









Savannas of the Brazilian semiarid region: what do we learn from floristics?

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ABSTRACT

The Cerrado represents the largest extension of savanna in South America. It occupies large stretches of central Brazil, being fragmented towards the Northeast, Southeast, and South regions of the country. Examples of disjunct patches of vegetation with savanna physiognomy within the Caatinga can be found in the Chapada Diamantina, the Chapada do Araripe, in small areas of southern Ceará State, and also in the coastal plains. This study recorded the floristic composition of four savannas within the Caatinga in northern Ceará State and evaluated the floristic relationships between these and other savannas, Cerrado and Caatinga sites. Periodic floristic collections recorded 247 species distributed among 162 genera and 55 families. Fifty-seven percent of the recorded species were of herbaceous or sub-shrubby habit, while the majority of the flora was of the therophytic life-form. Biogeographic analyses revealed that the study sites differ from typical Cerrado in flora and life-form spectra and have closer floristic relationships with Caatinga vegetation. The presence of floristic elements from the Cerrado, together with species from the Caatinga, in the study sites allows us to conclude that these savanna enclaves in the Caatinga are composed of a mixed flora with typical elements of these two Brazilian biomes.

Keywords: Brazil, Cerrado, floristics, savanna, semiarid, therophytes, vegetation comparisons

Introduction

Savannas are a group of phytophysionomies dominated by open habitats, where trees and shrubs are found sparsely distributed in the landscape and the ground is covered by a continuous herbaceous layer, often associated with natural fires (Eiten 1982; Pennington *et al.* 2006; Walter *et al.* 2008; Townsend *et al.* 2009). This vegetation typically occurs

under seasonal climate where rainfall is more regular and the dry season is less strong than in deciduous Seasonally Dry Forests (Pennington *et al.* 2006). In South America there are large expanses of savannas: the central Brazilian Cerrado, the Llanos between Venezuela and Colombia, the Gran Sabana in Venezuela, and the savannas of Northern Brazil and the Southern Guianas. The second largest biome in Brazil, the Cerrado, is represented by savannas with large numbers of endemic plant taxa (Eiten 1982; Ratter

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et al. 1997; Pennington *et al.* 2006; BFG 2015). The families with the largest number of species in the Cerrado flora are Fabaceae, Malpighiaceae, Myrtaceae, Melastomataceae, Poaceae and Rubiaceae. Nevertheless, in some localities, the vegetation can be dominated by species of *Vochysiaceae* (Ratter *et al.* 1997). The Brazil Flora Group's current data (BFG 2018) listed 33,099 angiosperm species for the whole of Brazil and, of these, 12,113 were recorded for the Cerrado biome, with 7,800 species listed for the cerrado *s.s.* vegetation (Souza *et al.* 2018).

The Brazilian Cerrado occupies a large area of central Brazil, also extending to Bolivia and Paraguay. It has very diversified and dynamic vegetation types and, according to the fire regime and substrate in each locality, physiognomies can vary from open grasslands (*campos limpos*, *campos sujos*, *campos brejosos*) to ecotonal forests known as *cerradão* and gallery forests (Eiten 1972; Gibbs *et al.* 1983; Ratter *et al.* 1997; Harley *et al.* 2005; Coutinho 2016). The most characteristic vegetation of the Cerrado domain is the cerrado *sensu stricto* (referred to as cerrado *s.s.* from here onwards), represented by a savanna with widely spaced shrubs and trees usually between 2-8 m height, displaying twisted and thickened, corky trunks, while the soil is covered by an herbaceous layer with a predominance of Poaceae and Cyperaceae and dicotyledoneous shrubs often with lignotuberous root systems (Eiten 1982; Gibbs *et al.* 1983; Ratter *et al.* 1997).

Apart from the 'core' area, savannas with species typical of the cerrado *s.s.* vegetation also occur in disjunct patches in other biomes in the Northern, Northeastern, Southeastern and Southern regions of Brazil (Eiten 1972; Ratter *et al.* 2003). Along the coastal environments of Brazil, the coastal savannas (Castro 1994; Castro & Martins 1999; Moro *et al.* 2011) appear to be associated with the tablelands of the *Formação Barreiras*, a flat 400 mya deposit in the coastal geomorphological unit found from Amapá to Rio de Janeiro states (Araí 2006; Balsamo *et al.* 2010) that is sometimes referred to as the *tabuleiros costeiros* (Castro 1994).

The best studied disjunct patches of savanna are those embedded within the Amazonian Rainforest biome (Devecchi *et al.* 2020). Biogeographical studies have shown that, although these sites have a typical savanna physiognomy and share very characteristic species with the cerrado vegetation of Central Brazil (like species of *Byrsonima*, *Qualea*, *Salvertia* and other genera), these patches of open habitats within the rainforest differ floristically from core cerrado sites, with a predominance of widespread and Amazonian species and a high species turnover from site to site (Devecchi *et al.* 2020).

Less studies are available for the savanna enclaves found within the semiarid Caatinga biome (caatinga-savannas hereafter). In Northeastern Brazil, savannas are found in the Chapada Diamantina (Bahia State), Chapada do Araripe (Ceará State) and in other areas of Bahia, Piauí, Ceará, Rio

Grande do Norte and Paraíba states (Figueiredo 1989; Costa *et al.* 2004; Juncá *et al.* 2005; Oliveira *et al.* 2012; Moro *et al.* 2015; 2016; Queiroz *et al.* 2017). While these caatinga-savannas appear to have floristic ties with the Cerrado of central Brazil, they also have species typical of the semiarid Caatinga (Castro 1994; Castro & Martins 1999).

Despite sharing the same macroclimate of the Caatinga, where the mean annual precipitation is less than 1000 mm with a longer, less predictable and more dramatic dry season than the Cerrado core area, the caatinga-savannas found in Northeastern Brazil develop on poor and acidic soils and are subject to wild fires (Moro *et al.* 2016; Queiroz *et al.* 2017). For example, the Chapada Diamantina and the Chapada do Araripe present a variety of substrates that support diverse plant physiognomies. In the Chapada Diamantina the areas of cerrado occur on clay soils while in the Chapada do Araripe the *cerradão* forests are found on oxisols, a class of soil constituted from mineral material that ranges from imperfectly to heavily drained, and that are naturally acidic and variable in depth (Costa *et al.* 2004; Rocha *et al.* 2005; Ribeiro-Silva *et al.* 2012; Santos *et al.* 2018).

Among the characteristic species commonly found between the typical cerrado and these caatinga savanna sites are *Bowdichia virgilioides*, *Curatella americana*, *Byrsonima crassifolia*, *Hancornia speciosa*, *Hymenaea*, *Salvertia convallariodora* and *Vatairea macrocarpa* (Costa *et al.* 2004; Moro *et al.* 2011; Oliveira *et al.* 2012; Moro *et al.* 2015; Silva-Moraes *et al.* 2018). All of these were listed as very widespread Cerrado species by Ratter & Dargie (1992) and Ratter *et al.* (2003). On the other hand, these Northeastern cerrados are also home to species that are commonly found in the Caatinga, such as *Centrosema brasilianum*, *Chamaecrista flexuosa*, *Cochlospermum vitifolium* and *Pityrocarpa moniliformis* (Castro 1994; Moro *et al.* 2011; Oliveira *et al.* 2012; Moro *et al.* 2014).

Mentions of Cerrado enclaves in Northeastern Brazil were made by several authors (Eiten 1982; Castro 1994; Castro & Martins 1999; Ratter & Dargie 1992; Ratter *et al.* 2003), together with putative floristic elements that might characterize them. Castro (1994) attempted to establish a relationship between such 'Cerrado areas' in Northeastern Brazil with the core Cerrado biome and showed floristic and phytosociological differences between cerrado areas from Piauí and São Paulo. While analysing the Cerrado as a whole, Ratter *et al.* (2003) have shown that the Northeastern Brazilian areas formed a cohesive group; however, the relationship between the caatinga vegetation with caatinga-savannas and the cerrado vegetation was not investigated further. The present work aims to document the flora of four caatinga-savanna enclaves and increase our understanding of the biogeographical links of these caatinga-savannas with typical cerrado and caatinga sites, evaluating their biogeographical relationships.



Materials and methods

Study area

The caatinga-savannas sampled by this study are located in the northeastern region of Ceará state, in the municipalities of Granja and Martinópolis (Fig. 1). The coordinates of the localities studied are listed in Table 1. The predominant climate in the municipalities is hot tropical mild semiarid, varying to hot tropical sub-humid at the limits of Granja with the Ibiapaba highlands, and hot tropical semiarid in Martinópolis, close to the central Ceará lowlands (IPECE 2007). The average annual temperature is around 27°C with an average annual precipitation of 1.115 mm in Granja and 1.009 in Martinópolis (FUNCEME 2019).

The localities studied in Granja (S1, S2 and S3) (Figs. 2A-C), comprise sandy, clay and stony soils. The vegetation physiognomies of these localities vary from open savannas similar to the *cerrado sensu stricto* (*cerrado s.s.*), according to the classification of Walter *et al.* (2015), from transition

zones between Caatinga-Cerrado, to forested physiognomies similar to more densely woody, ecotonal *cerradão* forests. S1 has soils ranging from sandy to clay, the herbaceous layer is well developed, and the trees and shrubs are sparsely distributed throughout the landscape. S2 is located over a quartzitic rock outcrop and it is a principal area of Caatinga-Cerrado ecotone studied. S3 is characterised by sandy and stony, lateritic soil with rocks formed in a process of intense weathering from the mother-rock, and rich in Fe and Al (Costa 1991). The study area in Martinópolis (S4) (Fig. 2D) has predominantly sandy soils that are stony in some sections, and support arboreal vegetation resembling a *cerradão*.

Floristic survey

Fertile plant specimens were collected in the four caatinga-savannas in expeditions carried out between May 2016 and August 2019. Appropriate herborization techniques were followed (Mori *et al.* 1989) and the herbarium samples were deposited in the Herbarium 'Professor Francisco José de Abreu Matos' (HUVA) of

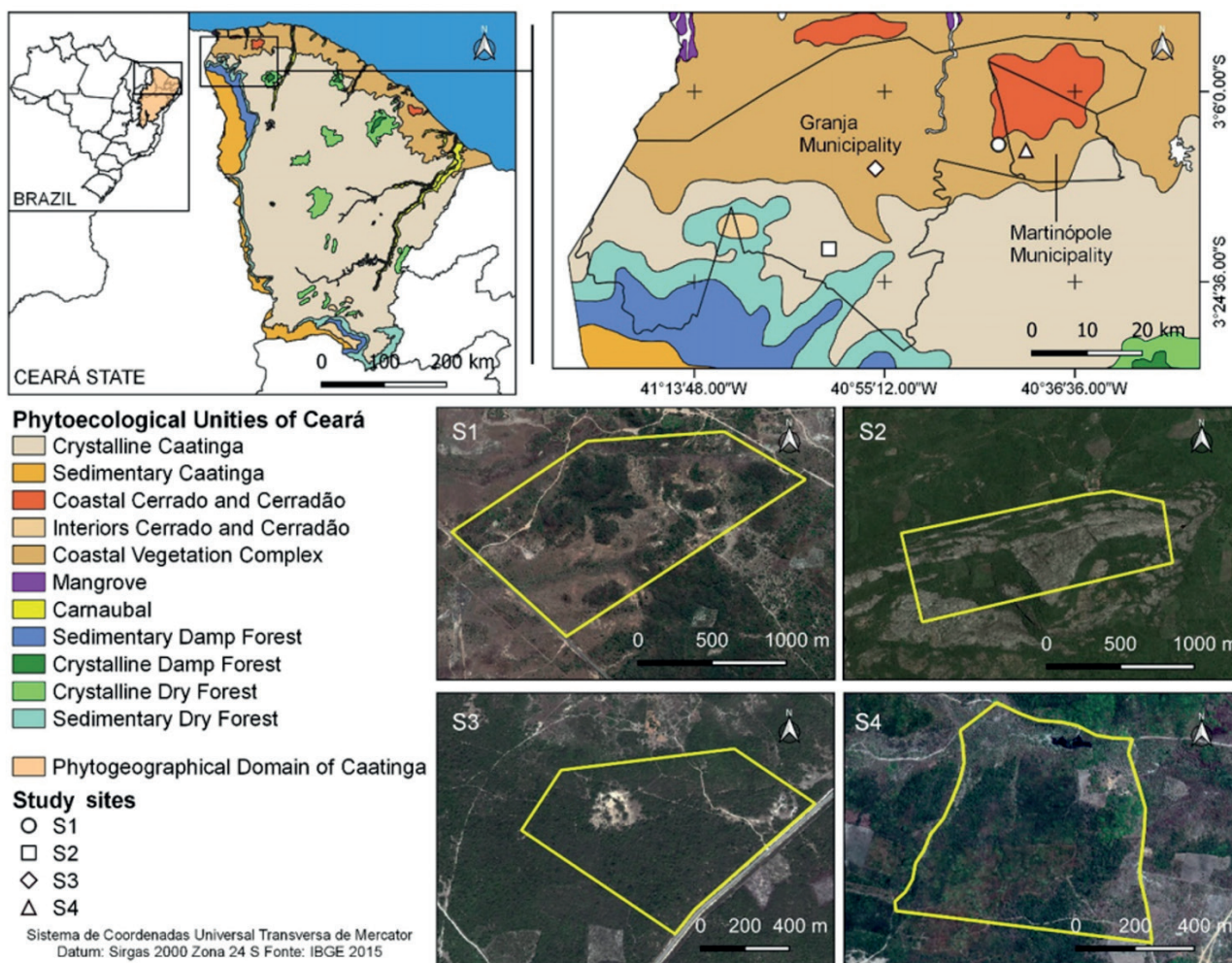


Figure 1. Location of the study areas in the municipalities of Granja and Martinópolis in Northern Ceará, Brazil. Source of satellite images: Google Earth 2020.

the Vale do Acaraú State University (UVA). Duplicates, when available, were sent to the herbaria EAC and HUEFS (herbarium acronyms according to Thiers 2021, continuously updated).

We consulted the relevant literature, such as the monographs of the Flora of Ceará (Menezes *et al.* 2013; Soares-Neto *et al.* 2014; Lima *et al.* 2018; Nepomuceno *et al.* 2018) and specialized taxonomic databases - Flora do Brasil 2020 (Flora do Brasil 2020 2019) and CRIA (2019), to identify the specimens. Plant specialists in the families Asteraceae, Bignoniaceae, Cyperaceae, Euphorbiaceae, Poaceae and Rubiaceae were consulted. Family circumscriptions follow the classification proposed by APG IV (2016), except for the Turneraceae, which was recognised as distinct from Passifloraceae (see Tokuoka

2012). Species names, their respective authors, geographic distribution and endemism are in accordance with BFG (2018). In addition, we classified each species into Raunkiaer life-forms to obtain the biological spectrum of the areas (Martins & Batalha 2011). The classification of Raunkiaer's life-forms follows the classification of Martins & Batalha (2011) and was observed in the field. When the life-form could not be defined *in situ*, data from the literature were consulted to determine the appropriate life-form.

To compare the life-form spectra of our sites with other vegetation types, we used an ordination analyses (NMS – non-metric multidimensional scaling using Eucliden distances) to contrast the spectra we compiled in our study sites with the spectra of other biomes, as compiled by Costa *et*

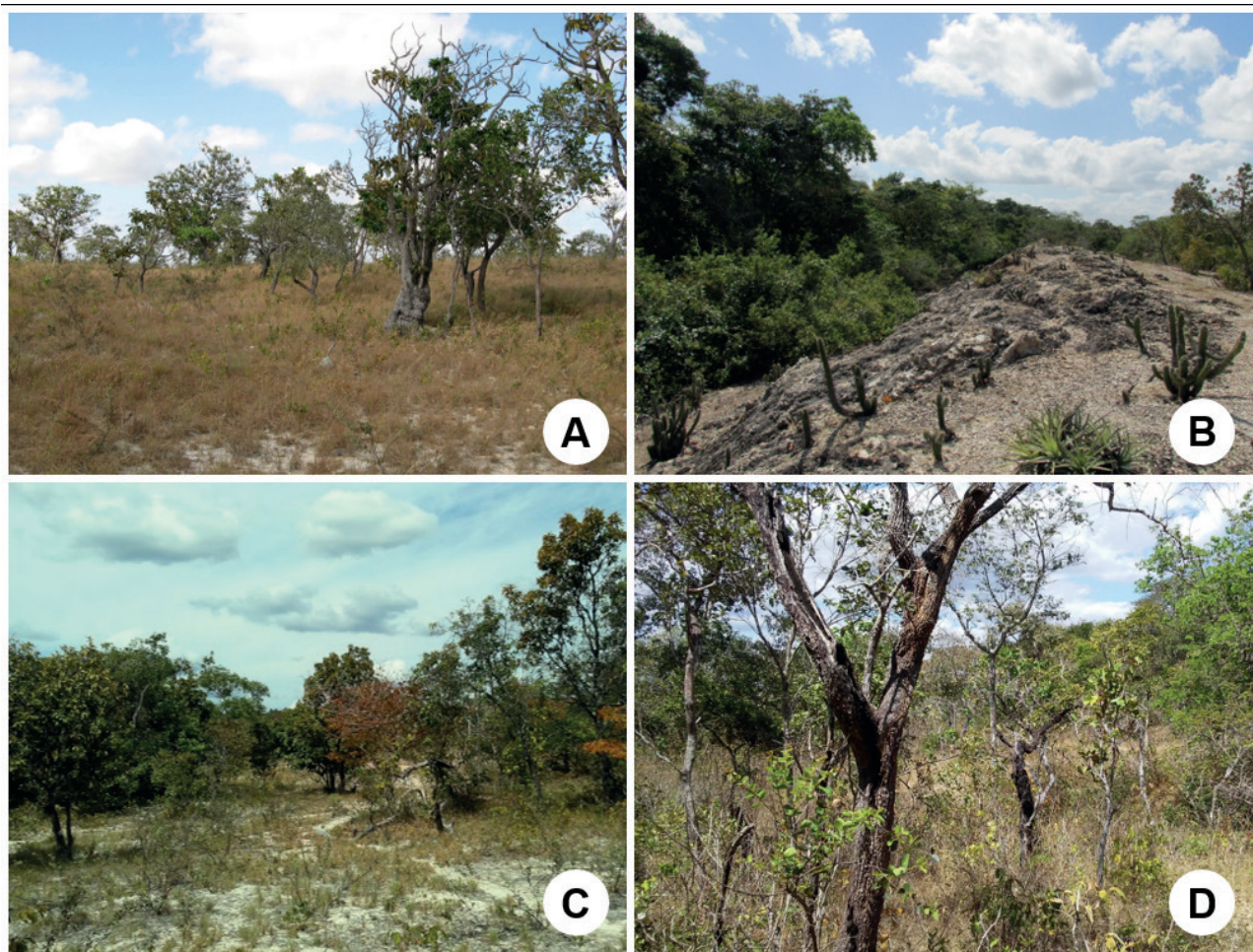


Figure 2. Landscapes of the study areas in Granja (**A**, **B**, **C**) and Martinópolis (**D**) in Northern Ceará. Granja, CE **A**) S1; **B**) S2; **C**) S3, Martinópolis **D**) S4. Photographs: **A-B**) E.B. Souza, **C-D**) I.V. Nepomuceno.

Table 1. Location, acronyms, vegetation type and geographical coordinates of the study areas.

Municipality	Location	Acronym	Vegetation	Coordinates
Granja	Papagaios	S1	Open savanna	03°11'11" S, 40°44'35" W
	São Miguel	S2	Ecotone between a savanna and typical caatinga vegetation	03°21'32" S, 41°01'24" W
	Vereda dos Tomás	S3	Savanna (both open and arboreal)	03°13'33" S, 40°55'49" W
Martinópolis	Bom Princípio	S4	Tall savanna (similar to arboreal cerrado, the <i>cerradão</i>)	03°11'51" S, 40°41'04" W

al. (2016) (<https://doi.org/10.6084/m9.figshare.12755876>, Tab. S1 in supplementary material).

Biogeographical analyses

We built a database with floristic lists of sites harbouring caatinga-savannas, typical caatinga and typical cerrado vegetation (<https://doi.org/10.6084/m9.figshare.12755876>, Tab. S2 in supplementary material). We only selected from the literature studies that included both woody (trees and shrubs) and non-woody (herbs and subshrubs) plant species. We then performed grouping (UPGMA - unweighted arithmetic average) analyses using Bray-Curtis distance (Gotelli & Ellison 2011; Legendre & Legendre 2012) to compare the general floristic resemblance between sites.

We made the UPGMA analyses for the woody component and also for the non-woody component in order to evaluate whether each vegetation layer has or has not different floristic affinities (<https://doi.org/10.6084/m9.figshare.12755876>, Tab. S2 in supplementary material). Lianas were removed from the analyses, because it was not possible to differentiate between woody and non-woody climbers using the Flora do Brasil 2020 (2019) database. We also compared the flora of caatinga-savannas, caatinga and cerrado sites using Venn diagrams for the woody and non-woody components using Venny 2.1 (<https://bioinfo.pcnb.csic.es/tools/venny/>).

Results

We recorded 246 species in the four sites, comprised of 162 genera and 55 families (Tab. 2, Fig. 3). The family Fabaceae (49 spp.), Rubiaceae (19 spp.), Convolvulaceae (17 spp.), Poaceae (11 spp.), Cyperaceae (10 spp.), Asteraceae (9 spp.), Lamiaceae (9 spp.) and Malvaceae (8 spp.) were the richest families, and represented 53.4 % of the flora. The genera *Ipomoea* and *Mimosa*, each with seven species, stood out as the most diverse, followed by *Borreria*, with six species and *Chamaecrista* and *Combretum* with five species each. Within the general flora, we found *Borreria* sp. nov., a new species yet to be described and 76 species endemic to Brazil, of which six are recorded only for Northeastern Brazil: *Stilpnopappus cearensis*, *Croton anisodontus*, *Mimosa ulbrichiana*, *Schultesia angustifolia*, *Hexasepalum gardneri* (and *Mitracarpus fernandesii* (BFG 2018).

Only six species were recorded in all four study areas: *Combretum laxum*, *Ipomoea eriocalyx*, *Cyperus schomburgkianus*, *Curatella americana*, *Bauhinia unguolata* and *Qualea parviflora*. In contrast with the small number of species occurring in the four areas, 158 species were collected only in one locality, 53 exclusive to S1, 52 in S2, 20 in S3 and 33 in S4.

The non-woody component represented 56.9 % of the total flora, with 113 herbaceous species and 27 sub-

shrubby species (Fig. 4). The woody component, with trees and shrubs, is constituted by 82 species. The shrubs vary between 1-6 m in height and mostly belong to the Fabaceae (6 spp.), Combretaceae (5 spp.) and Rubiaceae (5 spp.), while the trees, ranging in size from 2-12 m height, belong to the Fabaceae (15 spp.), Ochnaceae (4 spp.) and *Vochysiaceae* (4 spp.). Significant numbers of vines were recorded in our sites, 24 species in total, mainly Bignoniaceae (9 spp.) and Convolvulaceae (7 spp.).

Analysing the composition of the vegetation of each area separately, we observed the high richness of herbaceous species in the open habitats S1, S2, and S3, where herbs and subshrubs represent the majority of the flora (Fig. 4). Only in S4 it is possible to observe a similar number of herbaceous and tree species, 33 and 38 species, respectively, because this site has more closed vegetation. The climbers are divided between woody (9 spp.) and herbaceous climbers (15 spp.) and were recorded in higher numbers in S3.

The UPGMA analyses of separate life-forms has demonstrated that the flora of the savannas in the Caatinga is more closely related to the Caatinga biome than to the Cerrado biome. The grouping analysis of the woody component showed that all these caatinga-savannas formed a group, and that this group was closer to the caatinga vegetation than to the cerrado vegetation. An exception was the caatinga-savanna of the Chapada do Araripe, where the woody flora shares more species with the Cerrado (Fig. 5). The non-woody species displayed a similar pattern, with the caatinga-savannas being closer to the caatinga vegetation than to the cerrado vegetation, despite sharing some species with the cerrado (Fig. 6).

The Venn diagram shows that the savannas in the Caatinga have more species in common with the caatinga vegetation than with the cerrado (Fig. 7). In the database used here the caatinga-savannas shared 39 woody species with the cerrado vegetation, while 60 species are exclusive to these areas and 38 are shared with the caatinga vegetation (either on crystalline or sedimentary substrates) (Fig. 7A). In the Venn diagram for non-woody species, only 13 species from the caatinga-savannas are shared with the cerrado, while 22 species are shared with the caatinga and 90 are exclusive from the latter (Fig. 7B).

In order to document the structure of these sites, we recorded the Raunkier life-forms and observed that the therophytes, plants survive the drought in the form of seeds (Martins & Batalha 2011), represent the majority of the local flora (42.2 %), with 104 species (Fig. 8). The phanerophytes, species with buds exposed over 50 cm above the ground (Martins & Batalha 2011), represented the second largest group of species: 72 in total (29.3 %). Hemicyptophytes, plants that protect their buds at ground level, had 36 records totalling 14.6 %. A total of 25 species was classified as chamaephytes, individuals with buds that are protected between 50 cm and just above ground level (Martins & Batalha 2011), representing 10.2 % of the total.



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Table 2. Lists the species recorded in the caatinga savannas in the Caatinga of Northern Ceará. Th – Therophytes, Cr – Cryptophytes, He – Hemicryptophytes, Ch – Chamaephytes, Ph – Phanerophytes, PN - Popular Name, END – Endemism, BR – Endemic from Brazil, NE – Endemic from Northeastern Brazil, S1, S2 and S3 - Areas situated in the municipality of Granja - CE, S4 - Area situated in the municipality of the Martinópolis - CE. Collectors: EBS – Elnatan Bezerra de Souza, FAAN – Francisco Álvaro Almeida Nepomuceno, IVN – Izaíra Vasconcelos Nepomuceno.

Family	Species	Habit	Life-forms	PN	End	Occurrence				Voucher
						S1	S2	S3	S4	
Acanthaceae	<i>Elytraria imbricata</i> (Vahl.) Pers.	Herb	Th	-	-				X	EBS 5819
	<i>Ruellia paniculata</i> L.	Shrub	Th	melosa-roxa	-			X	X	EBS 5799, 4728
Amaranthaceae	<i>Gomphrena gardneri</i> Moq.	Herb	He	-	BR				X	EBS 5144
Amaryllidaceae	<i>Habranthus sylvaticus</i> Herb.	Herb	Cr	cebola-de-calango	BR	X				EBS 3754
Anacardiaceae	<i>Anacardium occidentale</i> L.	Tree	Ph	cajú	-		X	X		EBS 3159, 5790
	<i>Astronium fraxinifolium</i> Schott.	Tree	Ph	-	-				X	EBS 5818
Annonaceae	<i>Ephedranthus pisocarpus</i> R.E.Fr.	Tree	Ph	conduru	BR				X	EBS 4715
Apocynaceae	<i>Allamanda blanchetii</i> A.DC.	Tree	Ch	alamanda-roxa	BR	X				EBS 5044
	<i>Aspidosperma multiflorum</i> A.DC.	Tree	Ph	-	BR		X			EBS 5439
	<i>Himatanthus drasticus</i> (Mart.) Plumel.	Tree	Ph	janaguba	BR				X	EBS 3741
	<i>Mandevilla tenuifolia</i> (J.C. Mikan) Woodson	Subshrub	Th	jalapa-do-campo	-		X			EBS 3400
	<i>Tabernaemontana catharinensis</i> A.DC.	Tree	Ph	leiteiro	-		X			EBS 4471
Araceae	<i>Philodendron acutatum</i> Schott.	Herb	Ep	imbis	-		X			EBS 5758
	<i>Taccarum ulei</i> Engl. & K. Krause	Herb	Th	milho-de-cobra	BR				X	EBS 5163
Areceaceae	<i>Bactris major</i> Jacq.	Tree	Ph	tucum	-		X			EBS 5761
	<i>Copernicia prunifera</i> (Mill.) H.E. Moore	Tree	Ph	carnaúba	BR	X			X	IVN 99, EBS 5839
Asteraceae	<i>Aspilia bonplandiana</i> (Gardner) S.F.Blake	Herb	Th	margarida	BR		X	X		EBS 5752, 3621
	<i>Bidens pilosa</i> L.	Herb	Th	picão-preto	-		X			EBS 3398
	<i>Elephantopus hirtiflorus</i> DC.	Herb	He	língua-de-vaca	BR	X	X	X		EBS 3588, 5753, 3622
	<i>Lepidaploa</i> sp.	Herb	Th	-	-		X			EBS 4145
	<i>Pectis brevipendunculata</i> (Gardner) Sch.Bip.	Herb	Th	chá-de-moça	BR		X			EBS 3379
	<i>Praxelis diffusa</i> (Rich.) Pruski	Herb	Th	cambará	-		X			EBS 4103
	<i>Stilpnopappus cearensis</i> Huber	Herb	Th	-	NE	X				EBS 3605
	<i>Stilpnopappus pratensis</i> Mart. ex DC.	Herb	Th	-	BR	X		X	X	EBS 3485, 3487, 4730
	<i>Stilpnopappus trichospiroides</i> Mart. ex. DC.	Herb	Th	-	BR			X		EBS 3629
Bignoniaceae	<i>Adenocalymma subsessilifolium</i> DC.	Shrub	Ph	-	BR			X		EBS 3628
	<i>Adenocalymma validum</i> L.G. Lohmann	Climber	Ph	-	-				X	EBS 4713
	<i>Fridericia dispar</i> (Bureau ex K.Schum) L.G. Lohmann	Shrub	Ch	cipó-de-boi	BR		X			EBS 4126
	<i>Fridericia limae</i> (A.H. Gentry) L.G.Lohmann	Climber	Ch	cipó-de-bola	NE		X	X	X	EBS 5742, 5769, 5828
	<i>Fridericia platyphylla</i> (Cham.) L.G.Lohmann	Climber	Ch	cipó-una	-		X			EBS 3382
	<i>Fridericia subverticillata</i> (Bureau & K. Schum.) L.G. Lohmann	Climber	Ch	-	BR				X	EBS 4714
	<i>Fridericia triplinervia</i> (Mart. ex. DC.) L.G.Lohmann	Climber	Ch	-	-			X		EBS 3643
	<i>Neojobertia candolleana</i> (Mart. ex. DC.) Bureau & K. Schum.	Climber	Ph	-	BR			X		EBS 3635
Bixaceae	<i>Cochlospermum vitifolium</i> (Willd) Spreng	Tree	Ph	pacotê	-		X		X	FAAN 43, EBS 5809
Boraginaceae	<i>Cordia rufescens</i> A.DC.	Shrub	Ph	grão-de-galo	-	X				EBS 4926
Bromeliaceae	<i>Bromelia laciniosa</i> Mart. ex Schult. f.	Herb	He	macambira	BR		X			EBS 5762
	<i>Encholirium spectabile</i> Mart. ex Schult. & Schult.f.	Herb	He	macambira-de-flecha	BR		X			EBS 3158



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Table 2. Cont.

Family	Species	Habit	Life-forms	PN	End	Occurrence				Voucher
						S1	S2	S3	S4	
Cactaceae	<i>Cereus jamacaru</i> DC.	Tree	Ph	mandacaru	BR				X	EBS 5840
	<i>Pilosocereus catingicola</i> (Gürke) Byles & Rowley	Shrub	Ph	facheiro	BR				X	EBS 5841
	<i>Xiquexique gounellei</i> (F.A.C.Weber) Lavor & Calvente	Shrub	Ph	xique-xique	BR		X			EBS 5720
Chrysobalanaceae	<i>Hirtella ciliata</i> Mart. & Zucc	Tree	Ph	-	-	X			X	EBS 3164, 5836
Combretaceae	<i>Buchenavia tetraphylla</i> (Aubl.) R.A.Howard	Tree	Ph	perquiteira	-		X			EBS 4158
	<i>Combretum glaucocarpum</i> Mart.	Shrub	Ph	sipaúba, vaqueta	-		X			EBS 3385
	<i>Combretum hilarianum</i> D. Dietr.	Shrub	Ph	imbirdiba	-	X				EBS 3464
	<i>Combretum laxum</i> Jacq.	Shrub	Ph	cipó-de-bugio	-	X	X	X	X	EBS 4184, 5440, 5768, 4725
	<i>Combretum leprosum</i> Mart.	Shrub	Ph	mufumbo	-		X		X	EBS 4147, 5821
	<i>Combretum mellifluum</i> Eichler	Shrub	Ph	sipaúba	-		X			FAAN 37
Convolvulaceae	<i>Cuscuta racemosa</i> Mart.	Herb	He	cipó-chumbo	-	X		X		EBS 5222, 3466
	<i>Distimake cissoides</i> (Lam.) A.R. Simões & Staples	Climber	Th	-	-			X		EBS 3632
	<i>Evolvulus ericifolius</i> Mart. ex. Schrank.	Herb	Th	-	BR	X		X		EBS 5051, 3748
	<i>Evolvulus glomeratus</i> Ness. & Mart.	Subshrub	Th	azulzinha	-	X				EBS 5052
	<i>Evolvulus gypsophiloides</i> Moric.	Herb	Th	-	BR	X				EBS 4186
	<i>Evolvulus ovatus</i> Fernauld	Herb	Th	azulzinha	-	X	X	X		EBS 5684, 4112, 3499
	<i>Ipomoea asarifolia</i> (Ders.) Roem. & Schult.	Climber	Th	salsa	-			X	X	EBS 3496, 5810
	<i>Ipomoea bahiensis</i> Willd ex. Roem. & Schult.	Climber	Th	jetirana	BR		X			EBS 4107
	<i>Ipomoea bignonioides</i> Sims	Climber	Th	-	-				X	EBS 5164
	<i>Ipomoea calyprata</i> Dammer	Climber	Th	-	BR			X	X	EBS 5058, 5162
	<i>Ipomoea ericalyx</i> (Mart. ex. Choisy) Meisn.	Climber	Th	-	BR	X	X	X	X	EBS 5246, 4138, 3618, 5812
	<i>Ipomoea piurensis</i> O'Donell	Climber	Th	-	-			X		EBS 3497
	<i>Ipomoea subincana</i> (Choisy) Meisn.	Climber	Ph	-	BR	X		X		EBS 3423, 3620
	<i>Jacquemontia gracillima</i> Choisy	Herb	Th	jetirana	BR	X	X			EBS 3471, 4162
	<i>Jacquemontia gracilis</i> Choisy	Herb	Th	-	BR	X				EBS 3579
	<i>Jacquemontia tamnifolia</i> (L.) Griseb.	Herb	Th	-	-		X			EBS 4106
	<i>Operculina hamiltonii</i> (G. Don.) D.F.Austin & Stalpes	Climber	Cr	batatão	-			X		EBS 3498
Cyperaceae	<i>Bulbostylis capillaris</i> (L.) C.B. Clarke	Herb	He	-	-				X	EBS 5155
	<i>Bulbostylis conifera</i> (Kunth) C.B. Clarke	Herb	He	-	-	X				EBS 4930
	<i>Bulbostylis junciformis</i> (Kunth) C.B. Clarke	Herb	He	-	-	X				EBS 5041
	<i>Cyperus amabilis</i> Vahl.	Herb	Th	-	-				X	EBS 5134
	<i>Cyperus sesquiflorus</i> (Torr.) Mattf. & Kük.	Herb	He	junquinho	-				X	EBS 5137
	<i>Cyperus schomburgkianus</i> Ness.	Herb	He	tiririca	-	X	X	X	X	EBS 3477, 5348, 3492, 5145
	<i>Fimbristylis dichotoma</i> (L.) Vahl	Herb	He	-	BR	X			X	EBS 5239, 5169



Table 2. Cont.

Family	Species	Habit	Life-forms	PN	End	Occurrence				Voucher
						S1	S2	S3	S4	
Cyperaceae	<i>Rhynchospora holoschoenoides</i> (Rich.) Herter	Herb	He	-	-	X				EBS 3476
	<i>Rhynchospora nervosa</i> (Vahl) Boeckeler	Herb	Cr	capim-estrela	BR	X				EBS 4916
	<i>Scleria hirtella</i> Sw.	Herb	Cr	-	-	X				EBS 5248
Dilleniaceae	<i>Curatella americana</i> L.	Tree	Ph	lixreira	-	X	X	X	X	IVN 100, EBS 5434, 5770, 4718
	<i>Davilla cearensis</i> L.	Climber	Ch	-	BR		X			EBS 3160
Droseraceae	<i>Drosera sessilifolia</i> A.St.-Hil.	Herb	Th	-	-		X			EBS 5355
Eriocaulaceae	<i>Paepalanthus lamarckii</i> Kunth.	Herb	Th	-	-		X			EBS 4141
	<i>Paepalanthus cf. tortilis</i> (Bong.) Mart.	Herb	Th	-	BR		X			EBS 5345
Erythroxylaceae	<i>Erythroxylum laetevirens</i> O.E. Schulz.	Shrub	Ch	-	BR			X		EBS 5061
Euphorbiaceae	<i>Croton anisodontus</i> Müll.Arg.	Shrub	Ch	-	NE	X	X	X		EBS 5047, 4464, 5795
	<i>Croton glandulosus</i> L.	Herb	Th	carvão-branco	-				X	EBS 5156
	<i>Dalechampia scandens</i> L.	Climber	Th	-	-			X		EBS 3640
	<i>Euphorbia bahiensis</i> (Klotzsch & Garke) Boiss.	Herb	Th	-	-		X			EBS 3394
	<i>Microstachys corniculata</i> (Vahl.) Griseb.	Herb	Th	-	-	X				EBS 4483
	<i>Microstachys hispida</i> (Mart. & Zucc.) Govaerts	Herb	Th	-	-	X				EBS 3417
Fabaceae	<i>Aeschynomene benthamii</i> (Rudd.) Afr.Fern.	Subshurb	Th	-	BR	X				EBS 3592
	<i>Aeschynomene filosa</i> Mart.	Subshurb	He	-	-	X				EBS 5243
	<i>Aeschynomene histryx</i> Poir.	Herb	Th	-	-	X	X	X		EBS 3457, 3374, 3615
	<i>Aeschynomene mollicula</i> Kunth.	Subshurb	Th	-	-	X				EBS 5242
	<i>Amburana cearensis</i> (Allemão) A.C. Sm.	Tree	Ph	cumaru	-		X			EBS 5354
	<i>Andira cordata</i> Arroyo ex R.T. Penn. & H.C. Lima	Tree	Ph	-	BR				X	EBS 5830
	<i>Arachis dardani</i> Kaprov. & W.C. Greg.	Herb	Th	amendoim-de-carcará	BR	X				EBS 3375
	<i>Arachis pusilla</i> Benth.	Herb	Th	-	BR		X			EBS 4458
	<i>Bauhinia acuruana</i> Moric.	Shrub	Ch	-	BR		X			EBS 5357
	<i>Bauhinia cheilantha</i> (Bong.) Steud.	Shrub	Ch	-	-		X			EBS 5366
	<i>Bauhinia unguolata</i> L.	Shrub	Ph	pata-de-vaca	-	X	X	X	X	EBS 3155, 5743, 5775, 4721
	<i>Bowdichia virgilioides</i> Kunth.	Tree	Ph	sucupira	-	X				EBS 3152
	<i>Calopogonium mucunoides</i> Desv.	Climber	Th	-	-	X				EBS 5321
	<i>Centrosema brasilianum</i> (L.) Benth.	Climber	Th	centrosema	-	X	X			EBS 3601, 5749
	<i>Centrosema pascuorum</i> Mart. ex. Benth.	Climber	Th	centrosema, jetirana	-	X		X		EBS 5335, 3490
	<i>Chamaecrista diphylla</i> (L.) Greene	Herb	Th	-	-	X				EBS 3369
	<i>Chamaecrista flexuosa</i> (L.) Greene	Subshrub	He	-	-	X	X	X		EBS 5228, 3373, 5801
<i>Chamaecrista linearis</i> (H.S. Irwin & Barneby) Afr.Fern. & E.P. Nunes	Subshrub	Te	-	-	X				EBS 5319	



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Table 2. Cont.

Family	Species	Habit	Life-forms	PN	End	Occurrence				Voucher
						S1	S2	S3	S4	
Fabaceae	<i>Chamaecrista rotundifolia</i> (Pers.) Greene	Herb	Th	-	-	X	X			EBS 5240, 4457
	<i>Chamaecrista supplex</i> (Benth.) Britton & Ross ex Britton & Killip.	Herb	Th	-	-		X			EBS 4117
	<i>Chloroleucon foliolosum</i> (Benth.) G.P.Lewis	Tree	Ph	arapiraca	-		X			EBS 5721
	<i>Copaifera martii</i> Hayne	Tree	Ph	pau-d'óleo	-				X	EBS 5820
	<i>Dalbergia cearensis</i> Ducke.	Shrub	Ph	jacarandá-violeta	BR				X	EBS 5148
	<i>Dimorphandra mollis</i> Benth.	Tree	Ph	fava-danta	-			X		EBS 5779
	<i>Galactia jussiaeana</i> Kunth	Subshrub	He	-	-	X	X	X		EBS 4488, 4462, 3624
	<i>Hymenaea stigonocarpa</i> Mart. ex Hayne	Tree	Ph	jatobá-do-cerrado	-				X	EBS 5714
	<i>Machaerium acutifolium</i> Vogel.	Tree	Ph	jacarandá-do-campo	-				X	EBS 5817
	<i>Macroptilium lathyroides</i> (L.) Urb.	Climber	Ch	feijão-de-rola	-	X				EBS 5241
	<i>Mimosa camporum</i> Benth.	Subshrub	Th	-	-	X				EBS 4487
	<i>Mimosa hirsutissima</i> Mart.	Subshrub	Th	-	-	X			X	EBS 5229, 5153
	<i>Mimosa misera</i> Benth.	Subshrub	Th	-	BR	X				EBS 3467
	<i>Mimosa modesta</i> Mart.	Subshrub	Ch	-	BR	X				EBS 3450
	<i>Mimosa pigra</i> L.	Subshrub	Th	calumbi-d'água	-				X	EBS 5158
	<i>Mimosa somnians</i> Humb. & Bonpl. ex. Willd.	Subshrub	Ch	malícia	-	X				EBS 4484
	<i>Mimosa ulbrichiana</i> Harms	Subshrub	Th	-	NE	X		X		EBS 3463, 3489
	<i>Peltogyne confertiflora</i> (Mart. ex Hayne) Benth.	Tree	Ph	jatobá-de-brinco	-		X			EBS 5437
	<i>Piptadenia stipulacea</i> (Benth.) Ducke	Tree	Ph	jurema-branca	BR		X			EBS 5347
	<i>Pityrocarpa moniliformis</i> (Benth) Luckow & R.W.Jobson	Tree	Ph	angico-de-bezerro	BR	X	X	X		EBS 4914, 4467, 5763
	<i>Plathymenia reticulata</i> Benth.	Tree	Ph	candeia	-	X			X	EBS 5236, 5827
	<i>Senna alata</i> (L.) Roxb.	Shrub	Ch	fedegoso-gigante, mat- apastão	-		X			EBS 5721
	<i>Senna gardneri</i> (Benth.) H.S.Irwin & Barneby	Subshrub	Ch	-	-	X				EBS 3608
<i>Senna splendida</i> (Vogel) H.S.Irwin & Barneby	Shrub	Ch	-	-			X		EBS 5787	
<i>Senna trachypus</i> (Benth.) H.S.Irwin & Barneby	Shrub	Ch	besouro	BR	X	X	X		EBS 5245, 4120, 3634	
<i>Stryphnodendron coriaceum</i> Benth.	Tree	Ph	barbatimão-do-cerrado	BR				X	EBS 5824	
<i>Stylosanthes angustifolia</i> Vogel	Herb	Th	-	-	X	X			EBS 3448, 4120	
<i>Stylosanthes scabra</i> Vogel	Herb	Th	-	-			X		EBS 3627	
<i>Tephrosia purpurea</i> (L.) Pers.	Herb	He	-	-			X		EBS 3500	
<i>Vatairea sericea</i> (Ducke) Ducke	Tree	Ph	angelim-amargoso	-				X	EBS 5815	
<i>Zornia reticulata</i> Sm.	Herb	He	-	-	X				EBS 4922	
Gentianaceae	<i>Chelonanthus purpurascens</i> (Aubl.) Struwe, S.Nilsson & V.A.Albert	Herb	Th	-	-	X				EBS 4181
	<i>Schultesia angustifolia</i> Griseb	Herb	Th	-	NE	X				EBS 5225
	<i>Schultesia guianensis</i> (Aubl.) Malme	Herb	Th	mata-zombando	-	X				EBS 5223

Table 2. Cont.

Family	Species	Habit	Life-forms	PN	End	Occurrence				Voucher
						S1	S2	S3	S4	
Iridaceae	<i>Cipura paludosa</i> Aubl.	Herb	Cr	alho-do-mato	-	X				EBS 5033
	<i>Trimezia martinicensis</i> (Jacq.) Herb.	Herb	Cr	íris-amarela	-	X			X	EBS 5034, 5131
Krameriaceae	<i>Krameria tomentosa</i> A.St.-Hill.	Subshrub	Ch	carrapicho-de-cavalo	-	X	X		X	EBS 5036, 4463 5146
Lamiaceae	<i>Amasonia campestris</i> (Aubl.) Moldenke	Subshrub	Ch	flor-de-urubu	-	X			X	EBS 4485, 5143
	<i>Cyanocephalus rugosus</i> (Benth.) Harley & J.F.B.Pastore	Subshrub	Ch	-	-	X				EBS 4177
	<i>Eriope macrostachya</i> Mart. ex. Benth.	Herb	He	-	-			X		EBS 3633
	<i>Hyptis salzmannii</i> (Benth.) Harley	Subshrub	He	canela-de-urubu	-	X				EBS 5336
	<i>Hyptis atrorubens</i> Poit.	Subshrub	He	mentinha	-	X	X		X	EBS 5331, 5757, 5833
	<i>Hyptis lanceolata</i> Poir.	Subshrub	He	-	-	X				EBS 5233
	<i>Marsypianthes montana</i> Benth.	Herb	He	alfavaca-de-cheiro	BR	X	X		X	EBS 3475, 4459, 5140
	<i>Rhaphiodon echinus</i> Schauer	Herb	Th	betônica, falsa-menta	BR	X	X	X		EBS 3447, 4176, 3638
Lythraceae	<i>Vitex polygama</i> Cham.	Tree	Ph	tarumã	BR				X	EBS 5838
	<i>Ammannia auriculata</i> Willd.	Herb	Th	-	-	X				EBS 5317
	<i>Cuphea campestris</i> Koehne	Herb	Th	-	-	X	X		X	EBS 4475, 3406, 5138
	<i>Cuphea impatientifolia</i> A.St.-Hill	Herb	Th	-	BR	X			X	EBS 4477, 5154
Malpighiaceae	<i>Byrsonima coccolobifolia</i> Kunth.	Subshrub	Ph	murici-rosa	-		X	X		EBS 5744, 5805
	<i>Byrsonima crassifolia</i> (L.) Kunth.	Tree	Ph	murici-da-praia	-	X		X	X	EBS 4929, 3750, 5268
	<i>Janusia</i> sp.	Shrub	Ph	-			X			EBS 4128
	<i>Peixotoa</i> sp.	Climber	Ch	-			X			EBS 4146
	<i>Stigmaphyllon paralias</i> A.Juss.	Shrub	Ph	-	BR		X	X		EBS 5358, 5063
Malvaceae	<i>Helicteres heptandra</i> L.B.Sm.	Shrub	Ch	saca-rolha	-	X				EBS 5318
	<i>Pavonia cancellata</i> (L.) Cav.	Herb	He	-	-			X	X	EBS 3639, 5808
	<i>Sida ciliaris</i> L.	Herb	Th	-	-	X	X	X		EBS 3442, 4156, 3495
	<i>Sida cordifolia</i> L.	Subshrub	Th	-	-	X	X			EBS 4169, 4123
	<i>Sida linifolia</i> Cav.	Subshrub	Th	-	-			X	X	EBS 5796, 5834
	<i>Sterculia striata</i> A.St.-Hill & Naudin	Tree	Th	chichá	BR		X			EBS 3156
	<i>Waltheria indica</i> L.	Subshrub	He	douradinha	-	X	X	X		EBS 3611, FAAN 40, EBS 3641
<i>Waltheria operculata</i> Rose	Herb	Th	-	-	X	X	X		EBS 3472, 3381, 3493	
Melastomataceae	<i>Comolia villosa</i> (Aubl.) Triana	Herb	He	-	-		X			EBS 4461
	<i>Pterolepis perpusilla</i> (Naudin) Cogn.	Herb	Th	-	BR	X	X			EBS 5322, 5751
Myrtaceae	<i>Campomanesia aromatica</i> (Aubl.) Griseb	Shrub	Ph	guabiraba	-			X		EBS 5057
	<i>Campomanesia dichotoma</i> (O. Berg.) Mattos	Shrub	Ph	guabiraba	BR	X				EBS 4918
	<i>Myrcia guianensis</i> (Aubl.) DC.	Shrub	Ph	araçazinho	-	X			X	EBS 3755, 4726
	<i>Myrcia splendens</i> (Sw.) DC.	Shrub	Ph	guamirim-miúdo	BR		X	X	X	EBS 5435, 5804, 5829
Moraceae	<i>Ficus</i> sp.	Tree	Ph	-			X			EBS 4470



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Table 2. Cont.

Family	Species	Habit	Life-forms	PN	End	Occurrence				Voucher
						S1	S2	S3	S4	
Ochnaceae	<i>Ouratea castaneifolia</i> (DC.) Engl.	Tree	Ph	farinha-seca	-				X	IVN 89
	<i>Ouratea cuspidata</i> (A. St.-Hil.) Engl.	Tree	Ph	-	BR				X	IVN 77
	<i>Ouratea fieldingiana</i> (Garnder) Engl.	Tree	Ph	batiputá	-				X	IVN 81
	<i>Ouratea glaucescens</i> (A.St.-Hil.) Engl.	Tree	Ph	flor-de-ouro	BR			X	X	EBS 3749, 3735
Olacaceae	<i>Ximenia americana</i> L.	Tree	Ph	ameixa	-		X	X	X	EBS 5729, 5786, 3740
Orchidaceae	<i>Habernaria</i> sp.	Herb	Th	-	-			X		EBS 5054
	<i>Trichocentrum cepula</i> (Hoffmanns.) J.M.H.Shaw	Herb	Ep	dama-dançante	-		X			EBS 5759
Orobanchaceae	<i>Agalinis hispidula</i> (Mart.) D'Arcy	Herb	Th	-	-	X	X			EBS 5329, 4132
	<i>Buchnera rosea</i> Kunth	Herb	Th	-	-	X		X		EBS 5325, 3491
Oxalidaceae	<i>Oxalis divaricata</i> Mart. ex Zucc.	Herb	Th	azedinha	BR		X			EBS 4104
	<i>Oxalis psoraleoides</i> Kunth	Herb	Th	trevo	-	X	X			EBS 3670, 4460
Passifloraceae	<i>Passiflora foetida</i> L.	Climber	Th	maracujá-de-cheiro	-	X				EBS 4923
Phytolacaceae	<i>Microtea paniculata</i> Moq.	Herb	Th	-	-		X			EBS 3392
Plantaginaceae	<i>Bacopa angulata</i> (Benth.) Edwall	Herb	Th	-	BR	X	X			EBS 5237, 5360
	<i>Bacopa sessiliflora</i> (Benth.) Edwall	Herb	Th	-	-		X			EBS 5748
	<i>Tetraulacium veroniciforme</i> Turcz.	Herb	Th	-	BR	X	X			EBS 3441, 5756
Poaceae	<i>Andropogon angustatus</i> (J. Presl). Steud	Herb	He	-	-		X			EBS 4122
	<i>Aristida longifolia</i> Trin.	Herb	He	-	-	X				EBS 5320
	<i>Axonopus marginatus</i> (Trin.) Chase	Herb	He	capim-mimoso	-				X	EBS 5157
	<i>Isachne</i> sp.	Herb	Th	-	-		X			EBS 4152
	<i>Mesosetum annuum</i> Swallen	Herb	Th	-	-	X			X	EBS 5038, 5152
	<i>Paspalum maculosum</i> Trin.	Herb	He	canafistula	-	X				EBS 5037
	<i>Paspalum</i> sp.1	Herb	Th	-	-				X	EBS 5135
	<i>Paspalum</i> sp.2	Herb	Th	-	-				X	EBS 5147
	<i>Paspalum</i> sp.3	Herb	Th	-	-				X	EBS 5150
	<i>Streptostachys asperifolia</i> Desv.	Herb	Th	-	-			X	X	EBS 5055, 5159
<i>Trachypogon spicatus</i> (L. f.) Kuntze	Herb	He	-	-	X				EBS 5050	
Polygalaceae	<i>Asemeia</i> cf. <i>monticola</i> (Kunth.) J.F.B. Pastore & J.R. Abbott.	Herb	Th	-	-			X		EBS 5060
	<i>Bredemeyera floribunda</i> Willd.	Tree	Th	botica-inteira	-				X	EBS 4723
	<i>Polygala boliviensis</i> A.W.Benn.	Herb	Th	-	-	X	X			EBS 3488, 3363
	<i>Polygala glochidata</i> Kunth	Herb	Th	-	BR	X				EBS 3407
	<i>Polygala longicaulis</i> Kunth	Herb	Th	-	BR	X				EBS 5049
Rhamnaceae	<i>Polygala trichosperma</i> Jacq.	Herb	Th	-	-		X		X	EBS 4115, 5167
	<i>Gouania columnifolia</i> Reissek	Climber	Ph	-	-		X			EBS 5350
Rubiaceae	<i>Borreria latifolia</i> (Aubl.) K.Schum.	Herb	Th	-	-		X			EBS 4153
	<i>Borreria scabiosoides</i> Cham. & Schltldl.	Herb	He	-	-	X				EBS 5343
	<i>Borreria spinosa</i> Cham. et Schltldl.	Herb	He	vassourinha-de-botão	-	X		X		EBS -, 3503



Table 2. Cont.

Family	Species	Habit	Life-forms	PN	End	Occurrence				Voucher
						S1	S2	S3	S4	
Rubiaceae	<i>Borreria verticillata</i> (L.) G. Mey.	Subshrub	He	falsa-poaia	-	X			X	EBS 4479, 4724
	<i>Borreria tenella</i> (Kunth) Cham. & Schltdl.	Herb	Th	-	-		X	X		EBS 4150, 3612
	<i>Borreria</i> sp.nov.	Subshrub	He	-	-	X				EBS 5341
	<i>Cordia myrciifolia</i> (K. Schum.) C. Press. & Deplrete	Shrub	Ph	-	-				X	EBS 3737
	<i>Cordia rigida</i> (K. Schum.) Kuntze	Shrub	Ph	-	BR				X	EBS 3733
	<i>Guettarda viburnoides</i> Cham. & Schltdl.	Shrub	Ph	angislica	-			X	X	EBS 5783, 5161
	<i>Hexasepalum apiculatum</i> (Willd.) Delprete & J.H. Kirkbr.	Herb	Th	-	-	X		X		EBS 3478, 3614
	<i>Hexasepalum gardneri</i> (K. Schum.) J.H. Kirkbr.	Subshrub	Th	-	NE		X	X	X	EBS 4119, 3619, 4720
	<i>Hexasepalum teres</i> (Walter) J.H. Kikbr.	Herb	Th	-	-		X			EBS 4143
	<i>Mitracarpus fernandesii</i> E.L. Cabral, Sobrado & E.B. Souza	Herb	Th	-	NE	X	X	X		EBS 5323, 5356, 3646
	<i>Oldenlandia filicaulis</i> K.Schum.	Herb	Th	-	-		X			EBS 5351
	<i>Richardia grandiflora</i> (Cham & Schltdl.) Steud	Herb	Th	-	-		X			MCPT 14
	<i>Richardia scabra</i> L.	Herb	Th	-	-			X		EBS 3630
	<i>Rosenbergiodendron longiflorum</i> (Ruiz & Pav.) Fagerl.	Shrub	Ch	estrela-do-norte	-	X				EBS 5332
<i>Staelia virgata</i> (Link ex. Roem. & Schult.) K.Schum.	Herb	Th	-	-	X	X	X		EBS 3598, 4116, 3623	
<i>Tocoyena sellowiana</i> (Cham. & Schltdl.) K.Schum.	Shrub	Th	jeniparana	BR		X		X	EBS 4468, 4719	
Santalaceae	<i>Phoradendron</i> sp.	Herb	Th	erva-de-passarinho			X		EBS 3752	
Simaroubaceae	<i>Homalolepis cedron</i> (Planch.) Devecchi & Pirani	Shrub	Ph	-	-		X		EBS 5789	
	<i>Simarouba versicolor</i> A. St.-Hil.	Tree	Ph	mata-cachorro	-			X	EBS 5816	
Solanaceae	<i>Brunfelsia uniflora</i> (Pohl.) D.Don.	Shrub	Ch	manacá-de-jardim	-			X	EBS 5056	
	<i>Schwenckia americana</i> Rooyen ex L.	Herb	Th	-	-		X		EBS 5731	
	<i>Solanum crinitum</i> L.	Shrub	Ph	-	-		X		EBS 5740	
	<i>Solanum paniculatum</i> L.	Shrub	Ph	jurubeba	-		X		EBS 5734	
Turneraceae	<i>Turnera coerulea</i> DC.	Herb	Th	-	-	X	X		EBS 5231, 4455	
	<i>Piriqueta</i> sp.	Herb	Th	-	-	X			EBS 5235	
Urticaceae	<i>Cecropia concolor</i> Willd.	Tree	Ph	embaúba	BR		X		EBS 5738	
Verbenaceae	<i>Lantana camara</i> L.	Shrub	Ph	camará-chumbinho	-	X			EBS 4925	
	<i>Stachytarpheta cayennensis</i> (Riech.) Vahl.	Herb	He	gervão-azul	-	X			EBS 3456	
	<i>Stachytarpheta coccinea</i> Schauer	Herb	He	-	BR	X			EBS 3482	
Violaceae	<i>Hybanthus albus</i> (A. St.-Hill) Baill	Herb	Th	-	BR	X			EBS 3410	
	<i>Pombalia calceolaria</i> (L.) Paula-Souza	Herb	Th	ipeca-da-praia	-			X	EBS 5161	
Vochysiaceae	<i>Callisthene minor</i> Mart.	Tree	Ph	pau-de-pilão	BR		X	X	EBS 5738, 5822	
	<i>Qualea grandiflora</i> Mart.	Tree	Ph	pau-terra-de-folha-larga			X	X	EBS 5723, 5778	
	<i>Qualea parviflora</i> Mart.	Tree	Ph	pau-terra	-	X	X	X	EBS 5417, 5438, 3751, 3738	
	<i>Salvertia convallariodora</i> A.St.-Hill.	Tree	Ph	pau-de-colher	-	X		X	EBS 5415, 3746	
Xyridaceae	<i>Xyris cf. paradisiaca</i> Wand	Herb	Cr	-	BR		X		EBS 5353	



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Figure 3. Some species collected in the caatinga savanna studied. **A-D)** Species in common with the Cerrado, **E-H)** Species in common with the Caatinga. **A)** *Bowdichia virgilioides* Kunth., **B)** *Byrsonima coccolobifolia* Kunth., **C)** *Curatella americana* L., **D)** *Hirtella ciliata* Mart. & Zucc, **E)** *Copernicia prunifera* (Mill.) H.E. Moore, **F)** *Combretum leprosum* Mart., **G)** *Encholirium spectabile* Mart. ex Schult. & Schult.f., **H)** *Xiquexique gounellei* (F.A.C. Weber) Lavor & Calvente. Photographs: **A)** E.B. Souza, **B-H)** I.V. Nepomuceno.



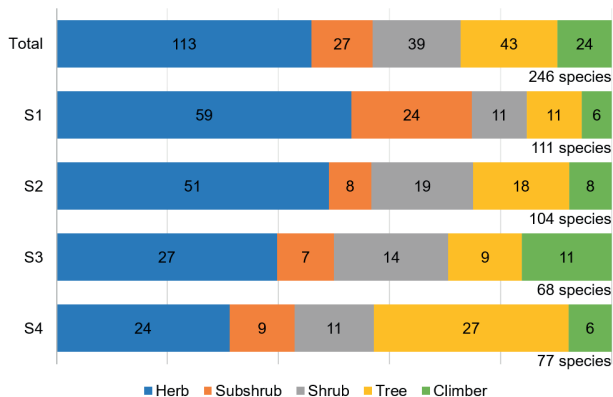


Figure 4. Spectrum of habit of the species recorded in each study area in Northern Ceará.

When we compared the Raunkiaer life-form spectra of our four sites with the spectra of other Brazilian biomes (Costa *et al.* 2016), we noted that these caatinga-savannas had spectra similar to the caatinga on crystalline substrates (Fig. 9), with a predominance of therophytes over other life-forms for most areas (Fig. 8). Therophytic species dominate in all areas, with the exception of S4, where we found a predominance of phanerophytes (39 spp.). Therophytes, phanerophytes, hemicryptophytes and chamaephytes are present in all the areas as the main life-forms, however other types are also found in smaller numbers. Cryptophytes, species that possess underground storage structures (Martins & Batalha 2011), were recorded in S1, S3 and S4. Only in S2 did we find epiphytic species, *Philodendron acutatum* and *Trichocentrum cepula* (Tab. 2).

For the NMS analyses performed with the Raunkiaer life-form spectra (Fig. 9) we observed that, while the standard biological spectrum of Raunkiaer is dominated by the phanerophytes, the caatinga-savanna and the caatinga in crystalline terrains are both composed of a majority of therophytes. The cerrado areas had a predominance of hemicryptophytes, as previously reported by other studies (Batalha & Martins 2002; Martins & Batalha 2011).

Discussion

The species richness in typical cerrado areas is variable, with a relatively low alpha diversity (number of species) while, in a few cases, it is possible to encounter more than 100 woody species occurring in a determined area (Felfili *et al.* 1992; Ratter & Dargie 1992; Ratter *et al.* 2003). When considering the four study areas we found a significant number of 82 species in the woody component, even though with low alpha diversity per area, with 22 species in S1, 35 in S2, 23 in S3 and 38 in S4. These numbers are in accordance with the average species per area that Ratter *et al.* (2003) obtained with the compilation of data from 376 localities of Cerrado vegetation in Brazil.

The Vochysiaceae is probably one of the more characteristic families of cerrado vegetation (Goodland & Ferri 1979). Six genera of this family occur in Brazil, with *Callisthene* Mart., *Qualea* Aubl. and *Vochysia* Aubl. being strongly associated with the cerrado and occurring in the surrounding biomes, whilst *Salvertia* A.St.-Hil. is typical of cerrado vegetation (Goodland & Ferri 1979; BFG 2018), but although our sites are many kilometres distant from the core Cerrado domain, we recorded *Callisthene* minor, *Qualea grandiflora* and *Salvertia convallariodora* in our caatinga-savannas. *Qualea grandiflora*, *Q. parviflora* and *Salvertia convallariodora* are commonly cited as widely distributed species in the Cerrado domain (Goodland & Ferri 1979; Felfili *et al.* 1992; Ratter & Dargie 1992; Ratter *et al.* 2003; Castro *et al.* 2007). These same species are also recorded in the Amazonian savannas (Miranda *et al.* 2006; Magnusson *et al.* 2008). Other examples of very common species in typical cerrado sites that were recorded in the studied caatinga-savannas were *Bowdichia virgilioides*, *Byrsonima coccolobifolia*, *Curatella americana* and *Hirtella ciliata* (Tab. 2, Fig. 3), but typical caatinga species like *Cereus jamacaru*, *Encholirium spectabile*, *Copernicia prunifera* and *Combretum leprosum* were also found in our sites, making them a mixture of floristic elements from both the Cerrado and Caatinga biomes (Moro *et al.* 2011).

The woody (shrubs + trees) component of our study sites is composed by many species common in cerrado vegetation of the core Cerrado biome. We recorded in our study sites *Astronium fraxinifolium*, *Bowdichia virgilioides*, *Byrsonima coccolobifolia*, *B. crassifolia*, *Curatella americana*, *Dimorphandra mollis*, *Hymenaea stigonocarpa*, *Machaerium acutifolium*, *Plathymenia reticulata*, *Qualea grandiflora*, *Q. parviflora* and *Salvertia convallariodora*, that are widely distributed in the core Cerrado areas, and compiled as common species by Ratter & Dargie (1992) and Ratter *et al.* (2003) and recorded in Souza *et al.*'s (2018) species list. Other species also common in the cerrado, such as *Anacardium occidentale*, *Copaifera martii*, *Hirtella ciliata* and *Ouratea castaneifolia*, were also recorded.

In the herbaceous layer we found the repeated occurrence of species that are commonly listed in Cerrado floras, such as the Asteraceae *Elephantopus hirtiflorus*, the Cyperaceae *Bulbostylis junciforme*, *Rynchospora nervosa*, *Scleria hirtella*, the Fabaceae *Chamaecrista diphylla*, *C. flexuosa*, *Zornia reticulata* and the Poaceae *Aristida longifolia*, *Axonopus marginatus* and *Trachypogon spicatus* (Batalha *et al.* 1997; Mantovani & Martins 1993; Costa *et al.* 2004; Tannus & Assis 2004; Magnusson *et al.* 2008; Moro *et al.* 2011; Oliveira *et al.* 2012; Ribeiro-Silva *et al.* 2012; Souza *et al.* 2018). We also flag here the occurrence of species typical of the Cerrado as abundant in the areas studied, with *Trachypogon spicatus* being widely recorded in the floristic lists of Brazilian Cerrado (Mantovani & Martins 1993; Oliveira *et al.* 2012; Souza *et al.* 2018) and in Ceará (Costa *et al.* 2004; Moro *et al.* 2011; Ribeiro-Silva *et al.* 2012).

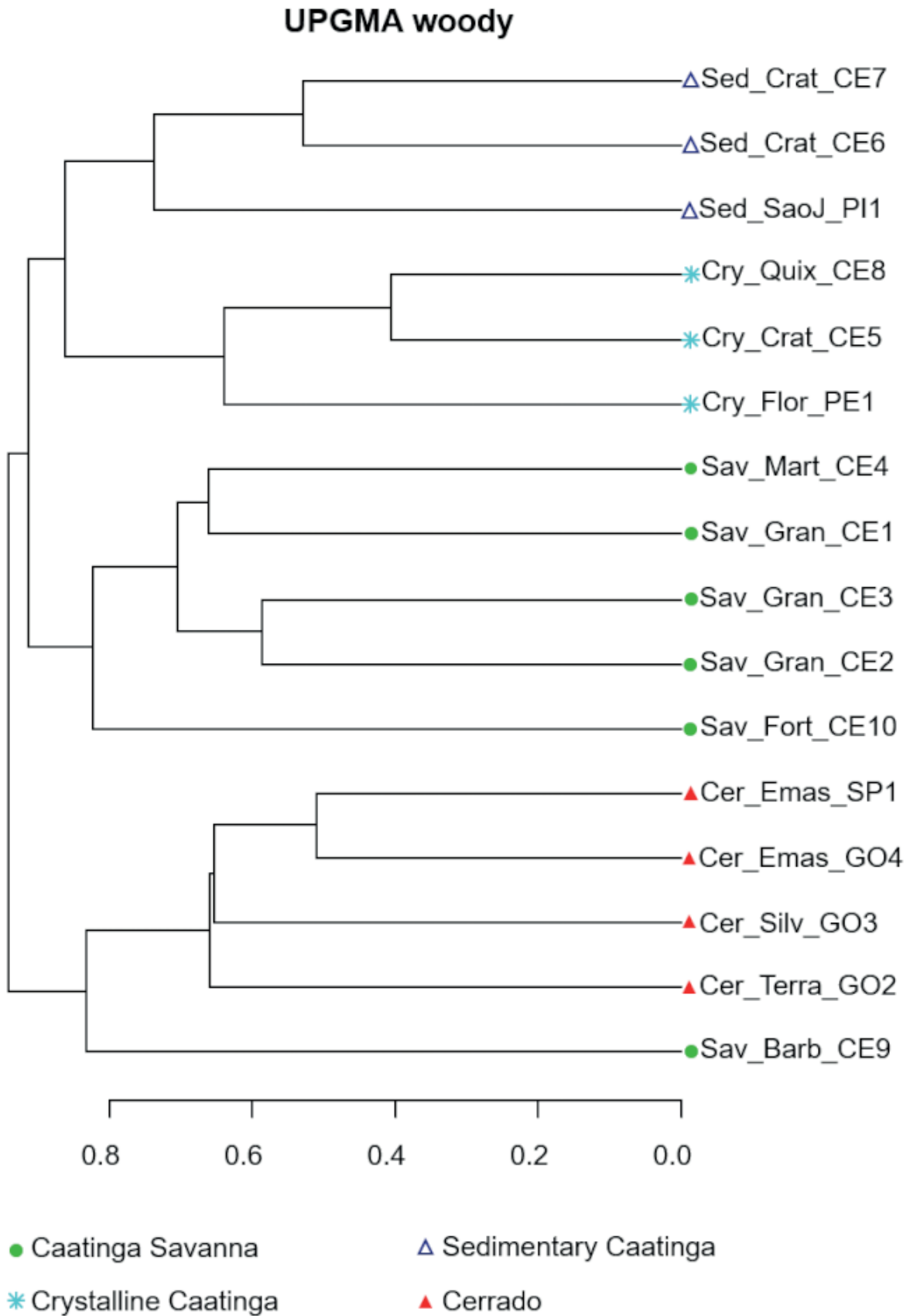


Figure 5. Dendrogram obtained in grouping analysis UPGMA with Bray-Curtis distance for woody component (cophenetic correlation coefficient = 0.910).



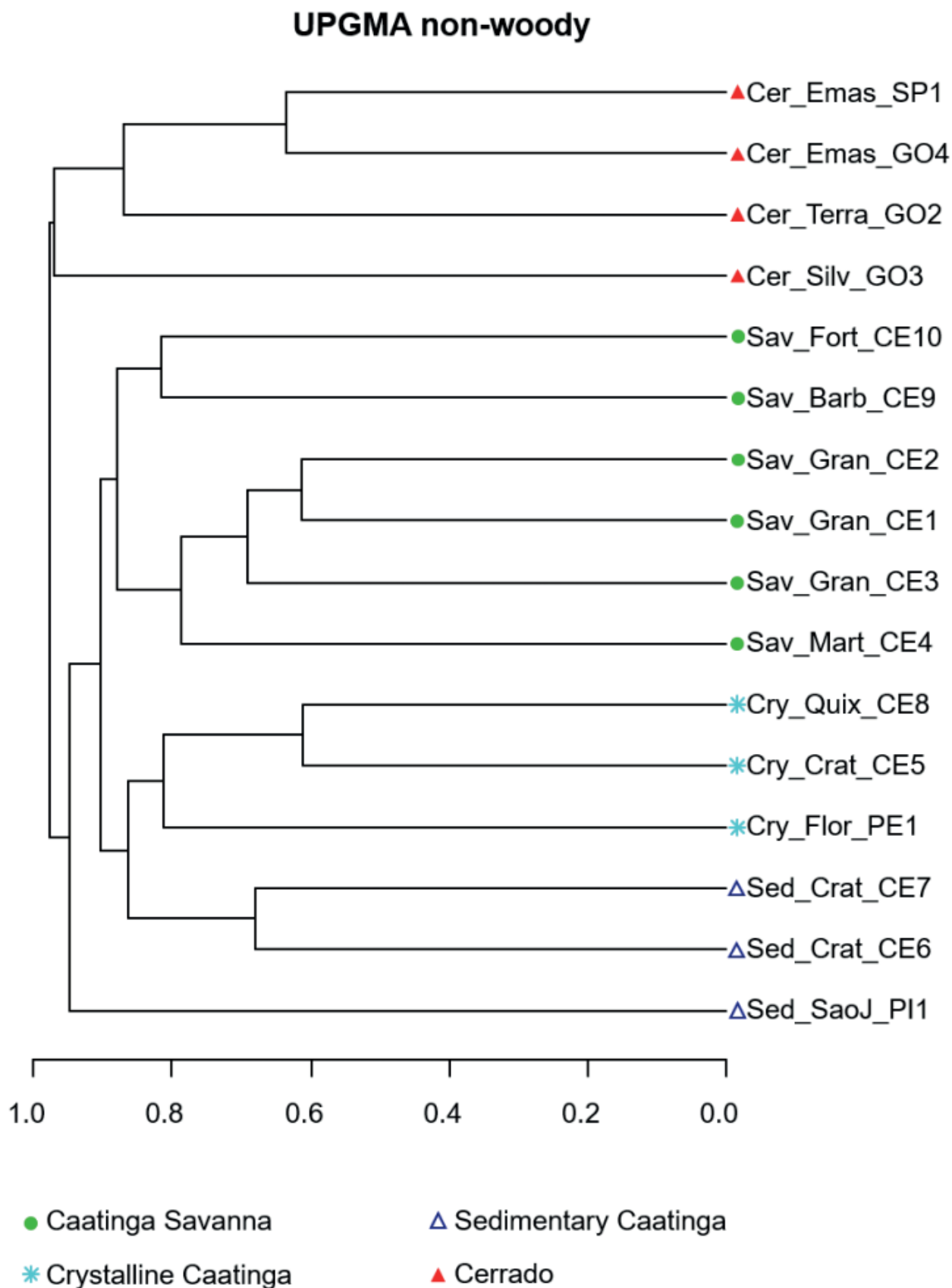


Figure 6. Dendrogram obtained in grouping analysis UPGMA with Bray-Curtis distance for non-woody component (cophenetic correlation coefficient = 0.920).

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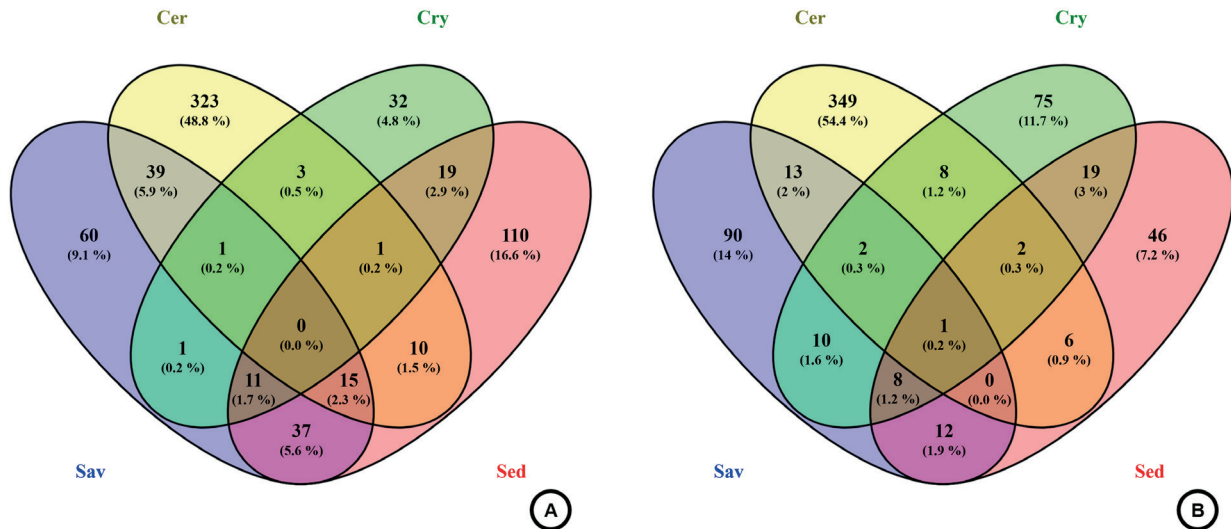


Figure 7. Venn diagrams showing the number species per area. **A)** Venn diagram for woody component. **B)** Venn diagram for non-woody component.

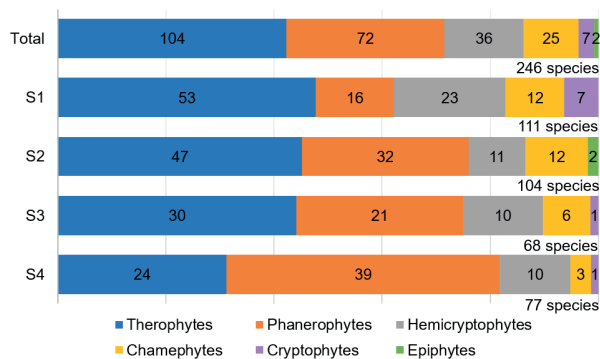


Figure 8. Spectrum of life-forms of the 246 species from the study area in Northern Ceará.

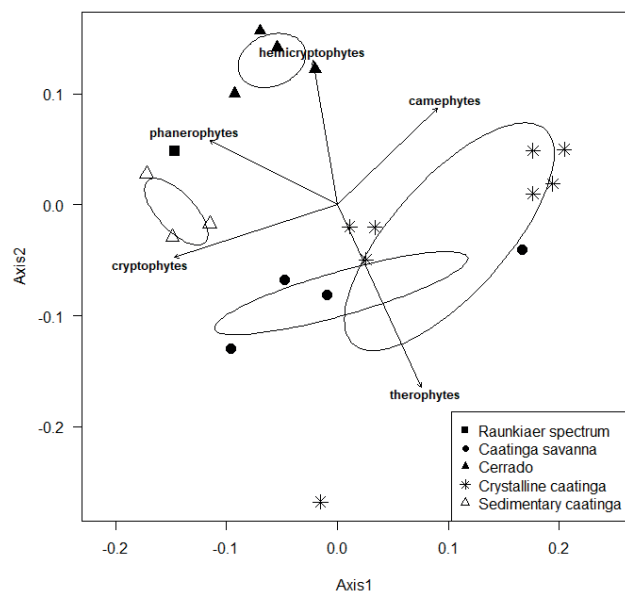


Figure 9. Non-metric multidimensional scaling (NMS) of caatinga-savannas, Caatinga and Cerrado (stress = 0.128).

In S1, the area with the highest richness of herbaceous plants, we observed trees and shrubs distributed sparsely in the environment with an herbaceous layer dominating the landscape (Fig. 2A). This configuration resembles the cerrado s.s. of central Brazil (Walter *et al.* 2015). In S2, we note a transition area between Caatinga and Cerrado, with shared species typical of both biomes, such as *Amburana cearensis*, *Combretum leprosum*, *Encholirium spectabile*, *Xiquexique gounellei* and *Ruellia paniculata*, common in the Caatinga (Araújo *et al.* 2011; Moro *et al.* 2014), and *Anacardium occidentale*, *Curatella americana*, *Byrsonima coccolobifolia*, *Qualea grandiflora* and *Q. parviflora* (Ratter & Dargie 1992; Ratter *et al.* 2003; Moro *et al.* 2011) common in the Cerrado (Fig. 2B). S3 presents a woody vegetation with trees reaching approximately 10 m in height, such as *Campomanesia aromatica*, *Curatella americana*, *Dimorphandra mollis*, *Qualea grandiflora* and *Q. parviflora*. In this sense it is similar to the cerrado, the forest facies of the Cerrado (Walter *et al.* 2015). However, in other stretches of the same study area, we found open areas with widely spaced trees and shrubs, such as *Anacardium occidentale*, *Byrsonima coccolobifolia* and *Myrcia splendens*, and a more continuous herbaceous layer, composed principally by the species *Elephantopus hirtiflorus*, *Cyperus schomburgkianus*, *Galactia jussieana* and *Streptostachys asperifolia*, a physiognomy which resembles that of cerrado s.s. (Fig. 2C) (Walter *et al.* 2015). S4 also presents a physiognomy similar to that of the cerrado at some sites and dense cerrado s.s. in others, (Fig. 2D), with many trees, namely *Andira cordata*, *Astronium fraxinifolium*, *Curatella americana*, *Himatanthus drasticus*, *Hirtella ciliata*, *Hymenaea stigonocarpa*, *Salvertia convallariodora* and *Stryphnodendron coriaceum* composing the landscape. Herbaceous species like the Poaceae *Axonopus marginatus*, *Mesosetum annum* e *Streptostachys asperifolia* and the Cyperaceae *Bulbostylis capilaris*, *Cyperus schomburgkianus* and *Fimbristylis dichotoma* are common in the herbaceous component of S4.

Despite sharing woody and non-woody species with the core Cerrado biome the total flora of caatinga-savannas is more similar to the surrounding caatinga vegetation. The typical savanna physiognomy that can be observed in these caatinga-savannas did not mean that typical caatinga species were excluded from these areas. We found here that most caatinga-savanna sites were floristically closer to the caatinga than to the cerrado. A remarkable exception was the woody community in the Chapada do Araripe savanna enclave, which presented a woody flora that is more similar to geographically distant cerrado areas of Goiás and São Paulo than to the surrounding Caatinga. It is possible that the deep, acidic soils from this region, together with higher rainfall and altitude may be the cause of this similarity (Costa *et al.* 2004; Ribeiro-Silva *et al.* 2012; Santos *et al.* 2018).

Batalha & Martins (2002 and 2004) compiled data from Raunkiaer life-forms in seven areas of Cerrado in Brazil and observed the predominance of hemicryptophytes, followed by phanerophytes and chamaephytes (Costa *et al.* 2004; Martins & Batalha (2011)), recording the largest occurrence of phanerophytes and hemicryptophytes in the Chapada do Araripe (CE) and in Itirapina (SP), respectively, and Tannus & Assis (2004) who established that hemicryptophytes were dominant in an area with open grassland. In our study areas, phanerophytes (29.3%) and hemicryptophytes (15%) have significant representativeness, although they are less rich than the therophytic life-form, which represented 42.3% of the plant species. Therophytes are predominant in desertic areas according to the Raunkiaer spectrum (Martins & Batalha 2011), whilst in Brazilian biomes they are more representative of the caatinga vegetation (Pennington *et al.* 2000; Costa *et al.* 2016), as seen in studies by Araújo *et al.* (2011) and Queiroz *et al.* (2015).

Despite being classified as physiognomically similar to the cerrado vegetation, our study areas had biological spectra different from other cerrado areas in Brazil and closer to the caatinga, with a high number of therophytic species. This fact could be related to the environmental conditions of the Caatinga biome, where these sites are located, with high temperatures and erratic rain regime and distribution, which favours therophytes, having short life-cycles that are adapted to water restriction and short or unpredictable growing seasons (Martins & Batalha 2011). Thus, the flora of the four studied caatinga-savannas is more similar to the caatinga vegetation than to the cerrado. Of the 247 species recorded in our areas, 150 are listed as occurring in the Caatinga biome as compiled by Moro *et al.* (2014). Also, we found that the therophytic life-form predominates, a similar situation with that recorded in caatinga vegetation (Araújo *et al.* 2011; Costa *et al.* 2016; Queiroz *et al.* 2015). The large number of therophytes found in the caatinga-savannas is very likely connected to the semiarid climate of the region with lower, less predictable precipitation in these savannas than in cerrados of central Brazil. Nevertheless, these

caatinga-savannas share a significant number of typical cerrado species do not present in typical caatinga sites.

Conclusion

The caatinga-savanna enclaves studied here are not fragments of typical cerrado vegetation, although possessing savanna physiognomy. The proximity of caatinga vegetation, which surrounds the patches, and the influence of the semiarid climate explain the larger number of therophytic species in relation to the phanerophytes and hemicryptophytes, since therophytes are the dominant life-form in the caatinga. Many species typical of the cerrado vegetation were found in our study areas. Apart from presenting a physiognomy similar to the cerrado *s.s.* and the taller and more closed *cerradão*, these areas have various typical species that occur in the 'core' Cerrado domain. Nevertheless, the local flora as a whole is closer to the caatinga vegetation than to the cerrado, with the exception of the Araripe savanna enclave. The flora of these enclaves is therefore characterised by a mixture of species typical of the Brazilian cerrado, widespread species and species typical from the caatinga vegetation.

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