indicating low weatherable calcium capital reserves. As already mentioned, a more conclusive evaluation of P-forms distribution across specific fractions requires sequential P fractionations. Nevertheless, these results illustrate differences in geochemical conditions of S_{MET} , S_{SED} and S_{KAR} . As the movement of P from primary minerals towards less soluble (Fe) and (Al)-bonded compounds requires continuous losses of Ca^{2+} and soil acidification, it is expected that soils with relatively higher pH (i.e. S_{MET} and S_{KAR}) should have higher levels of (Ca)-bonded compounds as opposed to S_{SED} sites. These results are consistent with the theoretical framework provided in Salcedo (2006). Indeed, soil P chemistry and behaviour are markedly complex. For example, Agbenin and Tiessen (1994) measured P-rich silt particles, concomitantly containing Ca, Fe and Al, which was suggested to be a mixture/impregnation of P-bearing primary minerals onto (oxy)hydroxides during erosive processes with limited leaching intensities typical of the Brazilian semiarid region.

As previously shown, differences in total $[\text{C}]_{\text{T}}$ and $[\text{N}]_{\text{T}}$ were not associated with the different geologic classes and/or RSGs. Soil texture, on the other hand, markedly influenced $[\text{C}]_{\text{T}}$ contents. Clayey soils, as mentioned already, have a relatively much higher SSA, allowing the formation of organo-mineral complexes, as well as providing physical protection for carbon particles inside their micropores. On the other hand, sandy soils have much lower SSA, along with a very reduced physical protection against SOC mineralisation (PALM et al., 2007, SANCHEZ, 2019). The current results echo these theoretical conceptions as both soil sand_f , silt_f and clay_f showed significant relationships with $[\text{C}]_{\text{T}}$ in the overall sampling context, with sand having a strong negative association with $[\text{C}]_{\text{T}}$. Contrary to the authors' expectations, MENEZES et al. (2021) found large SOC levels in coarse-textured Arenosols underlain Dense Caatinga. This superiority of SOC contents in Arenosols in Menezes and coworkers (2021) was assigned to the unsuitability of these soils for agriculture, corresponding to longer fallow periods, thus accumulating C for a longer time.

Considering geologic affiliations (and associated RSGs), S_{MET} sites had lower variability in their general texture when compared to S_{SED} sites and S_{KAR} sites, the latter showing considerably much finer textures and relatively high $[C]_T$ contents. Within S_{MET} sites, clay content tended to better account for variations in $[C]_T$ (Figure 2.10-c). Since all S_{ARE} , S_{LAC} and S_{HAC} soils are present in the S_{MET} category, the observed differences may reflect a spectrum of increasing SSA. Within S_{MET} category, however, the highest $[C]_T$ content (13.42 mg kg^{-1}) was found in a quartzite-derived S_{LAC} Leptosol (MCS-01), which might be hypothesised as being due to lower $[C]_T$ mineralisation rates. The conventional assumption that S_{HAC} soils stabilise more carbon than LAC kaolinitic-illitic soils was counteracted by Singh et al. (2017), who showed that contents of clay-sized smectites led to higher soil moisture, which in turn increased soil respiration and microbial biomass. The current results do not support the idea that S_{HAC} soils necessarily store more SOC than S_{LAC} soils, which appeared to be much more associated with particle size effects, levels of (oxi)hydr)oxides and Fe and Al bearing minerals and potentially T_A .

Although specific methods are required to specifically characterise clay mineralogy and (oxi)hydr)oxides species, soil total iron includes these forms as well as iron present in silicate minerals (SCHULTE, 2004). In conjunction with clay-sized aluminium species (e.g. kaolinite and gibbsite), (oxi)hydr)oxides are believed to be the most important soil constituents in the long-term persistence of SOC (KIRSTEN et al., 2021). The importance of pedogenic free iron oxides in storing SOC has been emphasised in several works in tropical soils (e.g. SINGH et al., 2017; QUESADA et al., 2020; KIRSTEN et al., 2021; BELLÈ et al., 2022). Therefore, these components likely similarly exert great importance on SOC persistence in Caatinga soils given the predominance of coarse-textured Caatinga soils (at least in the current study). Indeed, even small amounts of these constituents may significantly enhance the SOC storage capability. Ultimately, SOC levels should be controlled by the prevalent semiarid climate (i.e. high temperature and low moisture levels), proportions of free Fe and Al (oxy)hydroxides, Fe and Al bearing minerals, as well as varying levels of clay minerals from crystalline to amorphous allophane. The latter are usually assumed to hold the largest specific surface area among clay minerals (SINGH et al., 2017).

Climatic conditions have long been recognised as a major factor determining SOC build-up and decomposition (JENNY, 1980). In this respect, Figure 2.12 shows no apparent effect of P_A for $[C]_T$, $[N]_T$ and soil C/N ratio, whereas mean annual temperature (T_A) was associated with a decrease in $[C]_T$ levels for all sites considered together, but with a steeper

relationship considering only S_{SED} sites. Despite the relatively small variation in mean annual temperature among sites (from 20.5°C to 26.8 °C), these differences are hypothesised to be sufficient for catalysing SOC mineralisation, considering that mean values are affected by extreme values (as those in the warmest month and warmest year quarter), despite potential limitations arising from the minimum soil moisture levels required for biological activity. It has been reported that the release of physically protected and/or more recalcitrant SOC forms (such as aromatic compounds) is temperature-sensitive (DAVIDSON; JANSSENS, 2006; SANCHEZ, 2019). Thus, these forms may have lower rates of accumulation, yielding lower SOC contents over time at higher temperatures. An important concept underlying SOC decomposition is the temperature sensitivity of SOC decomposition, commonly expressed as changes in SOC decomposition every 10°C increases (Q_{10}), with studies showing a codependence of soil moisture and SOC recalcitrance (DAN et al., 2016; MOINET et al., 2020). Importantly, the results presented here are preliminary since conclusive statements regarding the potential effects of changes in temperature on SOC pools also should consider carbon dynamics in the soils and the sensitivity of SOC inputs via net primary production (NPP) (LLOYD; TAYLOR, 1994). Nevertheless, these results draw attention to the potential effects of increased temperatures on SOC mineralisation rates as a result of climate changes.

Mean annual temperature also had a negative effect on $[N]_T$ contents, but only for S_{SED} sites. Moreover, the relationship was stronger for $[C]_T$ rather than $[N]_T$, which suggests higher net carbon losses relatively to nitrogen, potentially present in more stable compounds. In addition, NO_x fluxes are considered an important biogenic source of nitrogen leaving arid and semiarid ecosystems (FEIG; MAMTIMIN; MEIXNER, 2008). NO_x and fluxes have been reported to be highly sensitive to temperature changes in these ecosystems, at least in part attributable to the fact that microbial populations should have distinct optimal temperatures, thus affecting gaseous N-fluxes (ARANIBAR et al., 2004).

An important consideration related to these results is that the nitrogen incorporated into soil organic pools represents an integrative ecosystem property, which is expected to reflect an integration of biogeochemical processes over time [e.g. nitrogen biological fixation (NBF)]. Some works reporting on NBF have been published for Caatinga over the last decade (e.g., FREITAS et al., 2010; DE SOUZA et al., 2012; FREITAS et al., 2012; DA SILVA et al., 2017), from which it is clear that despite the outstanding richness and abundance of legumes in Caatinga (QUEIROZ, 2006), the proportion of N_2 -fixing plants that effectively do so is commonly low. Nitrogen biological fixation is a highly-demanding process, which is more

likely to occur under higher rainfall levels (MCKEY, 1994), which may explain the low rates of NBF as found in the above-mentioned studies.

Relatively low phosphorus and high nitrogen availability have been found to influence symbiotic mechanisms instead of lacking nodulation in potentially N_2 fixing species (SILVA et al., 2017). Figures 2.11-a and 2.11-b provide further evidence of the coupled nature of the nitrogen, phosphorus and cations cycles (here represented by I_E). Both relationships were significant considering the whole dataset (Table 2.4-d), however, when considering geologically distinct soils separately, the relationship was significant only in S_{SED} sites. These results suggest that the influence of phosphorus and general fertility on the nitrogen cycle may be regulated under different geochemical circumstances, with some “sedimentary Caatingas” sites possibly susceptible to a relatively sluggish ecosystem nitrogen enrichment as compared to nutrient-rich sites across Caatinga.

Figure 2.17 (a-h) shows a series of weathering-associated relationships discriminated according to soil geologic affiliations. As anticipated in Section 2.4.4, $silt_f$ can be taken as a reasonable indicator of pedogenetic development, with less developed soils, in general, holding relatively higher silt contents as compared to highly weathered soils. Therefore, there is a strong association between soil $silt_f$ and \sum_{RB} , with the highest latter values being found in the three calcareous-derived S_{KAR} (Calcisol, Cambisol and Leptosol; PFF-01, GBR-1 and GBR-02, respectively). Such elevated contents, however, are thought to be the result of calcite secondary accumulation in stable compounds. The relatively high contents of silt in PFF-01, GBR-01 and GBR-02 soils are likely attributable to the presence of underlying calcilutites (i.e. predominantly silt or clay-sized limestones) widely present in the Jandaíra, Gabriel and Nova América geologic formations (PFF-01, GBR-01 and GBR-02, respectively). The $silt_f \times \sum_{RB}$ relationship was even stronger for S_{SED} sites, which encompass varying pedogenetic conditions, including quartz-rich Arenosols with nearly negligible silt contents (e.g. Arenosols of “Vazante Dunas” geologic unit), and pedogenically younger soils (i.e. Leptosol, Luvisol, Cambisol).

Regarding the relationships found between \sum_{RB} and total contents of iron zinc and manganese (Fe_T , Zn_T and Mn_T), it is noteworthy that soil total micronutrients reservoirs are the complex product of initial concentrations in parent materials and their subsequent interactions with pedogenic processes (WHITE; ZASOSKI, 1999). Indeed, both Fe_T and Zn_T had linear increases with \sum_{RB} across S_{SED} sites. On the other hand, Mn_T increased with \sum_{RB} increases only for the S_{MET} sites, suggesting general lower levels of Mn in S_{SED} soils (except for a Luvisol in JUV-01).

Despite higher micronutrient capital reserves, the S_{KAR} sites were slightly alkaline, potentially giving rise to limitations in the availability of most metallic micronutrients (optimally in slightly acid or acid soils). It has been shown that increases in aridity may indirectly lead to a shortage of metallic micronutrients mostly because of lower SOC inputs as well as aridity-induced soil pH increases (WHITE; ZASOSKI, 1999; MORENO-JIMÉNEZ et al., 2019). Thus, high soil pH caused by increased aridity might be a concern in a future scenario of lower precipitation amounts, at least in some Caatinga soils. The mechanisms whereby soil organic matter (SOM) improves metallic micronutrient availability have been comprehensively reviewed in DHALIWAL et al. (2019). In summary, SOM influences physicochemical reactions that improve levels of exchangeable and water-soluble plant-available micronutrients. Similar biogenic mechanisms may catalyse the conversion of unavailable to available micronutrient forms, thus counteracting potential micronutrient shortage issues in alkaline soils.

The elemental ratios of Figure 2.17 (e, f,) are additional weathering metrics. K/Zr ratios were markedly higher and less varying in S_{MET} and S_{KAR} sites. On the other hand, S_{SED} sites have shown more varying K/Zr ratios across the Σ_{RB} spectrum. This could be attributable to the predominance of quartz-rich Arenosols in the lower part of the spectrum, with K-bearing minerals (i.e. potassium feldspar or “K-spar”) virtually absent. The higher part of the spectrum is associated with Leptosols, Cambisols and Luvisols, i.e. less weathered soils associated with high values of K/Zr, which suggests higher levels of weatherable K-spars (in addition to available forms). The Ca/K relationship discriminates soils derived from plagioclase-bearing materials from those derived from K-spars-rich materials. Regardless of soil geologic affiliations, there were no differences in Ca/K with similar ranges for the S_{MET} and S_{SED} sites. It should be highlighted that, even under the same environmental conditions, weathering rates are not uniform. Rather, its susceptibility depends upon factors such as mineral assemblage, colour and texture (FONTES, 2012). Thus, minerals can be ordered according to weathering resistance. GOLDICH (1938) conceived a pioneer study where the resistance of primary minerals to weathering was linked to the magma crystallisation sequence. In other words, mafic or ferromagnesian minerals ($\downarrow Si$; $\uparrow Fe$; $\uparrow Mg$), which are formed first, are much more prone to weathering, tending to first disappear from sand_f and silt_f (FONTES, 2012), whereas felsic minerals ($\uparrow Si$; $\uparrow Al$) tend to resist more to weathering. Still, according to the weathering resistance sequence of GOLDICH (1938), K-spars are more resistant to Albite (Sodic Plagioclase), which in turn is more resistant than Anorthite (Calcic Plagioclase). Therefore, the Ca/K ratios shown in Figure 2.17-f), not only reveal the current lower abundance of plagioclase

products for virtually all sampled soils but it is also suggested that orthoclase K-spars minerals might persist for longer periods in soils.

Concerning the relationships among \sum_{RB} , $[P]_T$ and I_E (Figure 2.17-g and h), it has been suggested that similar general processes control, which is mostly governed by soil pH changes (QUESADA et al., 2010). At more alkaline pH, soil P reactions are mostly towards Ca-bonded compounds, which are more soluble as soil pH declines, as compared to Al and Fe-bonded P compounds, both later formed under acid reactions. Thus, with soil ageing and the tendency of base impoverishment and soil acidification, Ca-bonded P-forms compounds tend to be solubilised with an increasing abundance of Fe and Al-bonded P forms which have a higher P retention capacity, also undergoing slow but continuous losses of P out of the system (WALKER; SYERS, 1976; SANCHEZ; UEHARA, 1980). In parallel, clay activity tends to diminish (2: 1 clays \rightarrow 1: 1 clays), along with a decrease in specific surface area and associated surface charge density. As a result, a decrease in cations and anions retention capability is expected.

2.4.5 Soil morphology, effective rooting depth (R_{EF}) and water availability

During soil pedogenic development, physical and chemical constraints tend in opposite directions (QUESADA et al., 2010), with pedogenically incipient soils, in general, showing favourable chemical conditions for plant growth (i.e. greater nutrients availability) along with limiting soil physical properties (e.g. shallow depth). Except for Caatinga sedimentary terrains where soils are appreciably deep (≥ 2.0 m), Caatinga soils are morphologically distinct from common soils of other Brazilian regions, with conspicuous shallow soils (i.e. ≤ 0.5 m) or less shallow (i.e. ≥ 0.5 and ≤ 1.0) dominating the region (ARAÚJO FILHO et al., 2017). This characteristic itself may impose a marked physical constraint for root development, also affecting both soil physical support capability as well as the volume of exploitable soils for water and nutrient uptake. These relationships between soil physical properties and general fertility can be observed in this study. These patterns are largely represented across the S_{MET} and S_{SED} dichotomy, where the former usually exhibits favourable chemical conditions for plant growth, whereas the latter (excluding non-aggregated loose sands) tend to show more appropriate physical conditions to support plant growth as well as larger volumes of root-exploitable soils. These characteristics are known to be influenced by geomorphological features, where sloping terrains are more prone to continuous pedological rejuvenation processes and soil parent material exposure, and potentially also affect vegetation dynamics

(i.e. NPP, mortality and recruitment rates). An evaluation of the impact of soil physical properties on vegetation dynamics these dynamics remains to be undertaken in forthcoming work in the established permanent plots.

The results presented in Section 2.3.5 are consistent with observational field data and theoretical findings (GUSWA, 2010; SCHENK; JACKSON, 2002). Although R_{EF} can be assumed as a result of multiple factors, i.e. mean annual rainfall, soil texture class, depth of soil barriers, growth forms (e.g. tree, shrubs, herbs, grasses), stand species composition, water table depth (FAN et al., 2017), it seems logical that, in water-limited ecosystems, the climatic and hydrologic components may exert a pivotal influence on R_{EF} . From the water standpoint, optimal R_{EF} is thought to be achieved by the trade-off between carbon investments in root tissues and associated water uptake benefits as suggested by GUSWA (2010), who also found that deepest root systems were found when potential evapotranspiration approaches rainfall rates. And indeed, Figure 2.19 shows that deeper rooting zones tend to be found at lower CWD levels, i.e. towards a balance between rainfall and evapotranspiration levels. Laio, D'Odorico, and Ridolfi (2006) found the deepest root systems in coarse-textured soils where the rainfall rates were slightly lower than evaporative demands. Given the marked predominance of coarse-textured soils in the sampled soils of this work, the textural effect on R_{EF} may be obfuscated. As shown in Figure 2.18, R_{EF} values were highly variable across the sampled sites (0.3 – 2.0 m in non-restrictive soils; 0.35 to 1.75 in restrictive soils), even under similar climatic conditions. Beyond species characteristics, this overall variability may reflect local soil water status, infiltration rates and shallow water tables depth, relief-driven drainage barriers, as has been suggested by FAN et al. (2017). Interestingly, paired sites with similar or distinct soil conditions were located in similar positions across the $CWD \times R_{EF}$ environmental space (labelled in Figure 2.19), providing some evidence that nutritional characteristics may be less influential in R_{EF} , at least for the studied soils. For example, JUV-01 and CJU-01 (Luvisol and Arenosol, respectively) and CGR-01 and MCS-02 (also Luvisol and Arenosol, respectively), had quite dissimilar chemical and physical characteristics, but similar R_{EF} . Nevertheless, soils with similar conditions (namely PAT-01 and PAT-02, both Luvisols) also showed equivalent R_{EF} , GBR-01 and GBR-02 (Cambisol and Leptosol), which are chemically comparable but morphologically distinct (in terms of depth) also had equivalent R_{EF} . ARI-03 and ARI-04 (Alisol and Acrisol, respectively) support floristically similar semideciduous forests and have an equivalent P_A to CWD values, which may justify similar R_{EF} depths. Taken together, these results provide evidence of a climate-driven below-ground carbon investment in SDTFs

of Caatinga. Pinheiro, Costa e Araújo (2013) further suggested that R_{EF} may vary across different soil vegetation associations, with a marked capability of Caatinga to adapt to shallow soil profiles and a lack of spatial variability in R_{EF} within stands. Improved comprehension of plant rooting depth drivers is crucial to understanding global changes as Earth system models are particularly sensitive to the root depth parameter (FAN et al., 2017).

Finally, given that R_{EF} and general vegetation performance are believed to be largely driven by hydrologic parameters, Figure 2.20 shows that, contrary to what is often assumed, soils developed in sedimentary terrains, do not necessarily hold the higher maximum plant-available soil water contents (θ_P). Rather, the final water-holding capability is a function of both soil depth and soil texture-associated volumetric soil water (θ_V). Thus, θ_V among the deepest soil profiles (that is, 2 m) varied from 0.05 to 0.13 $\text{m}^3 \text{m}^{-3}$, whereas soils as shallow as 0.8 m were able to hold water volumes comparable to the deepest profiles (Figure 2.20). Overall θ_V was found to be low compared to clayey soils of other Brazilian regions, which is markedly due to the tendency of overall coarse textures found in many Caatinga soils, at least across the current sampling. These results can potentially contribute to regional modelling efforts to characterise soil hydrologic characteristics of Caatinga.

Conclusions

This work arose from the unique opportunity of studying a wide range of soils in much of the Caatinga Domain. It was shown that the common distinction often made between soils from ‘crystalline’ and ‘sedimentary’ terrains should be valid in most situations. However, there may be several exceptions. The properties of soils derived from sedimentary parent materials, metamorphic and chemical sedimentary calcareous rocks had marked differences, especially in terms of available cations, soil pH, and total (macro and micro) nutrient content. The simple model proposed in Table 2.5, including the $\sum_{RB} \times \text{pH}_{H_2O}$ term, represented 94% of the variation in soil \sum_B (available Ca + Mg + K + Na). Considering that methods to estimate the available and total bases are extremely time-consuming (especially sulfuric acid digestion – SAD) and given the high predictive power of the generated proposed model, the parameters could serve as a surrogate tool for estimating values from one method to another (if soil pH_{H_2O} values are also available).

The total phosphorus concentrations measured in this work are consistent with previous work that also measured $[P]_T$ in Caatinga soils. Karst-derived soils (S_{KAR}), however, showed

relatively higher P contents. These high contents are believed to be mostly present in low-solubility P forms, which should be counteracted by biological players. Additional sampling (including the biological component of the soil) in karst environments would be valuable to understand the dynamics of essential nutrients in these ecosystems.

Total soil carbon concentrations were best explained by the soil sand fraction. The mean annual temperature, however, also appeared to be related to both $[C]_T$ and $[N]_T$ in sedimentary environments. This is suggested to be due to the likely lower physical protection in soils resulting from sedimentary parent materials. Considering that soils of semiarid regions may play a considerable role in the global carbon sink (MENEZES et al., 2021), understanding the dynamics underlying the persistence of SOC in these soils is considerably important for global carbon emissions issues.

Soil $\delta^{15}N$ values were shown to be driven primarily by climatic parameters in Caatinga. This result is consistent with several studies showing the control of the climate on N isotopic signatures. Considering the extreme environmental variability of Caatinga, and echoing Swap et al. (2004), how could climate forces account so strongly for variation in isotopic composition changes? The soil $\delta^{15}N$ isoscape produced for the Caatinga region may potentially contribute to the understanding of the N cycle in this region. Furthermore, the results presented here suggest a cutoff of $0.8 \text{ m a}^{-1} P_A$, which is suggested to potentially be the point where I_E becomes more relevant than the climate in determining the isotopic composition in Caatinga soils. However, soils with I_E in the $40 - 80 \text{ mmol}_c \text{ kg}^{-1}$ range are particularly lacking in this study (Figure 2.16), and soil within this I_E range would be helpful to clarify the isotopic behaviour in less weathered/more fertile soils under different precipitation regimes.

Finally, the results presented here show that soils located in sedimentary terrains do not necessarily have a greater soil water-holding capability. On the one hand, deeper soils translate into potentially larger physical reservoirs; on the other hand, most deep soils in Caatinga are expected to hold coarse textures (that is, lower volumetric soil water content associated with texture).

Chapter 3

Soil and climate influence on above-ground woody biomass of
Brazilian SDTFs: a regional assessment in geologically distinct stands

Chapter 3 – Soil and climate influence on above-ground woody biomass of Brazilian Seasonally Dry Tropical Forests: a regional assessment in geologically distinct stands

3.1 Introduction

Stand-level above-ground biomass (AGB) integrates several processes, including primary productivity, tree recruitment, and mortality (LLOYD et al., 2009). Much of the research in the tropics concerning AGB has been carried out in rainforests (e.g. BARALOTO et al., 2011; LAURANCE et al., 1999; QUESADA et al., 2012; SULLIVAN et al., 2020), but seasonally dry tropical forests (herein SDTFs) are an important part of the story. This type of vegetation is usually associated with semiarid climates or freezing temperatures and, although they once have been estimated to represent 42% of the landmass covered by tropical forests (MURPHY; LUGO, 1986a), nowadays it is estimated that they are reduced to less than 10% of their original coverage in many countries (DRYFLOR, 2016), with a global gross loss of its coverage estimated to be 11% between 2001 and 2020 compared to the year 2000 (OCÓN et al., 2021). Moreover, despite storing relatively less carbon and having a simpler structure compared to their wetter counterparts (BECKNELL; KUCEK; POWERS, 2012a), SDTFs have been suggested to be increasingly relevant in carbon cycle inter-annual variability, with a substantial component of the record land carbon sink of 2011 (LE QUÉRÉ et al., 2013) associated with ecosystems of the Southern Hemisphere semiarid (POULTER et al., 2014). Therefore, understanding which environmental factors influence AGB accumulation is critical to understanding how global changes could affect this property and associated ecological services.

Above-ground ground biomass in Caatinga is known to be a multi-driven property, especially considering the human-modified characteristic of the region (SOUZA et al., 2019; CASTANHO et al., 2020a). An estimate from a satellite product showed that, in the year 2000, the stand-level AGB distribution was extremely heterogeneous across Caatinga (CASTANHO et al., 2000; Section 1.8, Chapter 1). Such a heterogenous distribution of AGB reflects human modifications, which led to a mosaic of stands ages, but also reflects the environmental influence, i.e. geologically derived soil substrates, AGB potential of species, and climate. The latter is considerably associated with different plant physiognomies and standing AGB across the region (CASTANHO et al., 2020b). For this reason, the opportunity to evaluate the influence of environmental drivers on the vegetation attributes of mature stands is relatively rare in the region. Considering that Caatinga usually exhibits negative water balances and high precipitation seasonality (SAMPAIO, 1995), SDTFs growing in the region should be primarily

limited by water availability, as for other SDTFs worldwide (MOONEY; BULLOCK; MEDINA, 1995; BECKNELL; KUCEK; POWERS, 2012; ALLEN et al., 2017).

Importantly, forecasted climate scenarios warn of potential changes in rainfall regimes in the tropical range by the end of the 21st century, and geographically comparative studies are essential to understand how SDTFs are sensitive or resistant to these changes (ALLEN et al., 2017). So far, most studies comprising larger or even global scales have only tested climate variables as AGB predictors (e.g. BECKNELL et al., 2012).

Among the few studies that have evaluated the influence of soil properties on AGB in semi-arid zones, Souza et al. (2019a) showed that soil properties (summarised as orthogonal axes) affect AGB, vegetation sprouting capacity, and community composition. Similarly, Maia et al. (2020a) reported interactions between soil attributes and climate shaping above-ground woody biomass and community assembly of SDTFs in the transition zone between the Cerrado and Caatinga biogeographic domains. Souza et al. (2019b) found a minor role in soil fertility to explain AGB in SDTFs in Catimbau National Park, Pernambuco state. Prado-Júnior et al. (2016) suggested a negative effect of soil calcium on SDTFs productivity, with no direct influence on initial standing AGB. Peña-Claros et al. (2012) have found a considerable role of soil fertility and texture to explain a suite of dry forest properties including basal area, stems density, species richness and taxonomic diversity. Interestingly, the effect of soil fertility was more pronounced in dry than in moist forests. Peña-Claros et al. (2012) argued that this counterintuitive effect was because the soils of moister forests in their study had a general high-fertility status, thus being less responsive to site variations in nutrient concentrations. Nevertheless, all these works were limited to relatively small geographic ranges. If, on the one hand, climate factors are believed to drive AGB over larger scales, factors such as soil properties and topography are likely to exert a greater influence at smaller scales, i.e., local to regional (SIEFERT et al., 2012). As the Brazilian Caatinga occupies an area of approximately 862,818 km², covering ca. 10.1% of Brazil's territory (IBGE, 2019a), both soil and climate are likely to affect AGB in the region.

In this context, noting the extreme environmental variability of Caatinga (Chapter 1), it should also be noted that not only has the complex geological history influenced the present flora assembly but also determined the parent soil parent materials found in the region. Therefore, accounting for the ability of most species to tolerate water-stressed conditions, geologically-derived soil parent materials are believed to be the main factor for plant species diversity and endemism (FERNANDES et al., 2022).

Generally speaking, it can be expected that the taxonomic/phylogenetic composition of a given community will reflect its respective functional attributes, with the latter ultimately being considered the mechanistic connection between plant species assembly and ecosystem functioning (LOHBECK et al., 2015; DÍAZ et al., 2006). Soil properties have already been demonstrated to influence the functional composition (Section 1.9, Chapter 1). For example, an inverse correlation between soil cations and wood density was reported by Quesada et al. (2012) and Lira-Martins, 2019). In turn, wood density might reflect different life histories and strategies to cope with environmental adversities. Soil nutrients may also influence other plant attributes, with Jager et al. (2015) examined the responses of functional traits to soil fertility and found a clear trend of species associated with low-fertility soils showing “slow leaves traits”, i.e. high wood density, low P, low N and high leaf mass dry content (LMDC) as opposed to species occupying high fertility soils.

Conceptually, if geologically-derived soil properties influence community attributes characteristics and the latter influence vegetation dynamics and standing biomass, geology can be seen as a major factor in shaping soil properties and, ultimately, influencing vegetation properties. Therefore, both community-weighted traits means (CWM), i.e. the mean trait values weighted by their relative abundance in a given community (LAVOREL et al., 2008), and functional diversity indices (MASON et al., 2005), that is, the patterns of how a given community fills a certain niche space can potentially provide valuable information in exploring these relationships (Section 1.9, Chapter 1).

Concerning the role of specific soil nutrients in driving vegetation properties, several studies have pointed out how the availability of soil nutrients can constrain vegetation performance and attributes. Nitrogen (N) and phosphorus (P) are essential nutrients without which plants cannot complete their life cycle. Both elements are involved in the key physiological process, with a marked influence on photosynthetic rates (DOMINGUES et al., 2010) and numerous other processes. For example, N is present in chlorophyll, nucleic acids (DNA and RNA), proteins and enzymes that regulate water and nutrient uptake, while P constitutes sugar phosphates, and nucleic acids, with a key role in energy absorption, storage, and conversion to adenosine triphosphate (ATP), a crucial biomolecule in biochemical reactions in plants (TAIZ; ZEIGER, 2014). Given that some of the Caatinga soils tend to show relatively low P contents (Chapter 1 and 2; SILVEIRA; ARAÚJO; SAMPAIO, 2006), phosphorus might be a concern in these soils, although field-based validation for this possibility in natural stands

is rare. On the other hand, N-availability in SDTFs is considered even higher than in humid places (ARANIBAR et al., 2004; SWAP et al., 2004; DA SILVA et al., 2017), which is also evidenced by high nitrogen concentrations and high $\delta^{15}\text{N}$ values commonly found in the leaves of Caatinga species (MARTINELLI et al., 2021).

Soil cations are also likely to play an important role in water-stressed environments. Potassium (K) is an osmotically active ion involved in several physiological processes and has already been shown to be an important modulator of the structure of tropical woody vegetation (LLOYD et al., 2015). Calcium (Ca), in turn, is involved in wood construction and the onset of cambial activity after periods of reduced physiological activity (FROMM, 2010). Furthermore, Ca is involved in the regulation of complex physiological responses to various abiotic stresses (SHARMA; KUMAR, 2021). Magnesium (Mg) is involved in essential plant processes such as photosynthesis and enzyme activation, so its deficiency can trigger barriers to plant survival (CHEN et al., 2018). Although sodium (Na) might be beneficial for some plants, its consumption should be less important than the previously mentioned cations. However, Na has been reported to potentially replace some K functions in plants (WAKEEL et al., 2011). High concentrations of Na salts are believed to be an issue in many semiarid areas, but only specific environments in the Caatinga are reported to exhibit high Na concentrations (i.e. some low valleys), largely due to the modern exorheic drainage pattern of the region (AB'SÁBER, 1974). Aluminium (Al) can impair root development when present in toxic concentrations (BOJÓRQUEZ-QUINTAL et al., 2017). In Caatinga, Al toxicity is more likely to potentially occur in some regions (e.g. in acid Alisols and Acrisols of the Parnaíba Basin) rather than in others with neutral to alkaline soils, where Al activity should be negligible. Essential micronutrients (B, Fe, Zn, Mn, Mo, Cu, and Cl) have been hypothesised to explain some variations in vegetation attributes, but little is known about this possible influence on Caatinga vegetation (SAMPAIO, 2010). Except for molybdenum, low availability of micronutrients is likely to occur at high soil pH (> 7), which can be the case for more alkaline soils in Caatinga.

In addition to the role of soils in achieving plant nutritional needs, soil properties play a decisive role in water availability. Soil texture, largely determined by original parental materials, is likely to be the most important soil property (PALM et al., 2007) influencing soil fertility, water holding capability, and the movement of water and gases (UPADHYAY; RAGHUBANSHI, 2020). Soil mineralogy and soil organic matter (SOM) are the two additional properties that contribute to soil water holding capacity (PALM et al., 2007).

Landscape physiography may also influence water retention in a given environment as topography influences the runoff process, also redistributing solutes in the landscape (MARKESTEIJN et al., 2010). Soil depth is also important, ultimately controlling the size of the potential plant-available water reservoir, and shallow soils are believed to be beneficial under certain circumstances. For example, Lloyd et al. (2015) demonstrated through numerical simulations that soil water availability is improved by the reduction in water losses due to drainage constraints (any impermeable layer). In contrast to deep well-drained soils typical of other Brazilian regions (e.g. *Cerrado* and *Amazônia*), impermeable layers are often found in the Caatinga region, particularly in soils of the Crystalline Domain, with the soil depth commonly reaching 0.5 - 1.0 m. In such conditions, barriers to water drainage can be beneficial in provisioning water to the vegetation, but such water is rapidly depleted in a few weeks if new rains do not occur (SAMPAIO, 2010).

Potentially complicating the analyses here is the fact that environmental predictors (and response variables) sampled over large geographical extensions have a high probability to show spatially autocorrelated data. QUESADA et al. (2012) provide a detailed overview of this matter and discuss alternative approaches to deal with spatially structured data. Briefly, spatial structures may be attributable to predictors, dependent variables only, and model residuals only, with these approaches, differently relating to underlying processes accounting for variation in a given response variable.

The current study reports on the climate, soil and vegetation properties of 29 SDTFs stands in the semiarid Caatinga that covers a rainfall gradient and different geological affiliations (i.e. metamorphic – S_{MET} , sedimentary – S_{SED} and karst – S_{KAR}), consequently exhibiting disparate edaphic properties. The following questions were addressed:

- 1) Do soil chemical and physical properties, climate, and their interactions influence the observed variability in stand-level above-ground woody biomass (AGB_W)?
- 2) Is the effect of climatic and edaphic factors the same for stands of different geological affiliations?
- 3) Does soil chemical characteristics and soil texture influence community-weighted mean traits, namely maximum stem diameter of adults (CWM_{dmax}) and wood density (CWM_{wd}) and their associated functional diversity metrics, namely function richness (F_{Ric}), functional evenness (F_{Eve}) and functional divergence (F_{Div})
- 4) Do functional properties account for variations in AGB_W ?

3.2 Material and Methods

3.2.1 Study sites

Data used here come from 29 sites distributed along the Brazilian Caatinga (Figure 1.2, Chapter 1), encompassing a wide range of edaphic conditions, from only slightly weathered soils mostly developed from metamorphic rocks (S_{MET}) to much more weathered soils from sedimentary parent materials (S_{SED}). Sampling included three vegetation stands in karst areas (S_{KAR}). Respective reference soil groups (RSGs) for each site can be accessed in Table 2.1, Chapter 2. Mean annual precipitation (P_A) ranged from 0.512 m a⁻¹ at CND-01 (Bahia) to 1.363 m a⁻¹ in PSC-02 (Piauí), whereas the mean annual temperature (T_A) ranged from 20.5 °C in MOR-01 (Bahia) to 26.8 °C at PFF-01 (Rio Grande do Norte). Above-sea level elevation of the sites varied from 99 m in PFF-01 to 944 m in MOR-01 (Table 2.1, Chapter 2). Vegetation structure varied from open canopies of only 4 – 7 m in height up to 25 – 30 m closed canopies. Study sites consisted of well-conserved old-growth stands. Sporadic grazing and occasional timber logging, however, could not be disregarded for some sites. The slope at the studied sites was typically flat, with a few exceptions (Table 2.1, Chapter 2). Vegetation inventory and soil sampling were undertaken in three intensive fieldwork campaigns (2017, 2018, and 2019), each for *ca.* two, three, and one month, respectively. Vegetation sampling was undertaken during the late wet season to reflect the maximum vegetative development.

3.2.2 Stand structure

Standardised floristic and structural inventories were carried out following the “The DryFlor Field Manual for Plot Establishment and Remeasurement” (MOONLIGHT et al., 2021). Briefly, a 100 x 50 m (0.5 ha) plot was established and sub-partitioned into 50 subplots (10 x 10 m or 0.01 ha) at each site. All trees having stems with a diameter either at breast height (DBH – 1.30 m from the ground level) or at 0.3 m from the ground level (DGL) \geq 5 cm were measured in all subplots. Trees were identified in the field at the species level and voucher specimens were incorporated into the Herbarium of Feira de Santana State University (HUEFS; Feira de Santana, Bahia, Brazil) collection.

3.2.3 Soil sampling and laboratory analyses

Comprehensively described in Sections 2.2.2 and 2.2.3, Chapter 2.

3.2.4 Maximum plant-available soil water (θ_p)

Comprehensively described in Section 2.2.6, Chapter 2.

3.2.5 Climatological data

Comprehensively described in Section 2.2.7, Chapter 2.

3.2.6 Geological surveying

Comprehensively described in Section 2.2.5, Chapter 2.

3.2.7 Above-ground woody biomass calculations

Estimates of individual tree above-ground woody biomass (AGB_W) were obtained using an allometric equation as provided in SAMPAIO and SILVA (2005). The Eqn. (3.1) considers only the diameter at the ground level (DGL) as the input variable according to:

$$AGB_W = 0.0644 \times DGL^{2.3948}, \quad \text{Eqn. (3.1)}$$

where AGB_W stands for the oven-dry above-ground tree biomass (kg), and DGL is the diameter at the ground level (cm).

A second equation provided in SAMPAIO and SILVA (2005) was used for estimating the biomass of cactus individuals. Such an equation was developed from individuals of *Cereus jamacaru* DC.:

$$AGB_C = 0.0268 \times DGL^{2.3440} \quad \text{Eqn. (3.2)}$$

Finally, palm tree biomass (only 35 individuals in the dataset) was estimated using equation 3.4 from SALDARRIAGA et al. (1988), viz.

$$\ln AGB_P = -6.3789 - 0.877 \ln X1 + 2.151 \ln X2, \quad \text{Eqn. (3.3)}$$

where AGB_P stands for the oven-dry above-ground palm tree biomass (kg), $X1$ stands for $1/DBH^2$ (diameter at breast height taken at 1.30 m from the ground), and $X2$ represents the palm tree height (H).

Further information on the chosen equations and a comparison with the dry forest global allometric equation (CHAVE et al., 2014) is provided in Supplementary Section S3.1 and Figure S3.1.

3.2.8 Community-weighted trait means (CWM) and functional diversity

Two community-weighted trait means were calculated: community-weighted maximum stem diameter (CWM_{dmax}) and community-weighted mean wood density (CWM_{wd}). Both are considered a “whole plant trait”. Species’ wood density values were extracted from the global wood density database (CHAVE et al., 2009, ZANNE ET AL. 2009). When unavailable at the species level, wood density values of genus or family were used. Botanical names were checked and adjusted according to the Brazilian Flora 2021 with the flora package version 0.3.5 (CARVALHO, 2020). The species’ maximum stem diameter reflects adult sizes and was calculated as the upper 0.95 percentile of those trees with a stem diameter $\geq 0.1 \times$ the diameter (cm) of the thickest tree observed in a given population. This approach was chosen because, within alternative approaches, it was shown to be the least sensitive to sample sizes as well as providing robust estimates for both large and smaller species (KING; DAVIES; NOOR, 2006). Each trait was weighted according to the individual species’ basal area, which is believed to better indicate plant performance than abundance (PRADO-JÚNIOR et al., 2016). Functional diversity indices, i.e. functional richness (F_{Ric}), functional divergence (F_{Div}) and functional evenness (F_{Eve}) were calculated using the *FD* package (LALIBERTÉ; LEGENDRE; SHIPLEY, 2022).

3.2.9 Data analysis

During the exploratory phase of the data, a correlation matrix reporting Kendall’s rank correlation coefficients (τ) and associated probabilities was built. In addition, OLS) linear regressions and graphical inspections were used to first assess the predictive ability of individual soil and climate predictors on AGB_w . Then, a linear mixed-effect model (LMM), along with a multi-model inference approach were used to investigate to which extent soil and climate associations account for AGB_w across the studied sites. Within each 0.5 ha plot (29 in total), two subplots of 0.25 ha were considered ($n=58$). The analytical design was thus subplots (0.25 ha) nested within plots (0.5 ha). This procedure was adopted to allow the inclusion of a higher number of variables into the same models with low risks of overfitting issues (Section 1.4.1 of Burnham and Anderson, 2002).

As many AGB_w candidate predictors were strongly correlated, pairwise variables with Pearson correlation ($r \geq |0.70|$) were never simultaneously included as candidate variables. Mean annual precipitation (P_A) and climatic water deficit CWD_{adj} were included to represent the overall water input and climatic water balance in studied ecosystems. The maximum

temperature of the warmest month (T_{MAX}) was included as the key thermal variable. T_{MAX} reflects high-temperature events throughout the year and can be used to examine if the function of a given community is affected by high-temperature anomalies (O'DONNELL; IGNIZIO, 2012).

Soil predictors were selected using similar criteria. Given that some soil properties were, as expected, correlated to each other [i.e. exchangeable cations, sum of bases (\sum_B), effective cation exchange capacity (I_E), and soil pH_{H_2O}], individual performances of these collinear predictors were assessed by replacing them one by one across the 'global model' of Eqn. (3.4) presented below. Thus, relative importance values (RIV), variance inflation values (VIF), global model marginal r^2 (r^2_m), global model AICc values, and graphical analysis of modelled responses were undertaken to compare the model performance of each alternative model. The *importance* function of the *MuMin* package (BARTON et al., 2020) represents the sum of the Akaike weights of all models that include a given variable in a given $\Delta AICc$ range. Relative importance values decreased following $I_E > [Ca]_{ex} > \sum_B > pH_{H_2O} > [Mg]_{ex} > [Na]_{ex} > [K]_{ex} > [Al]_{ex}$ (0.96, 0.95, 0.87, 0.64, 0.46, 0.39, 0.31 and 0.15 respectively). Despite I_E showing a slightly higher RIV than $[Ca]_{ex}$ (0.96 *versus* 0.95, respectively), the remaining evaluated criteria suggested that $[Ca]_{ex}$ is a better predictor. For instance, I_E had a higher VIF than $[Ca]_{ex}$ (3.51 and 3.25, respectively). Moreover, the global model of Eqn (3.4) including $[Ca]_{ex}$ as the "cation term" showed $r^2_m = 0.49$ and $AICc = 92.95$, *versus* $r^2_m = 0.46$ and $AICc = 94.67$ for I_E . Also of note is that $[Ca]_{ex}$ had a higher effect size in both full and conditional average models. That is, $[Ca]_{ex}$ showed $\beta_I = 0.38$ and $\beta_I = 0.39$ for the full and conditional average models, respectively, whereas I_E showed $\beta_I = 0.35$ and $\beta_I = 0.37$ for the full and conditional average models, respectively. Based on these metrics and $[Ca]_{ex}$ being the dominant cation in the soil sorptive complex of most study sites (Table 2.2 and Figure 2.3), subsequent analyses were performed by adopting the inclusion of $[Ca]_{ex}$. The alternative inclusion of I_E would lead to relatively similar results quantitatively speaking, but with small differences in interpretation due to the properties of the predictors.

Given the important role of these nutrients in plant functioning, soil total phosphorus $[P]_T$ and soil total nitrogen $[N]_T$ were also included as potential AGB_W predictors. Concerning soil physical properties, maximum plant-available soil water (θ_P) was calculated considering the full profile, i.e. the water until the maximum soil profile depth (any hardened layers usually impervious to water drainage or a maximum of two meters deep). Plant-available soil water considering only the layer whereby roots were observed ($^*\theta_P$) and potential interactions along

with soil depth and the presence (or absence) of a shallow impermeable layer (I_{LAYER}) were also tested.

Soil and climate values were considered at the plot level considering that subplots largely share similar climate and soil properties, especially considering the marked differences existing among sites. Variance inflation factor values (VIF) were also verified among the selected predictors, whereby none of them exceeded $VIF \geq 3$ (the exception was $[Ca]_{ex}$; $VIF = 3.25$). Much higher VIF values (i.e. ≥ 10) are usually considered a critical threshold (DORMANN et al., 2013).

To facilitate the interpretation of model coefficients, predictors were standardised (i.e. the mean of each predictor was subtracted from each observed value and then divided by the standard deviation), providing comparative scores, ‘effect size’, among predictors) using the *caret* package (MAX et al., 2020). Because the analysis strategy tacitly implied non-independent observations, sites were included as random structures in the model (HARRISON et al., 2018), accounting for the nestedness present in the analytical approach here undertaken (observations were correlated within sites).

Equation 3.4 expresses the global model built for the subsequent analysis:

$$\log(AGB_w) = \beta_0 + \beta_1\theta_P + \beta_2P_A + \beta_3[Ca]_{ex} + \beta_4CWD_{adj} + \beta_5\theta_P \times CWD_{adj} + \beta_6[Ca]_{ex} \times CWD_{adj} + \beta_7T_{MAX} + \beta_8\log[N]_t + \beta_9\log[P]_t + (1|site) + \varepsilon \quad \text{Eqn. (3.4)}$$

where β_0 represents the model intercept, $\beta_{1...(n)}$ represents coefficients associated with model terms and ε is the residual error.

Once fitted, the distribution of the model residual distribution was both statistically and graphically evaluated. The response variable was log-transformed to attain the assumption of normality and reduce the heterogeneity in the variance. Spatial correlograms with distance class increments as available in the *ncf* package (BJORNSTAD; CAI, 2020) were used to check for any spatial structuring of the models’ residues. Additionally, the potential presence of spatial structures was also evaluated through the recently developed approaches as described in Bauman et al. (2018a) and Bauman et al. (2018b). The *listw.candidates* function of the *adespatial* package (DRAY et al., 2021) was undertaken to test a small number of distance and graph-based spatial weighting matrices (SWM), resulting in no significant spatial dependencies in the model’s residues.

All possible combinations of predictors (including interaction terms) were tested with the aid of the *MuMin* package (BARTON, 2020). As an additional control of potential

(multi)collinearity issues, predictors with Pearson's correlation coefficient ($|r| \geq 0.6$) were prevented to be simultaneously included in the same models. This process generated 137 unique models, with the maximum number of predictors in each model being constrained to 6, thus ensuring approximately 10 observations *per* model term.

Subsequently, an information-theoretic (I-T) approach was used to deal with model uncertainty by selecting those models with $\Delta\text{AICc} < 4$ (BURNHAM; ANDERSON; HUYVAERT, 2011; HARRISON et al., 2018). Analyses were also run using $\Delta\text{AICc} < 2$ as a cutoff value with very similar results with no consequences for the interpretation of the results. From the 19 models retained ($\Delta\text{AICc} < 4$), coefficients were averaged through the *model.avg* function available in the *MuMin* package (BARTON, 2020). Model averaging was achieved through the function *model.avg* available in the *MuMin* R package (BARTON, 2020). The results of both full and conditional ('subset') average models are presented. The 'full' averaging approach dictates that each variable is included in every model (setting the coefficients to zero in the models where the term is absent), whereas the 'conditional' average approach considers only those models where the parameter appears (BARTON, 2020). In both cases, averaged coefficients were weighted according to Akaike weights. The full average is a type of shrinkage estimator, and coefficients of variables with weak support tend towards zero. The global model's marginal (r^2_m) and conditional (r^2_c) determination coefficients are also reported. The former reports only on fixed effects, while the latter refers to both fixed and random effects. The r^2 reported here consists of a revised statistic based on (NAKAGAWA; SCHIELZETH, 2013).

The *importance* function (also available in *MuMin*) was also used to calculate the relative importance value (RIV) of each model term. Model predictions were performed using the coefficients from the full average model. Importantly, the conditional average model coefficients are usually considered inappropriate for model predictions, whereas the full model coefficients (with shrinkage) are recommended in such instances (MAZEROLLE, 2020). Indeed, associated R packages do not even provide a function to make predictions with conditional model coefficients. Consequently, less supported averaged coefficients have little influence on modelled responses.

In addition, potential differences in AGB_W according to the geological grouping undertaken in this study (i.e. S_{SED} , S_{MET} and S_{KAR}) were evaluated through a non-parametric

robust Kruskal-Wallis test (χ^2). Subsequently, a series of LMM linear regressions were used to assess the predictive ability of individual soil and climate predictors on AGB_w within each category, with relationships, also shown for the entire dataset level.

Both evaluated CWM traits and functional diversity indices were also compared among geological categories using the Kruskal-Wallis test (χ^2), followed by the Wilcoxon-Mann-Whitney rank-sum test with Benjamin and Hochberg (BH) correction for multiple comparisons. In addition, bivariate linear relationships between CWM traits and functional diversity indices were tested through ordinary least squares (OLS) linear regression models. Finally, a Spearman's rank correlation coefficient (ρ) matrix was built to evaluate potential associations between soil chemical and physical properties and community functional properties. For the graphical representation of results, the *alphahull* package (PATEIRO-LÓPES; RODRÍGUEZ-CASAL, 2022) was used to constrain the heat maps simulations to the actual environmental envelope found in the dataset. Finally, all graphs were constructed using the *ggplot2* package (WICKHAM et al., 2021), and all analyses were carried out in the environment R version 4.1.1 (R CORE TEAM, 2021).

3.3 Results

In this work, the inclusion (or not) of spatial filters (here Moran Eigenvectors Maps; MEMs) in those models with spatially structured residuals was adopted. This is thought to reflect the influence of environmental predictors on a given response once the potential effects of other sources of variation have been filtered (e.g. endogenous processes attributable to species) (QUESADA et al., 2012). Interestingly, the studied response variable (AGB_w) did not show spatial structures, likely reflecting the patchy nature of AGB_w in Caatinga (CASTANHO et al., 2020a; CASTANHO et al., 2020b). On the other hand, some edaphic variables (mainly associated with cations) have shown moderate values of Global Moran's I (coefficient of spatial autocorrelation) (0.40 to 0.50; $p < 0.05$), likely reflecting patches of soils conditioned by geological substrates. Global Moran's I values for climatic variables were relatively higher (i.e. > 0.60 ; $p < 0.05$), which is expected to some extent for the interpolated climatic values undertaken in this study as for the geographic well as climatic patterns.

3.3.1 Above-ground woody biomass

In total, 18,201 stems ($DGL \geq 5$ cm) were recorded, of which 1,098 were *cacti* with 35 palm trees also found across 29 plots of 0.5 ha. The mean AGB_w was 32.55 ± 22.35 $Mg\ ha^{-1}$ (minimum = 4.87 $Mg\ ha^{-1}$ at CJU-01 and maximum = 85.65 $Mg\ ha^{-1}$ at JUV-01). Mean stem density (counts ha^{-1}) was 1255 ± 489 (minimum of 492 at CJU-01 and maximum = 2534 at SDA-02); mean basal area (B_A) was 12.9 ± 7.1 $m^2\ ha^{-1}$ (minimum of 2.44 $m^2\ ha^{-1}$ at CJU-01 and maximum of 28.79 at JUV-01). Above-ground woody biomass values did not differ among geological categories at $p < 0.05$ (Figure 3.1).

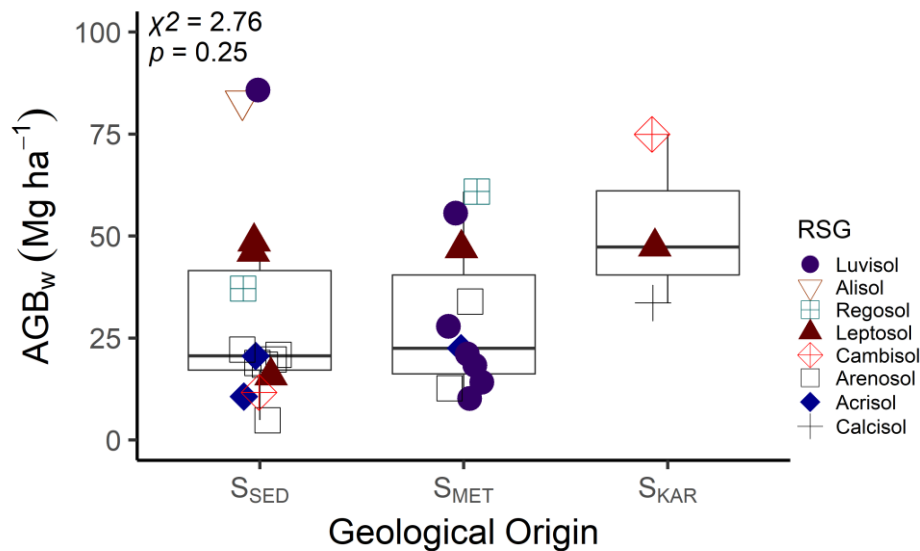


Figure 3.1: Above-ground woody biomass (AGB_w) values according to soil geological affiliation. Reference soil groups (RSGs) are shown.

Figures 3.2-a and 3.2-b show averaged coefficients, standard errors and confidence intervals resulting from conditional and full average models, respectively. The conditional model (Figure 3.2-a) furnishes the β coefficients averaged only from within those models where the variable appeared, i.e. P_A ($\beta = 0.28$); $[Ca]_{ex}$ ($\beta = 0.40$); $\Theta_P \times CWD_{adj}$ ($\beta = -0.25$); $[Ca]_{ex} \times CWD_{adj}$ ($\beta = -0.43$) and $[P]_t$ ($\beta = 0.23$). The β coefficients from the full averaged model (Figure 3.2-b) were shrunk towards zero for model terms with low frequency across the selected models.

Nevertheless, P_A ($\beta = 0.25$); $[Ca]_{ex}$ ($\beta = 0.38$) and $[Ca]_{ex} \times CWD_{adj}$ interaction ($\beta = -0.17$) remained as the most supported terms as they had relatively high β coefficients even in the full average model.

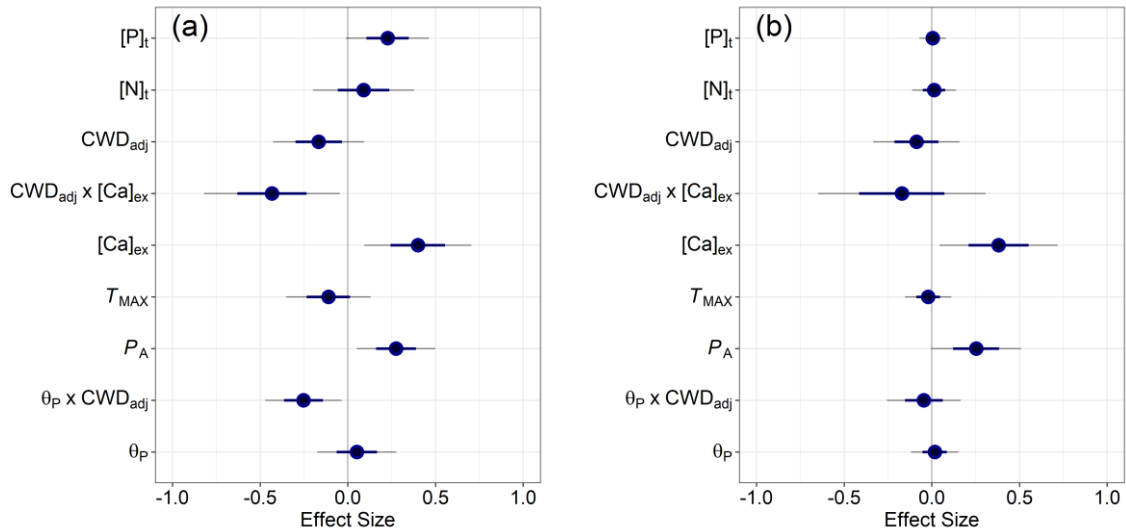


Figure 3.2: Edaphic and climatic AGB_w correlates in SDTFs of Caatinga. Points represent coefficients of averaged linear mixed effects models. a) Conditional average model coefficients; b) Full average model coefficients. In the full average model, poorly supported coefficients tend to be shrunken towards zero. Coefficients were standardised, thus representing changes in $\log(AGB_w)$ for one standard deviation change in the predictor variable (effect size). Error bars show standard error (dark blue) and 95% confidence interval (thin gray). Further information on “conditional” and “full” average models is provided in Section 3.2.9 of this thesis.

Figure 3.3 shows RIV for all terms included in the global model [Eqn. (3.5) above]. The retention of a variable across the models and associated RIV depends on the other variables included as ‘candidate predictors’, which may help explain some variables with relatively high RIV and low effect size (e.g. CWD_{adj}). It is of note that $[Ca]_{ex}$ and P_A , which showed the highest standardised coefficients for both conditional and full averaged models, also had the highest RIV (0.95 and 0.92, respectively). The RIV values below ≤ 0.9 were, in descending order, $CWD_{adj} = 0.53$, $[Ca]_{ex} \times CWD_{adj} = 0.40$, $\theta_P = 0.33$, $T_{MAX} = 0.18$, $\theta_P \times CWD_{adj} = 0.18$. The lowest RIV values were attributed to $[N]_t = 0.15$ and $[P]_t = 0.02$, which also corresponded to small effect sizes.

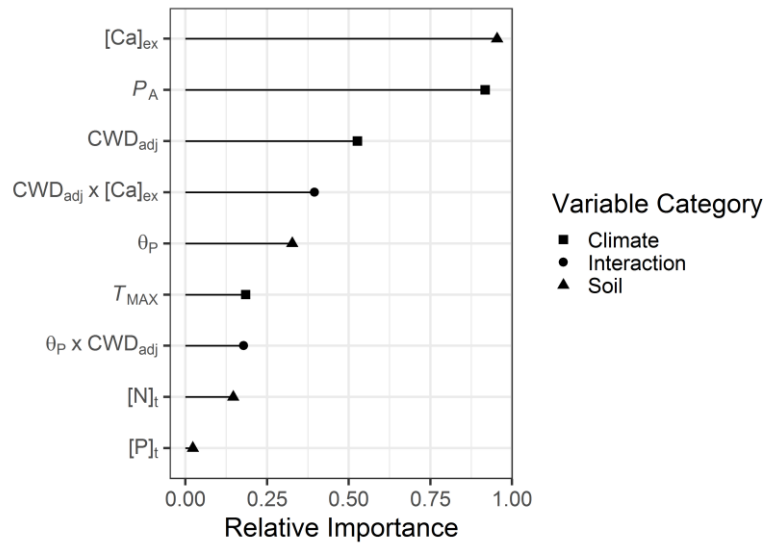


Figure 3.3: Relative importance values (RIV) of each variable included in the global model. Symbols represent variable categories.

As the interactive effects detected among variables were complex, Figures 3.4 and 3.5 illustrates the predicted responses of AGB_W through ‘heat maps’. The core idea behind this analysis is to show AGB_W predicted responses (\hat{AGB}_W) relate to environmental gradients by varying the interaction terms with all other model terms held constant (for instance, at their dataset average). Figure 3.4 shows \hat{AGB}_W as influenced by P_A held at: a) the dataset average - 1 standard deviation (SD); b) dataset average; c) dataset average + 1 SD; d) dataset average + 2 SD (0.6, 0.8, 1.01, 1.21 $m a^{-1}$, respectively). Simulations for all possible combinations within the maximum and minimum observed CWD_{adj} and θ_P environmental domain were performed. Actual AGB_W values are also shown in the specific panels associated with their respective P_A regimes.

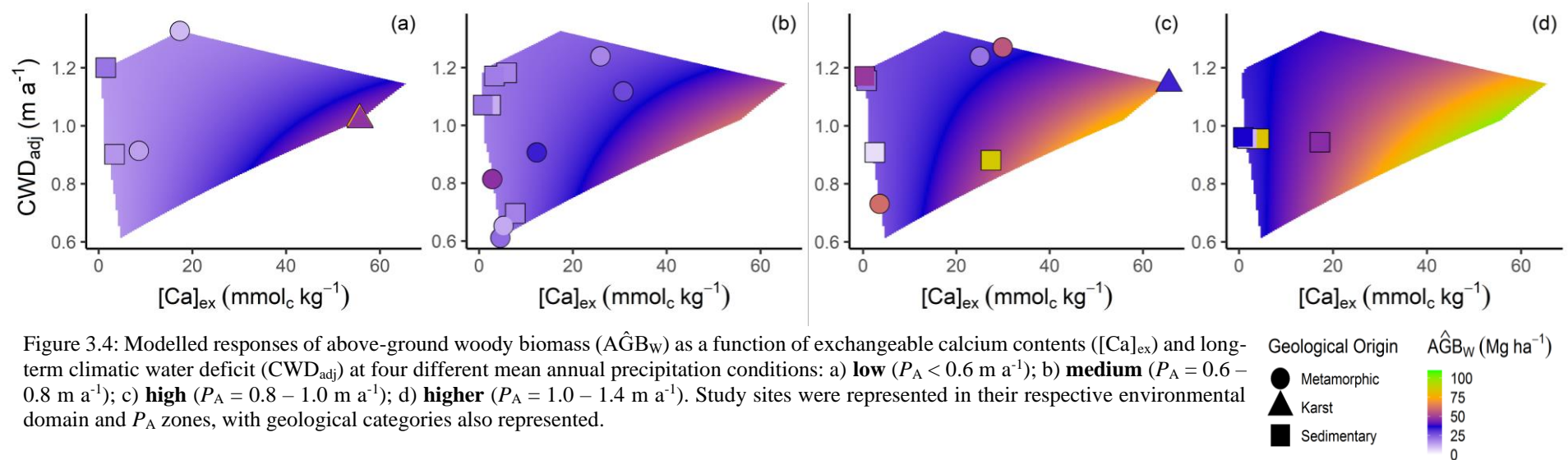
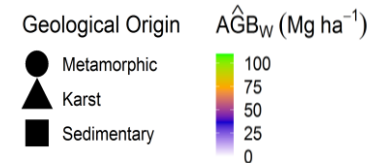
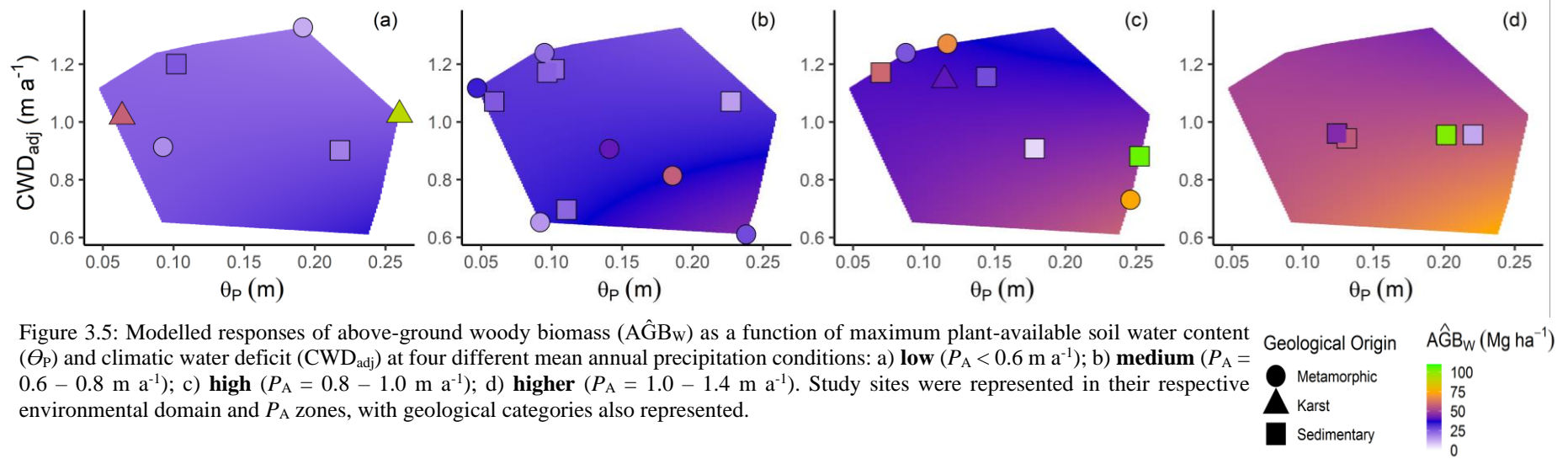


Figure 3.4: Modelled responses of above-ground woody biomass (\hat{AGB}_W) as a function of exchangeable calcium contents ($[Ca]_{ex}$) and long-term climatic water deficit (CWD_{adj}) at four different mean annual precipitation conditions: a) **low** ($P_A < 0.6 m a^{-1}$); b) **medium** ($P_A = 0.6 - 0.8 m a^{-1}$); c) **high** ($P_A = 0.8 - 1.0 m a^{-1}$); d) **higher** ($P_A = 1.0 - 1.4 m a^{-1}$). Study sites were represented in their respective environmental domain and P_A zones, with geological categories also represented.



The modelled responses presented in Figure 3.4 suggest that $[Ca]_{ex}$ levels strongly influence \hat{AGB}_W at any examined P_A zones. This effect, however, was also modulated by the intensity of the long-term climatic water deficit (CWD_{adj}). For example, when $[Ca]_{ex}$ is low (e.g. $5 \text{ mmol}_c \text{ kg}^{-1}$), \hat{AGB}_W was not inferred to vary markedly with changes in CWD_{adj} . However, at higher $[Ca]_{ex}$ (e.g. $40 \text{ mmol}_c \text{ kg}^{-1}$), the modelled influence of CWD_{adj} on \hat{AGB}_W increases. The magnitude of the effect was also sensitive (in an absolute sense) to the P_A regime. For example, at the lowest precipitation ($P_A = 0.6 \text{ m a}^{-1}$) and taking $[Ca]_{ex}$ as constant in $50.37 \text{ mmol}_c \text{ kg}^{-1}$, \hat{AGB}_W varies from 28.2 to 46.1 Mg ha^{-1} across the CWD_{adj} range (1.20 to 0.98 m a^{-1}). Nevertheless, for the highest precipitation zone ($P_A = 1.2 \text{ m a}^{-1}$), when $[Ca]_{ex}$ is $50.37 \text{ mmol}_c \text{ kg}^{-1}$, \hat{AGB}_W varies from 60.10 to 98.41 Mg ha^{-1} across the CWD_{adj} range (1.20 to 0.98 m a^{-1}). As the model has a log-linear nature, the exponentiated \hat{AGB}_W values (geometric means) differ in magnitude according to different levels of P_A , but the ratio of these variations was constant (64% for both cases). It is noteworthy that S_{SED} sites occur across almost the full range of CWD_{adj} , but with $[Ca]_{ex}$ levels, as expected (and except for JUV-01), at relatively low values ($\leq 10 \text{ mmol}_c \text{ kg}^{-1}$). On the other hand, S_{MET} sites showed large variability in CWD_{adj} , with $[Ca]_{ex}$ levels generally $\geq 10 \text{ mmol}_c \text{ kg}^{-1}$, whereas S_{KAR} sites always had invariably $[Ca]_{ex} \geq 50 \text{ mmol}_c \text{ kg}^{-1}$ and high CWD_{adj} values ($\geq 1.0 \text{ m a}^{-1}$). Moreover, only S_{SED} sites were encountered in the highest P_A zone (Figure 3.4-d).

Following the same approach, Figure 3.5 shows the interaction between maximum plant-available soil water (Θ_P) and annual climatic water deficit (CWD_{adj}) under four different P_A regimes. Models' predictions at all P_A zones show that \hat{AGB}_W levels increase with higher Θ_P and lower CWD_{adj} . Nonetheless, even sites with relatively high Θ_P tend to show low \hat{AGB}_W values when CWD_{adj} is high. For example, assuming two extremes P_A zones (Figure 3.5-a and 3.5-d), using $\Theta_P = 0.20 \text{ m}$ as a reference in the lower precipitation zone (Figure 3.5-a), when CWD_{adj} is at its minimum (0.62 m a^{-1}), the model predicts $\hat{AGB}_W = 27.80 \text{ Mg ha}^{-1}$. Conversely, when CWD_{adj} is at its maximum (1.29 m a^{-1}), the model predicts $\hat{AGB}_W = 16.60 \text{ Mg ha}^{-1}$. Using a similar approach for the wetter P_A zone (Figure 3.5-d), when $\Theta_P = 0.2 \text{ m}$, the model predicts $\hat{AGB}_W = 35.79 \text{ Mg ha}^{-1}$ when CWD_{adj} is in its maximum (1.29 m a^{-1}) and predicts $\hat{AGB}_W = 59.87 \text{ Mg ha}^{-1}$ when CWD_{adj} is in its minimum (0.62 m a^{-1}). Therefore, the modelled responses observed in Figure 3.5 suggest that the absolute magnitude of the interactive effect of $CWD_{adj} \times \Theta_P$ depends upon the prevailing P_A , with these differences proportionally occurring across all panels.



For this relationship, only S_{SED} sites were observed in the highest precipitation zone (Figure 3.5-d), which covers only intermediate levels of CWD_{adj} ($0.8 - 1.0 \text{ m a}^{-1}$).

Finally, predictions of \hat{AGB}_W levels as influenced by P_A were evaluated for four different $[Ca]_{ex}$ and θ_P combinations (Figure 3.6). Across the full P_A gradient, the following environmental conditions were simulated: a) both $[Ca]_{ex}$ and $\theta_P + 2 \text{ SD}$ above their dataset mean ($50.67 \text{ mmol}_c \text{ kg}^{-1}$ and $0.27 \text{ m}^3 \text{ m}^2$, respectively); b) $[Ca]_{ex}$ and $\theta_P + 1 \text{ SD}$ above their dataset mean ($32.65 \text{ mmol}_c \text{ kg}^{-1}$ and $0.21 \text{ m}^3 \text{ m}^2$, respectively); c) $[Ca]_{ex}$ and θ_P at their dataset mean ($14.62 \text{ mmol}_c \text{ kg}^{-1}$ and $0.15 \text{ m}^3 \text{ m}^2$, respectively); and d) $\theta_P - 1 \text{ SD}$ below the dataset mean ($0.08 \text{ m}^3 \text{ m}^2$) with $[Ca]_{ex}$ set to $1 \text{ mmol}_c \text{ kg}^{-1}$ (as a standard deviation subtraction for $[Ca]_{ex}$ would generate negative values). This is shown in Figure 3.6, which shows that, although \hat{AGB}_W increases with P_A levels, this relationship tends to become sharper as the soil conditions become more favourable [i.e. better nutritional levels (calcium) and greater maximum plant-available soil water content]. According to the model predictions, different Caatinga stands may show ca. threefold variation in \hat{AGB}_W depending upon the prevailing θ_P and $[Ca]_{ex}$, with the same relative differences at all evaluated P_A zones.

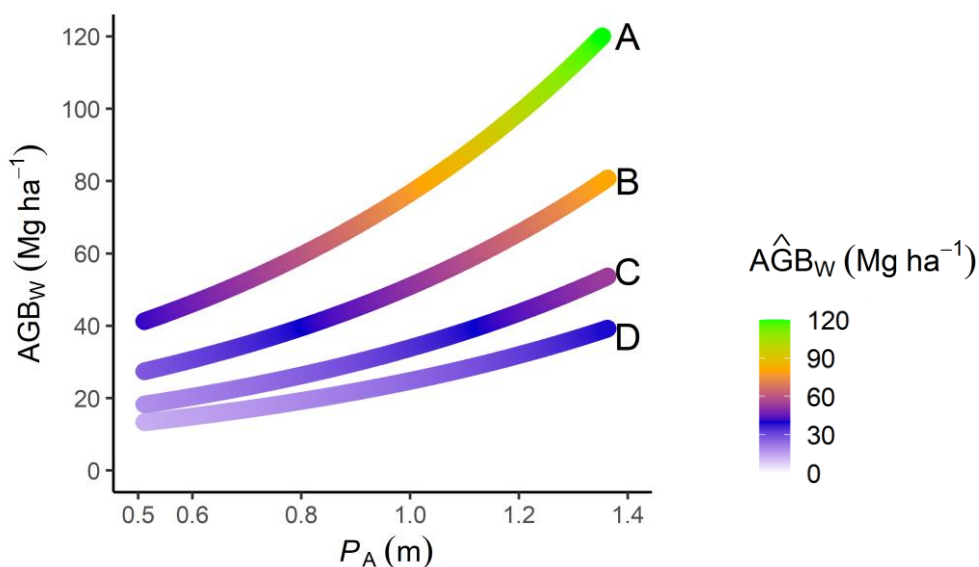


Figure 3.6: Modelled responses of above-ground woody biomass (\hat{AGB}_W) as a function of P_A at four different environmental conditions: **A) higher** maximum plant-available soil water content (θ_P) and higher exchangeable calcium ($[Ca]_{ex}$); i.e. both variables with $+ 2 \text{ SD}$ in relation to their average; **B) high** maximum plant-available soil water content (θ_P) and high exchangeable calcium ($[Ca]_{ex}$); i.e. both variables with $+ 1 \text{ SD}$ in relation to the average; **C) medium** maximum plant-available soil water content (θ_P) and medium exchangeable calcium ($[Ca]_{ex}$); both at their means; **D) low** maximum plant-available soil water content (θ_P) and low exchangeable calcium ($[Ca]_{ex}$); i.e. both variables with $- 1 \text{ SD}$ in relation to their average.

3.3.2 Assessing alternative models

To evaluate the ecological significance of climatic and edaphic drivers over AGB_w , an alternative set of models was tested. Initially, a model taking into account only the climatic terms expressed by Eqn. (3.5) was built:

$$\log(AGB_w) = \beta_0 + \beta_1 P_A + \beta_2 CWD_{adj} + \beta_3 T_{MAX} + (1|site) + \varepsilon \quad \text{Eqn. (3.5)}$$

As shown in Figure 3.7-a, a purely climatic model had negligible predictive power considering all data together, with $r^2_m = 0.07$ and $AICc = 94.52$.

Following the same approach, a model considering only soil chemical terms was tested,

$$\log(AGB_w) = \beta_0 + \beta_1 [Ca]_{ex} + \beta_2 \log[N]_t + \beta_3 \log[P]_t + (1|site) + \varepsilon \quad \text{Eqn. (3.6)}$$

Despite showing a better performance relative to the “only climate model” of Eqn. (3.5), the model fit was relatively poor ($r^2_m = 0.16$; $AICc = 91.26$; Figure 3.7-b).

Subsequently, the complexity of the model was increased by adding all climatic and edaphic terms (both chemical and physical; the latter represented by the plant-available soil water; θ_P) without any interactive terms, as expressed by Eqn. (3.7):

$$\log(AGB_w) = \beta_0 + \beta_1 P_A + \beta_2 [Ca]_{ex} + \beta_3 CWD_{adj} + \beta_4 T_{MAX} + \beta_5 \log[N]_t + \beta_6 \log[P]_t + \beta_7 \theta_P + (1|site) + \varepsilon \quad \text{Eqn. (3.7)}$$

The model fit of Eqn. (3.7) had a better performance than the previous models, however, yielding higher $AICc$ values ($r^2_m = 0.30$; $AICc = 96.6$). In addition, all possible models among variables in Eqn. (3.7) were tested using the *dredge* function of the *MuMin* package). Subsequently, those models with $\Delta AICc < 4$ were selected. From that analysis, it was found that $AICc$ ranged from 85.0 to 88.98, and r^2_m ranged from 0.26 to 0.29. In simple terms, any model from the selected set can perform better than running the model as in Eqn. (3.7).

As there is no available straightforward method for calculating the r^2_m of averaged models, the r^2_m reported in Figure 3.7-c refers to the r^2_m of the $AICc$ best-ranked model in the set.

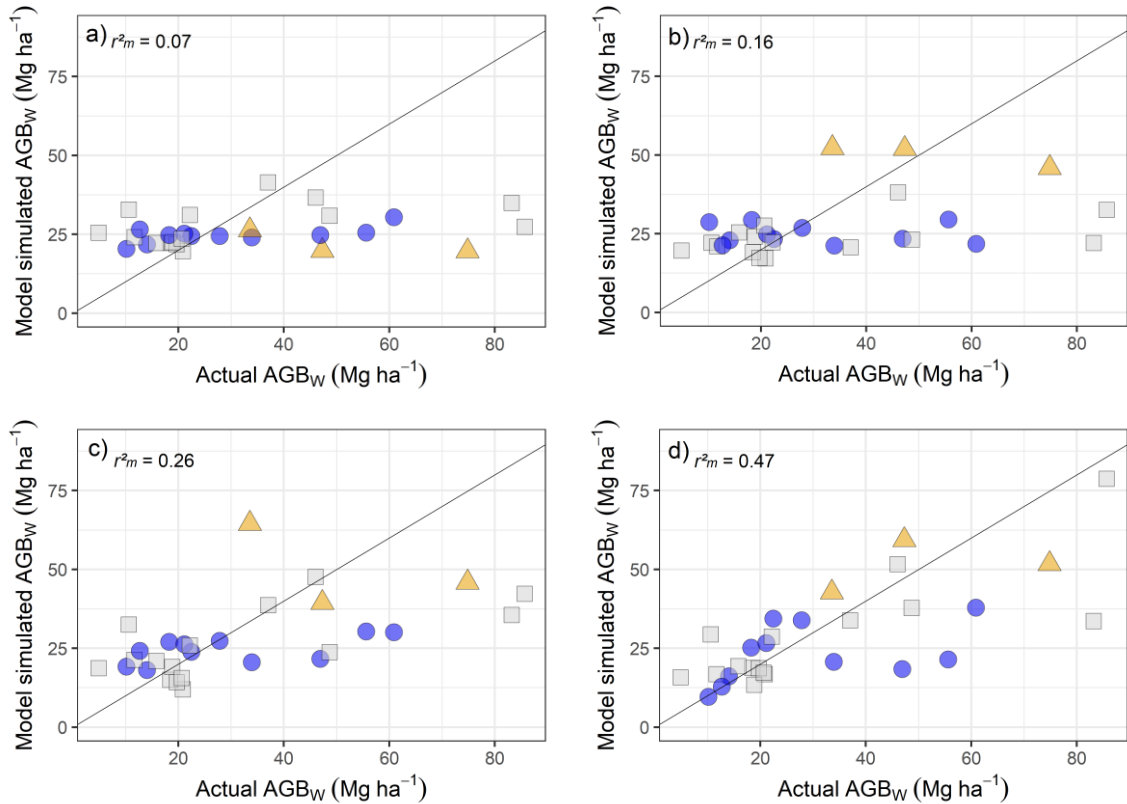


Figure 3.7: Differences of predictive ability among models with increasing complexity in accounting for AGB_w of Caatinga stands. **a)** “Only climate model”: $\log(AGB_w) = \beta_0 + \beta_1 P_A + \beta_2 CWD_{adj} + \beta_3 T_{MAX} + (1|site) + \varepsilon$; **b)** “Only soil model”: $\log(AGB_w) = \beta_0 + \beta_1 [Ca]_{ex} + \beta_2 \log[N]_T + \beta_3 \log[P]_T + (1|site) + \varepsilon$; **c)** “No interactions model”: $\log(AGB_w) = \beta_0 + \beta_1 P_A + \beta_2 [Ca]_{ex} + \beta_3 CWD_{adj} + \beta_4 T_{MAX} + \beta_5 \log[N]_T + \beta_6 \log[P]_T + \beta_7 \theta_P + (1|site) + \varepsilon$; **d)** “Full model”: $\log(AGB_w) = \beta_0 + \beta_1 \theta_P + \beta_2 P_A + \beta_3 [Ca]_{ex} + \beta_4 CWD_{adj} + \beta_5 \theta_P \times CWD_{adj} + \beta_6 [Ca]_{ex} \times CWD_{adj} + \beta_7 T_{MAX} + \beta_8 \log[N]_T + \beta_9 \log[P]_T + (1|site) + \varepsilon$. Marginal r^2 (r^2_m) values are provided. The respective geological affiliations of the study sites are shown.

Geological Origin

- Sedimentary
- Metamorphic
- ▲ Karst

Finally, the most complex tested model of Eqn (3.4), which includes potential interactive effects, yielded an $r^2_m = 0.49$ and $AICc = 86.0$. Then, when running all possible combinations among the terms in the model of Eqn. (3.4) and selecting those models with $\Delta AICc < 4$, $AICc$ values ranged from 84.9 to 88.8 and r^2_m ranged from 0.10 to 0.49, with the r^2_m value reported in Figure 3.7-d relative to the model with the lowest $AICc$ in the set evaluated. Conditional r^2 (r^2_c , including random effects) was 0.88 for the lowest $AICc$ model in the set.

3.3.3 Assessing AGB_w in geologically distinct stands

Table 3.1 shows the relationship between AGB_w and each individual selected soil and climate predictors (*log-linear* relationships). Considering the three geological classes together ($S_{\text{SED}} + S_{\text{MET}} + S_{\text{KAR}}$), several soil predictors showed significant effects, with coefficients (β) representing changes in $\log(\text{AGB}_w)$ for standard deviation change in the predictors, i.e. $[\text{Ca}]_{\text{ex}}$ ($\beta_I = 0.256$; $r^2 = 0.13$; $p = 0.04$), \sum_B ($\beta_I = 0.258$; $r^2 = 0.13$; $p = 0.04$), I_E ($\beta_I = 0.297$; $r^2 = 0.17$; $p = 0.02$) and f_{sand} ($\beta_I = -0.278$; $r^2 = 0.15$; $p = 0.03$), with no effects of any of the climatic or soil water storage variables detected ($p > 0.1$). No individual predictor at $p < 0.05$ could be considered superior to any other since the observed ΔAICc range was small for the significant relationships (≤ 2 for any comparison). Considering sites on the three geological classes separately, only effects related to soil were observed for the S_{SED} , i.e. $[\text{Ca}]_{\text{ex}}$ ($\beta_I = 0.385$; $r^2 = 0.25$; $p = 0.04$), $[\text{Mg}]_{\text{ex}}$ ($\beta_I = 0.367$; $r^2 = 0.23$; $p = 0.05$), \sum_B ($\beta_I = 0.408$; $r^2 = 0.23$; $p = 0.03$), I_E ($\beta_I = 0.434$; $r^2 = 0.28$; $p = 0.02$), with the ΔAICc range not exceeding two units. Concerning the S_{MET} , only mean annual precipitation (P_A) emerged as a significant predictor ($\beta_I = 0.432$, $r^2 = 0.50$; $p = 0.005$). Moreover, the AICc value for P_A was 25.9, which means that the ‘only P_A model’ at S_{MET} sites was superior compared to any other linear simple model. Because P_A was centred and scaled before the analysis, when P_A is on its average for those sites ($P_A = 0.76 \text{ m a}^{-1}$), the model prediction for $\text{AGB}_w = \exp(3.2042) = 24.74 \text{ Mg ha}^{-1}$ (model intercept), and an increase of 0.1 m a^{-1} in P_A represents an increase of $\exp(0.4321) = 1.54 \text{ Mg ha}^{-1}$ in AGB_w .

Given that only three independent observations are available for S_{KAR} sites, inferences regarding causal relationships of environmental variables *versus* AGB_w in these study sites are necessarily imprecise. At these sites, total SOC ($\beta_I = -0.376$; $r^2 = 0.66$; $p = 0.021$) and f_{sand} were significantly associated with AGB_w ($\beta_I = 0.359$; $r^2 = 0.61$; $p = 0.032$). Figure 3.8 shows the more significant relationships found between AGB_w and tested predictors. Regression assumptions (i.e. homoscedasticity and normality of residuals) were met and spatial structures (Moran’s I) in the residuals were not detected at $p < 0.05$.

Table 3.1: Individual predictors of above-ground woody biomass (AGB_W) according to site geology. Regression parameters were estimated through linear mixed- models (LMM). $[X]_{ex}$ = concentration of exchangeable cations in the brackets; \sum_B = soil sum of bases; I_E = soil effective cations exchange capacity; $[X]_T$ = total concentration of elements in the brackets; pH_{H_2O} = water-measured soil pH; f_{sand} , f_{silt} , f_{clay} = soil sand, silt and clay fractions; Θ_P = maximum plant- available soil water; Depth = soil depth; P_A = mean annual precipitation; CWD_{adj} = long-term mean annual climatic water deficit (multiplied by -1); ψ = precipitation seasonality index; T_{MAX} = mean annual temperature of the warmest month. Note: predictors were standardised, then coefficients (β) represent changes in log (AGB_W) per standard deviation changes in the predictor variables; significant relationships at $p \leq 0.05$ are shown in bold.

Variable	All ($S_{SED} + S_{MET} + S_{KAR}$; $n = 29$)					Sedimentary (S_{SED} ; $n = 15$)					Metamorphic (S_{MET} ; $n = 11$)					Karst (S_{KAR} ; $n = 3$)				
	β_1	SE	r^2	p	AICc	β_1	SE	r^2	p	AICc	β_1	SE	r^2	p	AICc	β_1	SE	r^2	p	AICc
$[Ca]_{ex}$	0.256	0.120	0.13	0.042	86.90	0.385	0.385	0.25	0.040	46.10	0.009	0.178	0.00	0.963	34.40	-0.292	0.155	0.42	0.108	12.30
$[Mg]_{ex}$	0.221	0.123	0.10	0.082	88.00	0.367	0.174	0.23	0.051	46.60	-0.140	0.173	0.05	0.437	33.70	0.116	0.207	0.07	0.613	14.60
$[K]_{ex}$	0.202	0.124	0.08	0.114	88.50	0.305	0.182	0.16	0.114	47.90	0.084	0.176	0.02	0.644	34.10	-0.225	0.286	0.25	0.286	13.60
$[Na]_{ex}$	-0.054	0.129	0.01	0.679	90.90	0.200	0.191	0.07	0.312	49.40	-0.282	0.157	0.22	0.100	31.50	-0.283	0.158	0.39	0.123	12.50
$[Al]_{ex}$	0.060	0.129	0.01	0.645	90.90	0.127	0.195	0.03	0.525	50.10	0.258	0.160	0.18	0.845	32.00	-0.280	0.159	0.38	0.128	12.60
\sum_B	0.258	0.120	0.13	0.040	86.80	0.408	0.167	0.28	0.028	45.50	-0.054	0.177	0.01	0.765	34.30	-0.234	0.171	0.27	0.219	13.50
I_E	0.297	0.117	0.17	0.017	85.30	0.434	0.163	0.31	0.018	44.70	0.008	0.178	0.00	0.966	34.40	-0.237	0.170	0.28	0.213	13.40
$[P]_T$	0.171	0.125	0.06	0.184	89.30	0.212	0.190	0.08	0.283	49.30	-0.308	0.152	0.26	0.068	30.90	-0.018	0.217	0.00	0.938	14.90
$[C]_T$	0.141	0.127	0.04	0.274	89.90	0.149	0.194	0.04	0.455	49.90	0.087	0.176	0.02	0.632	34.10	-0.376	0.121	0.66	0.021	9.40
$[N]_T$	0.224	0.123	0.10	0.077	87.90	0.251	0.187	0.11	0.198	48.80	-0.039	0.178	0.00	0.830	34.30	-0.170	0.194	0.15	0.444	14.20
pH_{H_2O}	0.190	0.124	0.07	0.137	88.80	0.124	0.195	0.03	0.534	50.10	-0.072	0.177	0.01	0.693	34.20	-0.047	0.216	0.01	0.841	14.90
f_{sand}	-0.278	0.119	0.15	0.026	86.10	-0.299	0.182	0.15	0.121	48.00	-0.069	0.177	0.01	0.705	34.20	0.359	0.129	0.61	0.032	10.10
f_{silt}	0.303	0.117	0.18	0.303	85.00	0.341	0.177	0.20	0.073	47.20	0.194	0.168	0.10	0.273	33.10	-0.095	0.210	0.05	0.681	14.70
f_{clay}	0.151	0.151	0.04	0.242	89.70	0.189	0.192	0.06	0.340	49.60	-0.058	0.177	0.01	0.750	34.30	-0.220	0.176	0.24	0.301	13.70
Θ_P	0.095	0.128	0.02	0.464	90.50	-0.019	0.198	0.00	0.925	50.50	0.182	0.170	0.09	0.307	33.30	0.309	0.149	0.46	0.084	11.90
Soil _{depth}	-0.120	0.127	0.03	0.354	90.20	-0.207	0.190	0.07	0.294	49.40	0.148	0.173	0.06	0.410	33.70	0.127	0.205	0.08	0.578	14.60
P_A	0.185	0.125	0.07	0.148	89.00	0.330	0.180	0.19	0.081	47.30	0.432	0.122	0.50	0.005	25.90	-0.287	0.156	0.40	0.116	12.40
CWD_{adj}	-0.034	0.129	0.00	0.793	91.00	0.000	0.200	0.00	0.999	50.50	-0.089	0.176	0.02	0.622	34.10	-0.279	0.159	0.38	0.129	12.60
ψ	0.199	0.124	0.08	0.119	88.60	0.202	0.191	0.07	0.305	49.40	0.230	0.164	0.15	0.188	32.60	-0.283	0.158	0.39	0.122	12.50
T_{MAX}	-0.005	0.129	0.00	0.969	91.10	0.010	0.197	0.00	0.969	50.50	0.026	0.178	0.02	0.888	34.30	-0.246	0.168	0.30	0.194	13.30

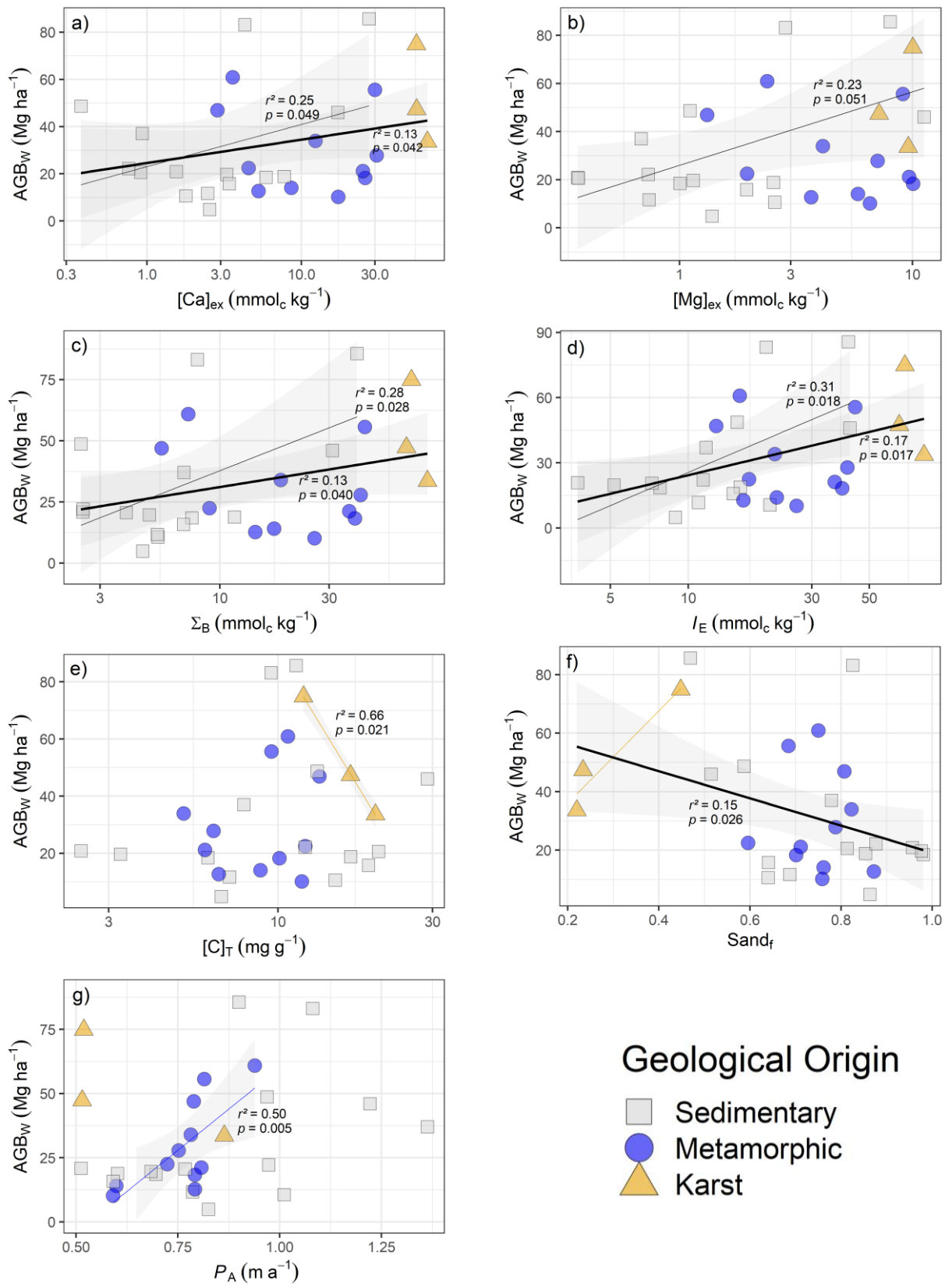


Figure 3.8: Observed variations in AGB_w as a function of selected edaphic and climatic predictors: a) [Ca]_{ex}; b) [Mg]_{ex}; c) Σ_B ; d) I_E ; e) [C]_T; f) Sand_{fraction}; g) P_A . Data points were discriminated according to their respective geological affiliations. Thinner lines represent linear fits for specific geological affiliations and coarser lines represent model fits at the entire sampling level. Shaded bands represent 0.95 confidence intervals.

3.3.4 Community-weighted trait means (CWM) and functional diversity

The community-weighted mean wood density (CWM_{wd}) was significantly lower at the S_{KAR} sites compared to both the S_{MET} and S_{SED} sites (Figure 3.9-a). On the contrary, the differences in the community-weighted mean maximum diameter (CWM_{dmax}) were not significant at $p \leq 0.05$ (Figure 3.9-b). Regarding the differences in the functional diversity indices, only F_{Ric} was significantly higher in S_{MET} compared to S_{SED} (Figure 3.9-c). Functional divergence (F_{Div}) was, in general, moderate to high and F_{Eve} was generally low to moderate in all categories (Figure 3.9-d; Figure 3.9-e).

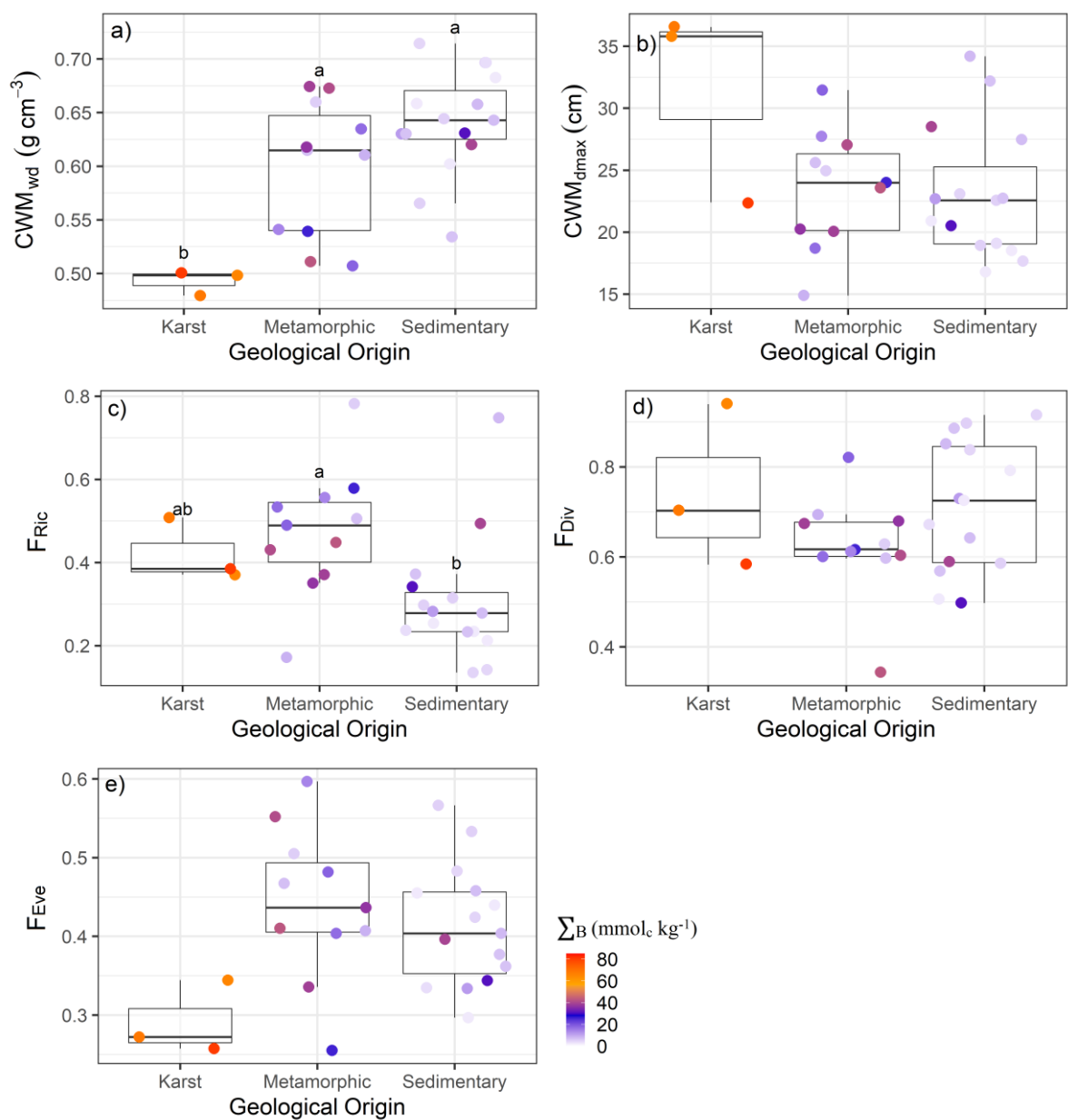


Figure 3.9: Community-weighted mean traits and functional diversity indices according to geological affiliations. a) Community-weighted mean wood density (wd); b) Community-weighted mean maximum diameter (dmax); c) Functional richness (F_{Ric}); d) Functional divergence (F_{Div}); e) Functional evenness (F_{Eve}).

Ordinary least squares linear regressions resulted in that AGB_w , considering all study sites together, was weakly associated with both ($r^2 = 0.20$; $p = 0.009$; Figure 3.10-a) and F_{Ric} ($r^2 = 0.17$; $p = 0.015$; Figure 3.10-b).

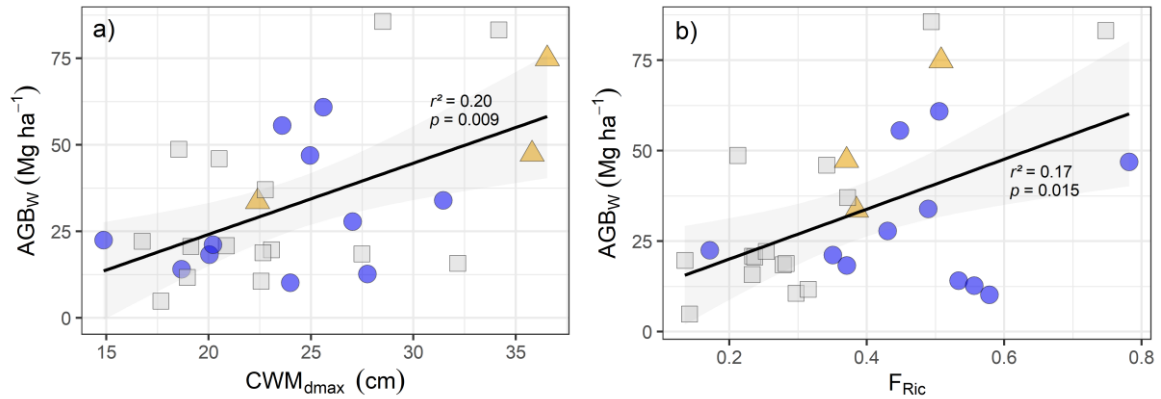


Figure 3.10: a) Predictive ability of CWM_{dmax} to explain variations in AGB_w ; b) Predictive ability of functional richness (F_{Ric}) to explain variations in AGB_w . Shaded bands represent 0.95 confidence intervals. Respective soil geological affiliations are shown.

Finally, a series of bivariate correlations between functional properties, soil chemical properties and soil texture (Table 3.2) showed that CWM_{wd} was inversely associated with CWM_{dmax} ($r = -0.49$; $p = 0.007$), $[Ca]_{ex}$ ($r = -0.50$; $p = 0.005$), $[Mg]_{ex}$ ($r = -0.43$; $p = 0.02$), \sum_B ($r = -0.55$, $p = 0.002$), $[K]_{ex}$ ($r = -0.36$; $p = 0.052$); I_E ($r = -0.55$, $p = 0.002$), $[Fe]_T$ ($r = -0.43$; $p = 0.023$), $[Zn]_T$ ($r = -0.40$; $p = 0.023$), $silt_f$ ($r = -0.56$; $p = 0.023$), and positively correlated with soil $sand_f$ ($r = 0.50$; $p = 0.006$). In turn, CWM_{dmax} was positively associated with F_{Ric} ($r = 0.53$; $p = 0.003$), $[Ca]_{ex}$ ($r = 0.45$; $p = 0.015$), and \sum_B ($r = 0.44$; $p = 0.016$). Functional richness (F_{Ric}) was positively associated with $[Ca]_{ex}$ ($r = 0.47$; $p = 0.010$), $[Mg]_{ex}$ ($r = 0.49$; $p = 0.007$), $[K]_{ex}$ ($r = 0.41$; $p = 0.027$), $[Na]_{ex}$ ($r = 0.38$; $p = 0.040$), \sum_B ($r = 0.55$; $p = 0.002$), I_E ($r = 0.53$; $p = 0.003$) and $[Zn]_T$ ($r = 0.37$; $p = 0.146$). Functional evenness (F_{Eve}) was inversely associated with $[C]_T$ ($r = -0.53$; $p = 0.003$), $[N]_T$ ($r = -0.63$; $p = 0.000$), $[Mn]_T$ ($r = -0.44$; $p = 0.016$). Finally, F_{Div} was negatively correlated with $[K]_{ex}$ ($r = -0.49$; $p = 0.007$) (Table 3.2).

Table 3.2: Spearman's rank correlation coefficient (ρ) amongst stand-level functional properties (namely CWM_{wd} , CWM_{dmax} , F_{Ric} , F_{Eve} and F_{Div} and selected soil chemical and physical properties, i.e. $[Ca]_{ex}$, $[Mg]_{ex}$, $[K]_{ex}$, $[Na]_{ex}$, $[Al]_{ex}$, Σ_B , I_E , soil pH_{H2O} , $sand_f$, $silt_f$, $clay_f$, $[C]_T$, $[N]_T$, soil C/N ratio, $[P]_T$, $[Fe]_T$, $[Mn]_T$ and $[Zn]_T$. Significant correlations at $p \leq 0.05$ are shown in bold. Red represents negative correlations and blue represents positive correlations. Significant correlations at $p \leq 0.05$ are shown in bold.

Variable	CWM_{wd}	CWM_{dmax}	F_{Ric}	F_{Eve}	F_{Div}
CWM_{wd}	-	-0.49	-0.33	0.18	0.10
CWM_{dmax}	-0.49	-	0.53	0.03	0.14
F_{Ric}	-0.33	0.53	-	-0.02	-0.33
F_{Eve}	0.18	0.03	-0.02	-	0.00
F_{Div}	0.10	0.14	-0.33	0.00	-
$[Ca]_{ex}$	-0.50	0.45	0.47	-0.29	-0.16
$[Mg]_{ex}$	-0.43	0.29	0.49	-0.26	-0.11
$[K]_{ex}$	-0.36	0.16	0.41	-0.29	-0.49
$[Na]_{ex}$	-0.13	-0.24	0.38	0.04	-0.32
$[Al]_{ex}$	0.21	-0.33	-0.13	0.14	0.08
Σ_B	-0.55	0.44	0.55	-0.32	-0.23
I_E	-0.55	0.31	0.53	-0.32	-0.15
pH_{H2O}	-0.32	0.31	0.29	-0.17	-0.16
$[P]_T$	-0.32	0.14	0.19	-0.33	-0.19
$[C]_T$	-0.16	-0.08	-0.05	-0.53	0.10
$[N]_T$	-0.26	0.06	0.11	-0.63	0.01
Soil C/N	0.22	-0.14	-0.27	0.07	0.30
$[Fe]_T$	-0.42	-0.01	0.13	-0.24	-0.14
$[Mn]_T$	-0.29	0.13	0.21	-0.44	-0.11
$[Zn]_T$	-0.40	0.16	0.37	-0.17	-0.01
$sand_f$	0.50	-0.06	-0.14	0.30	0.13
$silt_f$	-0.56	0.24	0.20	-0.32	-0.17
$clay_f$	-0.23	-0.20	0.07	-0.25	-0.07

3.4 Discussion

3.4.1 Study particularities

In this chapter, the most influential environmental drivers on stand-level AGB_w of Caatinga's seasonally dry communities were explored. To my knowledge, this work is the first to encompass study plots over a biome-wide geographical extension using standardised soil and vegetation sampling protocols in Caatinga. Such a large spatial scale also implies that the task of disentangling environmental forces accounting for AGB_w in Caatinga is not straightforward. This is because this region, despite having a common prevailing hot semiarid climate, is extremely patchy in terms of geodiversity (including both land-forms and geological substrates or parent materials, as shown in detail in Chapters 1 and 2). In addition, intricate evolutionary processes gave rise to a highly diversified flora and distinct physiognomies (QUEIROZ, 2006; QUEIROZ, 2017; FERNANDES et al., 2022), which means that the dry-adapted plant species of each community could respond differently to environmental effects.

As pointed out by CASTANHO et al. (2020a), for any study of above-ground biomass in Caatinga, it is necessary to specify which factors are under evaluation. In a broad sense, these factors are environmental drivers (soil + climate; macro variability), land-use effects on a given stand (meso variability) and successional age (micro variability) (*sensu* CASTANHO et al., 2020a). This study aimed to evaluate environmental drivers leading AGB_w. Given the highly human-modified history of the biome (AB' SABER, 1974), it is recognised that at least some of the stands evaluated here must have undergone more impactful human interference in the past. However, as there is no record of significantly impactful activities over the last decades, stands characteristics were assumed as the result of the maximum environment potential (or their resources limitation), therefore "mature" or "old-growth". Moreover, the impacts of eventual timber logging or grazing activities were assumed to not interfere significantly in the results presented here. Furthermore, the post-disturbance recovery of SDTFs is expected to be relatively rapid (3 – 5 decades), which might be attributable to the simpler structure of this vegetation type compared to moister forests (BECKNELL et al., 2012).

3.4.2 Biome-wide AGB_w is driven by complex interactions

The fundamental hypothesis that stand-level AGB_w in Caatinga is driven by complex interactions among climate, soil chemical, and physical properties rather than climatic variables alone was tested with the most interesting patterns highlighted in Figures 3.4 and 3.5. The results presented here show that, indeed, when considered in a multivariate context, P_A and soil cation levels (calcium) accounted more expressively for AGB_w in both conditional and full average models, while the interaction terms, i.e. $[Ca]_{ex} \times CWD_{adj}$ and $\theta_P \times CWD_{adj}$, had lower but still meaningful effect sizes in the full average model.

Despite high temperatures potentially triggering tree mortality through carbon starvation and hydraulic failure (MCDOWELL et al., 2018), with an associated lower AGB_w over time, there was no evidence that higher T_{MAX} has an influence on AGB_w across the evaluated stands. The most likely reason for the ability of Caatinga trees to cope with high-temperature events is that these species have evolved to tolerate high-temperature and through mechanisms of both avoidance (e.g. changes in leaf morphology) and tolerance (e.g. accumulation of osmoprotectants) to conserve the photosynthetic machinery (MATHUR; AGRAWAL; JAJOO, 2014; JAJOO; ALLAKHVERDIEV, 2017). Despite the tendency to high temperatures in Caatinga throughout the year, the typical drought-deciduous leaf habit of Caatinga species implies that, during the drier months, resources should be allocated to other plant processes instead of sustaining the high-cost leaves and photosynthetic apparatus.

Variations in total P and N appeared to be less important in determining AGB_w in the studied stands. Although they had small effect sizes in the conditional averaged model, the coefficients for both nutrients approached zero in the full average model and had low relative importance values. However, this does not mean that these nutrients are not important for the structure of the vegetation in Caatinga. Fertilisation experiment studies such as those presented in Kaspari et al. (2008) or the undergoing Amazon Fertilisation Experiment (AFEX) would be of great interest to determine how these nutrients affect productivity and biomass accumulation in the long term. I recognise that more accurate measures of N and P availability are lacking in this study. For comparison purposes, QUESADA et al. (2010) found a wide variation in $[P]_T$ in Amazon Forest soils, with a considerable number of soils showing $<200 \text{ mg kg}^{-1} \text{ P}$, including several Ferralsols that support high AGB_w values ($<300 \text{ Mg ha}^{-1}$). Furthermore, Quesada et al. (2012) have found that total soil P was the most important factor accounting for wood production. Therefore, the soil total P might be taken as a reasonable surrogate for the general

availability of P. Ecosystem buffering capacity has been described in which P from less bioavailable pools can become available if available P becomes scarce in the soil (KITAYAMA; MAJALAP-LEE; AIBA, 2000; QUESADA et al., 2010).

Similarly, N cannot be completely ruled out in driving AGB_w. Caatinga has been described as a hotspot for N fixation, although *in situ* and experimental research revealed that a small proportion of potentially nodulating species effectively do so (FREITAS et al., 2010; SILVA et al., 2017). Furthermore, high foliar N concentrations and high foliar $\delta^{15}\text{N}$ have been reported in Caatinga, which is suggested to be the result of the high availability of N (FREITAS et al., 2010; MARTINELLI et al., 2021). It should be noted that all Caatinga sites included in the study by Martinelli et al. (2021) are also part of this study. Although Caatinga soils are generally assumed to be fertile, the sampling includes some fairly infertile soils (e.g. Hyperdystric Arenosol in CJU-01). Thus, the premise that high soil general fertility is linked to high higher N pools may not be necessarily observed in the field. However, N availability in Caatinga seems somewhat controversy. This is because, although some potential indicators of high N-availability such as high $\delta^{15}\text{N}$ signals reported from both soils and leaves of Caatinga (e.g. FREITAS et al., 2010; MARTINELLI et al., 2021), N₂O emissions in Caatinga were reported to be even lower than in Cerrado (RIBEIRO et al., 2016; MARTINELLI et al., 2021). In addition, as for tropical savannas (LLOYD et al., 2009), it is not clear to what extent N or P may limit photosynthetic rates in Caatinga. Photosynthetic capacity was shown to correlate with foliar N and P in tropical savannas, especially in drier areas (DOMINGUES et al., 2010). At the same time, higher foliar N and C/N ratios were found in Caatinga compared to other Brazilian biomes (MARTINELLI et al., 2021). In general, deciduous trees require a high amount of nutrients (LLOYD et al., 2009) and have already been shown to resorb N much more efficiently from senescing leaves than evergreen shrubs and trees (AERTS, 1996). However, the extent to which nutrient use efficiency, i.e. nutrient resorption from senescing leaves (VITOUSEK, 1982; 1984) takes place in Caatinga is still little studied.

Mean annual precipitation (P_A) became relevant in driving AGB_w only in a multivariate context. This was, in part, contrary to the initial expectation as in the words of BECKNELL et al. (2012), “..., *the ecology and climate of SDTF suggest that water availability, even expressed through a coarse index like mean annual precipitation, is highly likely to play a role in SDTF biomass content*”. However, the P_A range in this study is within the dry end spectrum of global SDTFs, that is, 17 of 29 study plots had $P_A \leq 0.8$, with only four study plots with $P_A \geq 1.0$ m. Menezes et al. (2021) pointed out that Caatinga forests are even drier than the hilly Mexican

“very dry deciduous forests” studied by LEBRIJA-TREJOS et al. (2008), in which P_A is around 0.9 m. The P_A of 0.9 m has also been suggested as a threshold level for AGB_W by BECKENELL et al. (2012), who found a lower and higher AGB_W below and above this mark, respectively (in this study, there were no differences in AGB_W according to this threshold; results not shown). Therefore, it is plausible that the effects of P_A on driving AGB_W become more pronounced at higher P_A levels than observed in this study. Furthermore, the results presented here suggest that P_A is indeed important over a biome-range level, but its effect is conditioned by other abiotic covariates.

Regarding the maximum climatological water deficit tested in this study (CWD), even the wettest site in the dataset showed a negative annual balance of -0.6 m. Maximum climatological water deficit (CWD) has been demonstrated to influence allometric relationships in tropical trees (CHAVE et al., 2014) and represents to what degree a certain place is water-stressed. Despite the small effect sizes of CWD and associated interactions with soil chemical and physical parameters, it was decided to proceed with model simulations, since coefficients were high in those models where these terms were retained. Therefore, it is suggested that soil properties also mediate vegetation responses to climate on small scales (MAIA et al., 2020a).

The influence of other cations (that were not included in the main model of Eqn. (3.4) on AGB_W cannot be ruled out. For example, potassium might play a key role in modulating tropical woody vegetation (SCHRODT et al., 2015; LLOYD et al., 2015). Similarly, magnesium can alter vegetation growth under severe deficiency. This is because this element is involved in several biochemical and physiological processes, acting in photosynthesis, synthesis of proteins and acid nucleic acids, and enzyme activation, in addition to improving the problems of aluminium toxicity (CHEN et al., 2018). Although relatively high exchangeable aluminium is found in some S_{SED} sites, no evidence of its potential negative effects was found. Detrimental aluminium effects (DELHAIZE; RYAN, 1995) have been observed in castor (*Ricinus communis* L.) under experimental conditions in Caatinga (DE LIMA et al., 2014), but should rarely affect vegetation performance under moderate to high soil pH conditions common to this region. Exchangeable sodium appeared only in small amounts (only two study soils exceeded $1 \text{ mmol}_c \text{ kg}^{-1}$). Six important woody native species of Caatinga had a high capacity to tolerate low to moderate salinity levels, while only one specie (*Myracrodruon urundeuva* M. Allem.) could tolerate a high salinity level (BESSA et al., 2017).

Concerning the potential beneficial effects of calcium itself [included in the main model of Eqn. (3.4)], in addition to the fundamental role of calcium in providing structural support for plant cells, it is known that calcium also has an equally important role in several mechanisms associated with responses to plant abiotic stress. For example, exogenous calcium ion treatment considerably improves antioxidant activities in grasses under heat stress (JIANG; HUANG, 2001), also conferring greater osmoprotection by increasing glycine betaine (an important osmoprotectant) in *Catharanthus roseus* under water deficit (JALEEL et al., 2007). Furthermore, several mechanisms involving calcium signal decoding elements have been described. Such mechanisms refer to a complex and regulated signalling network, in which plants can respond specifically to different abiotic stresses and these responses are known to be largely mediated by the cytosolic concentration of Ca^{2+} (SONG et al., 2008; SHARMA; KUMAR, 2021). In turn, extracellular and calcium cytosolic concentration $[\text{Ca}^{2+}]_{\text{cyt}}$ are controlled by the soil $[\text{Ca}^{2+}]$ as well as transpiration rates in *Arabidopsis thaliana* (SONG et al., 2008). Calcium-mediated stress-induced responses were also studied in roots (WILKINS et al., 2016), and the authors pointed out that calcium is also important for exocytosis in growth and that roots also have to endure various abiotic stresses as they exploit the soil in search of water and nutrients. Therefore, regardless of the mechanisms considered to justify the importance of calcium, and contrary to the potential nutrient imbalance and calcium toxicity as suggested by PRADO-JUNIOR et al. (2016), results here suggest that calcium is of pivotal importance for the semi-arid Caatinga (Figure 3.4). That is, under similar (high) water stress conditions (higher CWD_{adj}), soils that afford greater calcium availability seem to be able to maintain a higher AGB_w over time.

Lastly, the interactive effect between maximum plant-available soil water (θ_P) and maximum climatological water deficit (CWD_{adj}) suggests that soils with higher θ_P are likely to mitigate the negative effects of suboptimal precipitation regimes. Precipitation seasonality and soil moisture gradients were also found to be the most important variables determining manifold vegetation parameters in sites including transitions between Caatinga, Atlantic Forest, and Cerrado (TERRA et al., 2018). Therefore, a higher θ_P may represent an important buffering agent by which plants can benefit even after the end of wet season rains. I recognise the limitations of using a pedotransfer function instead of a field-measured water-holding capability. However, the index used here is believed to provide much better information compared to the commonly used coarse textural fractions to represent soil water-holding capacity per unit volume. Furthermore, the field-measured maximum effective soil depth

(rarely measured in the field) embedded in Θ_P should reflect the size of the reservoir from which plants can potentially extract water.

3.4.3 Is the effect of climatic and edaphic factors the same for stands of different geological affiliations?

Several studies have already pointed out that Caatinga plant communities are particularly associated with geologically distinct substrates (e.g. ANDRADE-LIMA, 1981; DA COSTA et al., 2015; QUEIROZ, 2006; MORO et al., 2016; QUEIROZ et al., 2017; FERNANDES et al., 2022). Furthermore, the community composition of stands growing in karst and dunes environments is recognised by their unique species composition and high levels of endemism (QUEIROZ et al., 2017; FERNANDES et al., 2020). These differences in community compositions are thought to reflect species suitability to edaphic conditions, but also reflect the available regional pool of species (i.e. geographical proximity).

The present-day assembly of plant lineages was identified to be primarily the result of ancient biogeographical changes, with later post-climate-induced changes in the vegetation responsible for most *in situ* speciation events (FERNANDES et al., 2022). Furthermore, the main pathway of species in Caatinga must have occurred from surrounding regions (i.e. Atlantic Forest and Cerrado), mostly represented by lineages carrying drought tolerance traits (FERNANDES et al., 2022). Nevertheless, another key point behind the suitability of the environment to host such species is that, beyond the critical environmental filter that Caatinga species are subjected to (i.e. relatively low water availability), species thrive in distinct geologically-determined edaphic conditions. In addition to physical and chemical soil characteristics, other commonly unmeasured subsidiary factors are likewise controlled by geological processes (e.g. shallow rocky soils in the *Depressão Sertaneja*) (FERNANDES et al., 2022).

The results presented in Figure 3.8 and Table 3.1 suggest that different community compositions overlying geologic-edaphically distinct substrates may be primarily limited by different resources. To help understand these results, it is worth mentioning that much of the research on resource limitation in plant ecology has been put forward through economics analogies (*sensu* BLOOM; CHAPIN; MOONEY, 1985). From this perspective, it seems reasonable to assume that light availability, i.e. photon flux density (PFD), should rarely limit the typical open canopies communities with low cloud coverage of the seasonally dry Caatinga.

On the other hand, the importance of water or nutrients in limiting a given community should be determined by the relative availability of each resource. Hence, plants should adjust in both the short and long-term (acclimation and genetic adaptation, respectively) to achieve a similar benefit-to-cost ratio related to the expenditure of each resource (BLOOM; CHAPIN; MOONEY, 1985). This conceptual framework may help explain why biomass stocks are not higher considering geological affiliations (Figure 2.1). That is, despite the relatively higher availability in S_{MET} - and S_{KAR} -associated communities, the latter does not have relatively higher biomass or, still, plants from nutrient-poor sites can adjust their physiology according to available resources.

In addition, nutritional needs can vary significantly across species, genotypes of a species, among tissues of a single plant, and according to ontogenetic stages (BLOOM; CHAPIN; MOONEY, 1985). Therefore, determining the limitations across plant communities is a difficult task. Plants have evolved to tolerate varying levels of resource availability, and a community dominated by a given (or a set of) species is expected to also show varying physiological traits to cope with the available nutrient supplies (CHAPIN; VITOUSEK; VAN CLEVE, 1986).

Concerning water availability, several mechanisms to cope with water stress have been extensively studied and include morphological, physiological, and biochemical adaptations such as activation of osmotic-stress signalling, ion transport, stomatal closure, leaf drop (inducing lower leaf area), improving water use efficiency - WUE (OSAKABE et al., 2014; MESQUITA; DANTAS; CAIRO, 2018). Similarly to nutrients, species may have different levels of tolerance to water stress. For example, MESQUITA; DANTAS; CAIRO (2018), experimentally studying six native species of the same site, found that all species have undergone a decrease in transpiration rate and stomatal conductance under lower soil moisture conditions. However, only two species (*Myracrodruon urundeuva* M. Allem. and *Cnidocolus bahianus* (ULE) Pax & Hoffm.) had significant negative effects on net photosynthesis. An interesting example of species adaptation to a constrained environment in the current dataset is the dominance of the sclerophyllous *Copaifera coriacea* in both plots at the sedimentary “Dunas de São Francisco”, for which P_A does not exceed 0.7 m a^{-1} and the aridity index is high ($AI \approx 0.28$, $AI = \text{precipitation/potential evapotranspiration}$; SOUZA et al., 2021). Sclerophylly is a trait commonly associated with drought tolerance but was also reported to predominate in P-deficient soils of humid and semiarid regions (MEDINA; GARCIA; CUEVAS, 1990). Therefore, the dominance of *C. coriacea* in the studied sand dunes may be

attributable to the potential capacity of this species to thrive in both water- and P-limited environments.

In the last instance, the weighted composition of a given community and associated functional properties are expected to reflect its general resistance or tolerance to drought stress, as well as its capacity to cope with nutrient-poor environments. Therefore, the AGB_W and predictor relationships of Figure 3.8 and Table 3.1 indicate that soil cation concentrations play a significant role in AGB_W throughout the biome, including different community compositions. The soil sand content was also influential when considering all sites together, probably reflecting nutrient levels, but also because fast-draining sandy soils are known to induce greater water stress in plants in seasonal environments (MAIA et al., 2020a). Furthermore, sandier textures have been associated with increased mechanical instability (QUESADA et al., 2012).

The positive effect of both exchangeable $[Ca]_{ex}$ and $[Mg]_{ex}$ (also reflected in \sum_B and I_E) at S_{SED} sites can be interpreted as an indication that these cations can be relatively more limiting than water in these environments. Both calcium and magnesium are essential for plants, participating in several physiological and biochemical processes (Section 3.4.2). On the contrary, stands growing on mostly nutrient-rich S_{MET} terrains appeared to be more limited by rainfall total amounts, with the relationship found between AGB_W and P_A being considerably strong ($r^2 = 0.50$; $p = 0.005$), interestingly close to the relationship presented in a global synthesis of AGB_W in dry forests (BECKNELL et al., 2012), who found $r^2 = 0.55$ ($p < 0.000$) for the same relationship. However, the slope of their relationship was much higher, where an increase of 1.0 m a^{-1} in P_A accounted for an increase of 187 Mg ha^{-1} in AGB_W , with these values being comparable to the relationship found in the global compilation of MARTÍNEZ-YRÍZAR (1995). Considering that AGB_W appeared to respond sharply to increases in P_A in both studies (BECKNELL et al., 2012; MARTÍNEZ-YRÍZAR, 1995), it is arguable that their evaluated stands probably grow on more nutrient-rich soils, even though their studies did not incorporate the relevant soil information. Moreover, most stands included in BECKNELL et al. (2012) had mean annual rainfall levels close to the maximum limit according to Murphy and Lugo's (1986) definition of SDTFs (i.e. 2000 mm a^{-1}) and with a much higher AGB_W ($100 - 334 \text{ Mg ha}^{-1}$) than the values commonly found in the dry Caatinga.

Another implicit aspect of soil water availability is the fact that a reduction in the soil water supply is expected to impair significantly nutrient availability and this can be summarised in a few underlying reasons (*sensu* BLOOM; CHAPIN; MOONEY, 1985): (1) the

movement of water towards the roots is diminished and, as a consequence, mass flow of nutrients onwards the roots also decreases; (2) As a result of soil drying, contact of roots and soil particles decreases due to shrinkage of both limiting nutrient diffusion; (3) Increased soil cation concentrations leads to the formation of less soluble cation-bonded compounds; (4) mineralisation rates are also expected to decrease, likely reducing the release of nutrients from organic matter to the soil. Therefore, since the supply of nutrients is generally relatively higher in S_{MET} sites, increased water availability can be expected to improve the nutritional status of these ecosystems.

Given that only three independent observations are available for the S_{KAR} category, I am unable to provide conclusive results about the environmental drivers of AGB_W in the S_{KAR} sites. However, it is still noteworthy that AGB_W in GBR-01 (Cambisol) was 58% higher than in GBR-02 (Leptosol). Although these study plots share virtually the same climatic conditions and very close edaphic properties, the soil was markedly shallower in GBR-02. Therefore, it may potentially be a case of bad anchorage to large trees, which often leads to lower AGB_W (QUESADA et al., 2012). Within the S_{KAR} sites, PFF-01 showed the lowest AGB_W even with annual precipitation being 0.3 m higher than the other S_{KAR} stands. This could potentially be due to adverse soil morphological properties (i.e. high rock and gravel levels; shallow depth), community characteristics or even potential uncounted human interference since PFF-01 was close to several small farms surrounding the municipalities of Mossoró and Baraúna, Rio Grande do Norte.

3.4.4 AGB_W , functional diversity and soil properties

Complementary bivariate analyses showed that the community-weighted mean wood density (CWM_{wd}) was not associated with AGB_W , while the mean maximum stem diameter (CWM_{dmax}) accounted for a small but significant variation in AGB_W ($r^2 = 0.20$; $p = 0.009$, Figure 3.10-a). Furthermore, among the components of functional diversity (F_{Ric} , F_{Div} , and F_{Eve}), only F_{Ric} was related to AGB_W ($r^2 = 0.17$; $p = 0.015$; Figure 3.10-b). These results are partially in agreement with Prado-Junior et al. (2016), who found that CWM_{wd} also accounted for only a low proportion of the variance in the initial standing AGB_W , and with F_{Div} and F_{Eve} accounting for variations in AGB_W instead of F_{Ric} found in this work. It should be noted that the functional diversity indices used in the study by Prado-Junior et al. (2016) also included CWM_{sla} (specific leaf area), although this trait appeared to influence only the growth of surviving trees throughout their recensus.

Higher functional richness is assumed to imply niche complementarity, in which species can take advantage of resources in different manners. For example, assuming that tree diameter is, in general, allometrically associated with other vegetative characteristics (e.g. tree height, crown area, roots depth), a range of species' maximum stem diameter is very likely to reflect life histories and resource partitioning in a given community (VILÀ et al., 2013; PRADO-JUNIOR et al., 2016). The results presented here suggest that relationships found for a given set of communities (and/or at smaller spatial scales) may not necessarily reflect the same patterns of trait economic spectrum on broader geographical scales or when considering other communities.

Although wood density presumably influences biomass storage (since high wood density trees hold more biomass per unit of wood volume), this influence did not translate into differences in standing AGB_w in this study. This lack of ability of CWM_{wd} in predicting AGB_w was maintained even alternatively using the global allometric equation for dry forests, which includes wood density as an input variable (CHAVE et al., 2014). The CWM_{wd} itself had an inverse relationship with CWD_{dmax} , indicating a trend for thicker trees of low wood density or the inverse, likely reflecting different plant life histories. For example, the ecological meaning of high (or low) wood density can be broadly interpreted from the physical and biochemical points of view. In this respect, and contrary to the general idea that high wood densities provide higher strength (i.e. resistance to stem breakage), Larjavaara and Muller-Landau, 2010) showed that this may not always be true. This is because the resistance to stem breakage is proportional to the construction costs, and the latter also depends on the diameter of the trunk. Therefore, trunks with varying wood density but the same length can have identical construction costs, and trees with low wood density are more resistant to stem breakage compared to high wood density trees under the same construction costs (LARJAVAARA; MULLER-LANDAU, 2010). However, higher costs of maintaining respiration were shown to be associated with thicker trunk diameter (BOSC; DE GRANDCOURT; LOUSTAU, 2003; LARJAVAARA; MULLER-LANDAU, 2010), the latter unlikely being the most appropriate strategy for a Caatinga tree.

In addition to the physical aspects related to wood density, inverse correlations between CWM_{wd} and soil $[Ca]_{ex}$, $[Mg]_{ex}$, $[K]_{ex}$, \sum_B , I_E , $[Fe]_T$, $[Zn]_T$ and $silt_f$, and a positive correlation with $sand_f$ (Table 3.2) were found. Interestingly, the lowest CWM_{wd} was observed in S_{KAR} stands and with a clear trend for higher wood density values in S_{SED} sites, the latter with relatively lower cations availability (Chapter 2, Table 2.2). This indicates a greater abundance

of individuals with low wood density in soils with greater availability of metallic cations. Potential mechanisms underlying these relationships have already been comprehensively characterised in detail by QUESADA et al. (2012) in the context of tropical rainforests. Regarding the semiarid Caatinga, these relationships are thought to reflect primarily water-economy strategies. For instance, S_{KAR} GBR-01 and GBR-02 are within the sites with the lowest mean annual precipitation levels in the dataset (both showing P_A 0.51 m a⁻¹) and are fairly dominated by the low wood density *Commiphora leptophloeos* (Mart.). As wood density is generally well correlated with xylem density (SARMIENTO et al., 2011), those individuals with low wood density can exhibit greater sapwood water capacitance compared to individuals with high wood density, and therefore, greater availability of osmotically active cations may improve the capacitive efficiency of these plant cells (QUESADA et al., 2012). Similarly, given that an inverse association between wood density and parenchymatic tissues (responsible for storing water, nutrients and carbohydrates) can be established, an inverse association between wood density and osmotically active cations can also be reasonably expected (LIRA-MARTINS et al., 2019). This association has been suggested as an evolutionary strategy for plants to cope with potential cavitation in xylem conduits given the high susceptibility of low-wood-density plants to embolism (LIRA-MARTINS et al., 2019). Despite the less apparent causal effect of both $[Zn]_T$ $[Fe]_T$ on reflecting lower values of wood density, Zn has already been shown to improve the activity of osmoregulation substances under drought stress (WU et al., 2015). In contrast, stands with lower availability of osmotically active cations tended to exhibit high CWM_{wd} values, which is likely to reflect a long-term strategy for lower susceptibility to hydraulic failure. Finally, the inverse relationship between CWM_{wd} and soil $silt_f$ and wood density and the positive relationship with $sand_f$ are likely to reflect the nutrient relationships described above. Furthermore, soil texture is expected to correlate with mechanical stability, which in turn was shown to also affect wood density (QUESADA et al., 2012).

The community-weighted mean maximum stem diameter (CWM_{dmax}) was positively associated with F_{Ric} , indicating that stands with thicker adults are also those that fill more niche space. Regarding the relationships between CWM_{dmax} and soil properties, only $[Ca]_{ex}$ and \sum_B were positively associated with CWM_{dmax} , suggesting that only soil bases, rather than I_E (which includes $[Al]_{ex}$), are important for secondary growth in plants. The relationship between eutrophic soils and stem growth was recently observed by Angl elico et al. (2021), who found individuals of *Enterolobium contortisiliquum* (Vell.) with greater stem diameter in eutrophic

soils compared to oligotrophic soils in the Brazilian Cerrado. Furthermore, in their study, the cell fibres and pits between the cell vessels were higher in eutrophic soils than in oligotrophic soils, providing evidence that soil conditions influence the wood anatomical characteristics.

Except for $[Al]_{ex}$, F_{Ric} was positively related to all soil cation metrics evaluated (including I_E) and $[Zn]_T$ of the soil. This result suggests that the varying levels of these cations in the soils reflect physiological adjustments of the trees to achieve the most cost-effective balance between secondary growth and woody density. Indeed, environmental gradients are expected to influence community functional traits, which are determined by the distribution of resources (LIU et al., 2012). Therefore, it seems reasonable to expect that the varying availability levels of these elements provide means for both acquisitive and conservative species to establish, which is reflected in higher F_{Ric} . Jager et al. (2015) observed a coordinated variation of several independent plant traits according to soil fertility degree in a warm forest in New Zealand.

Functional evenness (F_{Eve}) was negatively associated with soil $[C]_T$, $[N]_T$, and $[Mn]_T$. Although in a first evaluation there did not appear to be any causal relationship, this is hypothesised to potentially reflect organic matter quality. For instance, given that the recalcitrance of soil organic carbon (SOC) is influenced by the quality of organic matter produced by the vegetation (WANG et al., 2015), stands with low F_{Eve} may indicate that the niche space is mostly filled towards species with thinner stems of high wood density, these being potentially associated with the “slow” leaf traits described by Jager et al., 2015 (that is, low SLA, low P and N and high thickness and dry matter content – LDMC). All of these traits are likely to influence the recalcitrance of carbon compounds and their residence time in soils, which in turn may reflect higher SOC values over time.

Functional divergence (F_{Div}) was negatively correlated with soil $[K]_{ex}$. If, as soil $[K]_{ex}$ values increase, traits of the most abundant species occur towards the centre of the niche space (low F_{Div}) (MASON et al., 2005), then the niche differentiation should be relatively small. This also means that competition for resources should be higher in those communities showing low F_{Div} (MASON et al., 2005). Finally, considering the functional traits and diversity metrics explored here, even though only CWM_{wd} and F_{Ric} were significantly different across geological categories (Figure 3.9), several soil properties when considered on a continuous basis, had marked associations with all functional metrics included in this study. This provides evidence

for the multi-driven influence of soil properties on the vegetation function and how this may result in variations in biomass stocks over time.

3.5 Conclusions

This work encompassed a biome-wide spatial scale that allowed evaluating complex environmental interactions that account for variations in AGB_W . Specifically, AGB_W was found to be a product of climate and soil properties. Indeed, along the entire mean annual precipitation gradient observed in this work, changes in soil properties [i.e. from harsh to more favourable conditions in terms of nutrients availability (represented by calcium) and maximum plant-available soil water] were associated with an approximately three-fold increase in above-ground woody biomass (Figure 3.6). Furthermore, edaphic properties were suggested to be more limiting in sedimentary environments, whereas total annual rainfall amounts appeared to be more influential in metamorphic/crystalline environments. Soil properties were also shown to influence community trait values and functional diversity indexes, with CWM_{dmax} and F_{Ric} weakly predicting AGB_W . Therefore, the alternative “biomass ratio” and ‘niche complementarity’, based on the two traits evaluated here, were considered less supported as drivers of AGB_W variations in Caatinga, which is suggested to be primarily driven by environmental controls.

Supplementary topic

S3.1 – Biomass equations

Woody volume estimates are critical when leading a forest inventory or making management decisions in plantations, with native forest inventories usually showing more obstacles, such as species diversity (i.e. the allometric behaviour varies from species to species) and variable ages among trees (NAZARENO et al., 2021). Nevertheless, despite the hindrances to obtaining reliable woody estimates, allometric equations have been traditionally used in ecology with a relatively safe margin of error.

Allometric equations remain relatively scarce for Caatinga's trees and there is no 'silver bullet' to obtain fully reliable estimates for the entire region. Most studies apply the Caatinga-specific equation (SAMPAIO; SILVA, 2006) or the global equation for dry forests (CHAVE et al., 2014), widely used at a global level in the tropics. Recent studies proposed using averaged values of the mentioned equations as a manner to reduce biomass estimates uncertainties (e.g. MAIA et al., 2020a; MAIA et al., 2020b). Sampaio and Silva's work provides multiple possibilities to predict AGB_w , i.e. equations based only on stem diameter at the breast height (DBH) or stem diameter at ground level (DGL), or different combinations of stem area at the ground level (AGL) and stem area at breast height (ABH) with total tree height (H) and woody density (ρ).

Regarding only DGL or DBH equations available in the work of Sampaio and Silva (2005), either equation was considered suitable for calculating above-ground biomass as the authors found a very strong relationship between each other ($r^2 = 0.92$). It is noteworthy that some authors claim that the DGL equation should be preferred in Caatinga since it allows for easier measurements in common multitrunked trees of Caatinga, the reason why it is widely used in phytosociological studies across the region (RODAL; SAMPAIO; FIGUEIREDO, 2013).

Further comparison was performed between Sampaio and Silva's DBH equations and the global equation for dry forests (CHAVE et al., 2014), widely used to estimate biomass in the tropics. Biomass values estimated through the global equation for dry forests for each standing tree were obtained through the *BIOMASS* package version 2.1.6 (RÉJOU-MÉCHAIN et al., 2021). Considering the two available ways to calculate trees' biomasses, a slightly modified equation from RÉJOU-MÉCHAIN ET AL. (2021) was used, whereby the inputs are wood density, diameter at breast height (DBH) and E (a measure of environmental stress estimated from the site coordinates). Wood density values for each specie were obtained from

the global wood density database (CHAVE et al., 2009, ZANNE ET AL. 2009), attributed to family, genus or species when available. Botanical names were checked and adjusted according to the Brazilian Flora 2021 with the *flora* package version 0.3.5 (CARVALHO, 2020). On average, Sampaio and Silva's DBH equation was 19% greater than Chave and coworkers' equation, with the equations being highly correlated ($r = 0.96$).

Whatever theoretical consideration about observed differences among these equations and because the best fit was, in general, attained with DGL equations (Table 2 of Sampaio and Silva's original work), which was adopted in this work, also supported by the fact Sampaio and Silva's equation was developed in the same region of this study. Furthermore, specific equations for *cacti* and palm species were used to avoid overestimated AGB_w values in some cases (a difference of 8 Mg ha⁻¹ was recorded in SJO-01 when using the general Sampaio and Silva's general equation for Caatinga species for *cacti* individuals). Figure S3.1 shows the relative difference in AGB_w calculated through the chosen equation and the other three alternative methods. It is noteworthy that calculated AGB_w had relatively high variations depending on the allometric equation, and the reasons underlying such variations are briefly discussed. First, assuming an inclusion criterion for trees' measurements (for instance, DGL or $DBH \geq 5$ cm), it is expected that stem count differences will arise. Often, a tree with DGL = 5 cm (or slightly higher) shows $DBH < 5$ cm, commonly yielding a greater stem count for DGL rather than DBH. The opposite might also happen where trees usually branch at a certain height (e.g. higher than 30 cm), which is the case for five of the study sites. Despite such a pattern, a comparison between Sampaio and Silva's DGL and DBH equations using our original data resulted in a very high Pearson's correlation coefficient ($r = 0.99$), even though the values obtained with the DBH equation were 41% greater on average. This discrepancy can be attributable to the α parameters of these equations (0.0644; 0.1730 for DGL and DBH equations, respectively), thereby even small changes in both α and b coefficients might represent a great difference in trees' volumes, especially for large trees (SAMPAIO; SILVA, 2005).

Another source of variation might be attributable to the presence of *cacti* species. Of course, the difference should be minimal at stands where *cacti* rarely occur or are absent (which usually is not the case for many Caatinga places). However, where *cacti* species occur in a larger proportion, one might overestimate AGB_w values up to 8 Mg ha⁻¹ (as noted in SJO-01) if the general equation for trees is used. It is due to the peculiar columnar format (MAUSETH; KIESLING; OSTOLAZA, 2002) and specific allometric relationships present in most *cacti* species. For example, a strong anisometric relationship was shown for *Cereus giganteus*, i.e.

taller specimens tended to be markedly thinner than younger, shorter counterparts (NIKLAS; BUCHMAN, 1994).

Since only 35 palm individuals are present in the dataset, it would not be expected to influence the AGB_W values at the plot levels significantly. In any case, palms are also known to show peculiar allometric relationships, and their heights do not necessarily vary proportionately with diameter, which is should be related to a series of mechanical architecture strategies (RICH, 1986, ALVES; MARTINS; SANTOS, 2004).

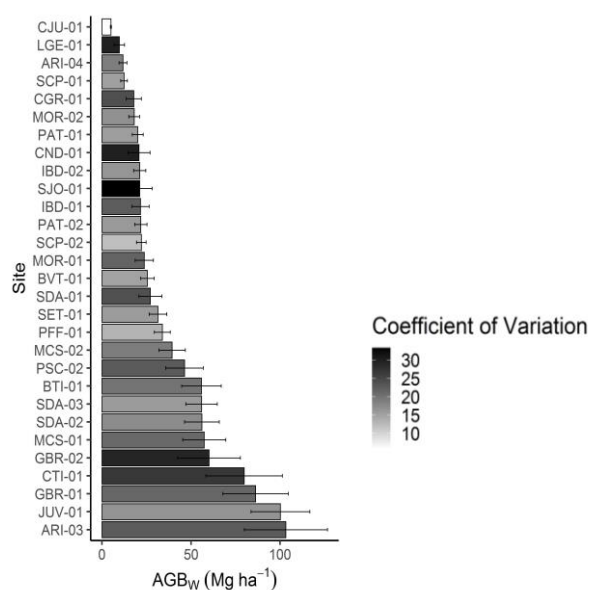


Figure S3.1: AGB_W average values \pm standard deviations and coefficient of variation (CV%) relative to alternative equations.

Finally, the bulk of differences found in AGB_W estimates using the pantropical equation for dry forests (which uses DBH as diameter input) might be owed to woody densities (ρ) entrances as well as the environmental stress factor (E). The former may vary significantly among and within tree species in dry forests, with recent work assuming a general average value of 0.55 g cm^{-3} for all Caatinga species (CASTANHO et al., 2020a). This value was used in satellite retrieval for carbon stock estimates for the entire biome (CASTANHO et al., 2020a), nearly achieving AGB_W as for the Caatinga-specific equation. However, we must observe that Caatinga species commonly (by no means always) attain higher wood density values. For example, the nine tree species used for Sampaio and Silva (2005) to develop their allometric equation showed an average woody density of 0.87 g cm^{-3} , but the authors also noted that several Caatinga species hold low wood densities values (such as *Jatropha Molissima* Pohl). Thus, it is argued that, if possible, appropriate average wood density values should be weighted according to the species assemblage in each community. The average wood densities retrieved

from the global wood density database ranged from 0.50 to 0.72 g cm⁻³, with most sites showing average values ≥ 0.60 g cm⁻³. In addition, the environmental stress factor (E) has been shown to influence the tropical trees' allometry and is obtained according to climatic water deficit, temperature seasonality, and precipitation seasonality (see CHAVE et al., 2014). Since E varied from 0.32 to 1.10 among our study sites, AGB_w estimates through the pantropical equation for dry forests can be expected to vary significantly compared to other equations which do not include these parameters.

Chapter 4

Conclusions

Chapter 4 – Conclusions

The main objectives of this study were to provide a detailed approach to Caatinga soils and to evaluate how their properties influence the properties of vegetation. Across the 29 studied sites, soils belonging to three distinct geological affiliations had consistent differences. However, some properties varied more than others. For example, soil effective cation exchange capacity and soil total reserve of bases (taken as a measure of nutrient total capital reserves) decreased following $S_{\text{KAR}} > S_{\text{MET}} > S_{\text{SED}}$. Total soil phosphorus concentrations, although showing high overall variability, were considerably higher only at the S_{KAR} sites. These results are thought to reflect the weathering status as well as soil parent materials quality. Reference soil groups were found to also reflect geological origins, with S_{KAR} soils mainly associated with low pedogenic stages (that is, Leptosols, Cambisols, and Calcisols), S_{MET} soils mainly associated with intermediate pedogenetic stages (i.e. Luvisols), and S_{SED} mainly associated with Arenosols, the latter usually being the residual product of old weathered quartz-rich soil parent materials or recently deposited sands.

The nitrogen dynamic in Caatinga was shown to be strongly modulated by climatic forces as indicated by isotope discrimination, with modelled soil $\delta^{15}\text{N}$ responses (“The Soil $\delta^{15}\text{N}$ Isoscape for Caatinga”) showing a clear convergence between soil $\delta^{15}\text{N}$ and climatic patterns. However, further evidence suggests that the pedogenetic stage (reflected by I_{E}), may also explain part of the variation in soil $\delta^{15}\text{N}$ values, especially at the wetter sites. In addition to geomorphological aspects, soil pedogenetic stages are suggested to explain the remaining unexplained variance when using purely climatic variables to explain $\delta^{15}\text{N}$ patterns in semiarid environments.

Using a geographic comparison approach, it was possible to compare the environmental drivers that influence AGB_{w} . In summary, AGB_{w} was found to be the product of complex interactions between soils and climate in Caatinga. The inclusion of additional S_{KAR} sites would be of great interest in better understand which environmental forces shape vegetation structure and function of vegetation at these sites. Furthermore, soil properties influenced vegetation functional traits and associated functional diversity indexes, that is, the frequency pattern in which traits occur in the communities studied. Collectively, these results provide information on the multiple ways soils can influence vegetation properties.

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