



Floristic and taxonomic diversity of angiosperms in several vegetation types of the *Caatinga* Phytogeographic Domain

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Key words:

- Chapada Diamantina
- Endemism
- Extinction Risk
- Richness

Abstract

This study describes the angiosperm composition of four natural (Crystalline *Caatinga*, Rupestrian Grassland, Rocky Outcrop, Tropical Rainforest) and three anthropized (Aquatic Ecosystem, Crystalline *Caatinga*, Tropical Rainforest) vegetation types within the *Caatinga* Phytogeographic Domain, and compares habit diversity and the richness of Brazilian endangered, native, and exotic species. A total of 428 species across 85 families and 296 genera were identified between 2018 and 2020. Species richness varied from 11 to 191 among vegetation types, with natural Crystalline *Caatinga* (191) and natural Tropical Rainforest (129) being the richest. The ranking of families and genera by species richness differed among vegetation types. Notably, 84.35% of the species were unique to one vegetation type, highlighting their distinct compositions. Subshrub/shrub and Herb species (together) were predominant in natural Crystalline *Caatinga* (105 spp.), Rupestrian Grassland (20), Rocky Outcrop (20), and anthropized Tropical Rainforest (9). Tree and subshrub/shrub species were prevalent in natural Tropical Rainforest (79), while Herb species were predominant in Aquatic Ecosystem (25). The percentage of native species ranged from 87.43% to 96.67% in natural vegetation and from 72.73% to 91.67% in anthropized vegetation. Forty-five of the species, including *Lafoensia glyptocarpa*, are endangered, with prevalence in natural Crystalline *Caatinga* and natural Tropical Rainforest.

Palavras-chave:

- Chapada Diamantina
- Endemismo
- Risco de Extinção
- Riqueza de espécies

Resumo

Este estudo descreveu a composição de angiospermas em quatro tipos de vegetação natural (Caatinga Cristalina, Campo Rupestre, Afloramento Rochoso, Floresta Tropical) e três tipos antropizados (Ecossistema Aquático, Caatinga Cristalina, Floresta Tropical) dentro do Domínio Fitogeográfico da Caatinga, comparando a diversidade de hábitos e a riqueza de espécies ameaçadas, nativas e exóticas no Brasil. Entre 2018 e 2020, foram identificadas 428 espécies, em 85 famílias e 296 gêneros. A riqueza de espécies variou de 11 a 191 entre os tipos de vegetação, com a Caatinga Cristalina natural (191) e a Floresta Tropical natural (129) sendo as mais ricas. Diferenças foram observadas na classificação das famílias e gêneros mais ricos em espécies entre os tipos de vegetação. Notavelmente, 84,35% das espécies foram exclusivas de um tipo de vegetação, destacando suas composições distintas. Espécies de subarbustos/arbustos e ervas (juntos) foram predominantes na Caatinga Cristalina natural (105 spp.), Campo Rupestre (20), Afloramento Rochoso (20) e Floresta Tropical Pluvial antropizada (nove). Espécies de árvores e subarbustos/arbustos foram prevalentes na Floresta Tropical Pluvial natural (79), enquanto ervas foram predominantes em Ecossistemas Aquáticos (25). A porcentagem de espécies nativas variou de 87,43% a 96,67% na vegetação natural e de 72,73% a 91,67% nos tipos antropizados. Quarenta e cinco espécies, incluindo *Lafoensia glyptocarpa*, estão ameaçadas de extinção, com prevalência na Caatinga Cristalina natural e na Floresta Tropical Pluvial natural.

Original Papers

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Introduction

In Brazil, a phytogeographical domain is a subcontinental geographical area where the vegetation of a major biome predominates, interspersed with patches of vegetation from smaller biomes (Queiroz *et al.* 2017). This mosaic of vegetation is closely linked to a region's climate, soil, and topography (Queiroz *et al.* 2017). The *Caatinga* Phytogeographic Domain (CPD), located in the semi-arid region of Northeast Brazil, encompasses the largest continuous expanse of the Seasonally Dry Tropical Forest (SDTF) Biome in the Neotropics, situated alongside smaller patches of three other biomes: Tropical Rainforest, Savanna, and Rupestrian Grassland (Queiroz *et al.* 2017; Fernandes & Queiroz 2018).

Two major floristic subgroups have been identified within the SDTF areas of the CPD based on floristic composition and plant biogeography: Crystalline *Caatinga* and Sedimentary *Caatinga*. A less common subgroup, Tall Deciduous and Semi-Deciduous *Caatinga* Forest, is also recognized, with vegetation growing on specific soil types (Moro *et al.* 2014; Queiroz *et al.* 2017). Additionally, the SDTF within the CPD ecosystem types characterized by taxonomic oligarchies, such as Rocky Outcrop and natural or anthropized Aquatic Ecosystem (Queiroz *et al.* 2017).

Although the CPD features extensive natural vegetation mosaics with a high diversity of species native to Brazil and endemic to this domain, it has undergone significant transformation. It is estimated that 80% of the original vegetation of the CPD has been altered by chronic human activities (Jesus *et al.* 2022). These activities include wood cutting, livestock farming, and agriculture, particularly in areas of Crystalline and Sedimentary *Caatinga* vegetation (Albuquerque *et al.* 2012; Melo *et al.* 2019; Jesus *et al.* 2022). As a result, large areas now have little to no Herb vegetation, and the remaining subshrub/shrub component exhibits low taxonomic and functional diversity (Pifano *et al.* 2023). This component is mainly represented by pioneer exotic species, characterized by low stature and wide spacing of individuals on exposed soil (Pifano *et al.* 2023). Over time, chronic anthropogenic disturbances within the CPD have led to a reduction in the richness of native Brazilian species and those endemic to this domain, in addition to the extinction of species with local and small populations (Albuquerque *et al.* 2017). This impact is particularly evident in the woody component and the species dependent on it, such as Climber/Twiners/Vine species (Albuquerque *et al.* 2017; Ribeiro *et al.* 2019; Vieira *et al.* 2022).

The assembly of plant communities within the CPD and its floristic subgroups is strongly

influenced by temperature and precipitation, both of which are directly related to the altitudinal gradient (Queiroz *et al.* 2017). At higher elevations in Brazil, such as the mountain ranges and plateaus of the CPD, temperatures are generally lower compared to lowland areas (Alvares *et al.* 2013). These higher, cooler regions also typically receive more rainfall than the lowlands, primarily due to the phenomenon of orographic rainfall (Velloso *et al.* 2002). This increased precipitation supports the tall and dense vegetation of Tropical Rainforest and Deciduous or Semi-Deciduous Forest vegetation types in the higher regions of the CPD (Moro *et al.* 2015). Rupestrian Grassland and Rocky Outcrop vegetation types are also commonly found at these altitudes (Queiroz *et al.* 2017). In contrast, the lower and drier areas of the CPD are predominantly composed of deciduous subshrub/shrub (Moro *et al.* 2015). These areas are mainly made up of Sedimentary *Caatinga*, as well as by vegetation from terrestrial or aquatic ecosystems transformed by chronic anthropogenic activities (Queiroz *et al.* 2017).

Checklists of plants from the CPD, encompassing large areas of SDTF and irregularly spaced patches of Tropical Forest, Savanna, or Campo Rupestre (*sensu* Queiroz *et al.* 2017), have been produced in the last 10 years based on data compiled from publications (Moro *et al.* 2014) or from Herbarium and botanical collections available on digital platforms (Fernandes *et al.* 2020). Despite the contributions of these publications to advancing the knowledge of plant diversity in the CPD, a portion of the taxonomic and biogeographic information about species in this domain remains unknown due to the lack of access to their habitats. It is estimated that less than 50% of the territory of the CPD has at least one plant collection or study with taxonomic and/or phytosociological objectives (Moro *et al.* 2014). These expeditions tend to be spatially biased, occurring mainly in low areas of Sedimentary *Caatinga* vegetation (Moro *et al.* 2014; Pifano *et al.* 2023).

Extensive areas in the highlands of the CPD still require comprehensive checklists to address deficiencies in knowledge of plant taxonomic diversity (Nascimento *et al.* 2010). Chapada Diamantina is one such region with significant knowledge gaps regarding plant diversity, although several studies have locally addressed these gaps within this chapada (Conceição & Giulietti 2002; Conceição & Pirani 2005, 2007; Costa *et al.* 2009; Ramalho *et al.* 2009; França *et al.* 2010; Nascimento *et al.* 2010; Couto *et al.* 2011; Santos *et al.* 2020). Situated in the southernmost part of the CPD, Chapada Diamantina exhibits pronounced altitudinal and rainfall gradients (Velloso *et al.* 2002) and features a socio-ecological system where human populations

depend on forest resources for activities such as firewood collection and livestock grazing (Bragagnolo *et al.* 2021). This has given rise to a diverse range of aquatic and terrestrial ecosystems, both natural and anthropized, within the chapada (Velloso *et al.* 2002), highlighting the need for further taxonomic and ecological studies of the plants in these environments (Juncá *et al.* 2005). This need is particularly critical given the changes in plant beta diversity projected for the region by the end of the century due to climate change (Moura *et al.* 2023). According to these researchers, the southernmost region of the CPD, including Chapada Diamantina, may experience the extinction of numerous plant species and biotic homogenization by 2100 because of climate change impacts. Therefore, increasing floristic surveys in natural or anthropized areas within Chapada Diamantina could help fill knowledge gaps regarding plant diversity, while also supporting species conservation.

Gaps in biodiversity knowledge are mainly due to the poor quality and reliability of taxonomic and biogeographic data, which are limited by human investigative capacity (Hortal *et al.* 2015). These gaps highlight the disparity between the number of described species and the actual number of species (Linnean Shortfall), and reveal geographic biases in species distribution data (Wallacean Shortfall), turning taxonomic diversity hotspots into mere maps of collection effort (Lomolino 2004). These checklists also facilitate comparisons between anthropized and native vegetation in terms of composition, habit diversity, and the richness of Brazilian endangered, native or exotic species, as well as endemic species of the CPD.

Thus, this study aimed to expand knowledge of the taxonomic diversity of angiosperms in different types of natural and anthropized vegetation within the CPD, focusing on a region in the Northern Piedmont of Chapada Diamantina. The resulting checklist will allow comparisons to be made between anthropized and natural vegetations regarding composition, habit diversity, and the richness of Brazilian endangered, native or exotic species (naturalized or cultivated), as well as endemic species of the CPD.

Material and Methods

Study Area

The study area is in Serra de Santana of the Northern Piedmont of Chapada Diamantina in the state of Bahia, between the cities of Jaguarari and Senhor do Bonfim (411 and 375 km from the capital Salvador, respectively). This mountain range is situated between latitudes 10°26'75.79"S and 10°39'34.57"S and longitudes 40°20'83.42"W and 40°18'72.59"W, with elevation ranging from 500

to 1,000 m (Fig. 1). It is in the geo-environmental unit of the Chapada Diamantina complex (Souza & Oliveira 2006; Barbosa 2012).

The climate of the study area is subtropical with hot summers, during which the temperature is always above 22 °C. The annual precipitation ranges 580–640 mm, and the soil is Dystrophic Yellow Latosol (Souza & Filho 2011). An expedition to survey the study area identified in Serra de Santana different types of vegetation described for the CPD (*sensu* Queiroz *et al.* 2017), namely: anthropized Aquatic Ecosystem (AEC, Fig.2a), anthropized Crystalline *Caatinga* (CCa, Fig.2b), natural Crystalline *Caatinga* (CCn, Fig.2c), Rupestrian Grassland (RG, Fig.2d), Rocky Outcrop (RO, Fig.2e), anthropized Tropical Rainforest (TRFa), and natural Tropical Rainforest (TRFn, Fig.2f). The first three vegetation types were observed in low regions of the study area (500m–700m), while the other types of were recorded in higher areas (above 700m).

Data Collection

Floristic survey expeditions were conducted in the study area between July 2018 and July 2020. The floristic survey adopted an unsystematic walking method within the sites of each investigated vegetation type. Collection efforts within each site were terminated upon reaching stabilization of taxonomic diversity. Three to six samples (branches in reproductive stage or entire individuals) were collected per morphospecies recorded at the study sites. The collected biological material was preserved in the field, following established protocols for aquatic and terrestrial plants (Mori *et al.* 1985; Peixoto & Maia 2013). Three to six exsiccates were produced for each sampled species (*sensu* Mori *et al.* 1985), which were incorporated into the collection of the Herbário de Referência do Sertão Nordestino (HRSN) (Herbarium of the Northeastern Sertão, in English) at the Universidade Federal do Vale do São Francisco (UNIVASF) (Federal University of São Francisco Valley, in English).

Species were identified using taxonomic keys available in the literature (*e.g.*, Souza & Lorenzi 2012) or by comparison with exsiccates deposited in the HRSN. Assistance was sought from taxonomists with expertise on respective families for the identification of some species. The systematic classification of families followed APG IV (2016). The Flora e Funga do Brasil database (2025, continuously updated) was used to verify the scientific names of the species (excluding synonyms or non-accepted names) and their respective authors, as well as to classify the species according to geographic origin (native, naturalized or cultivated in Brazil, or no information), endemism to Brazil and/or CPD, and habit (Climber/Twiners/Vine, epiphytes, herb, palm, subshrub/shrub and

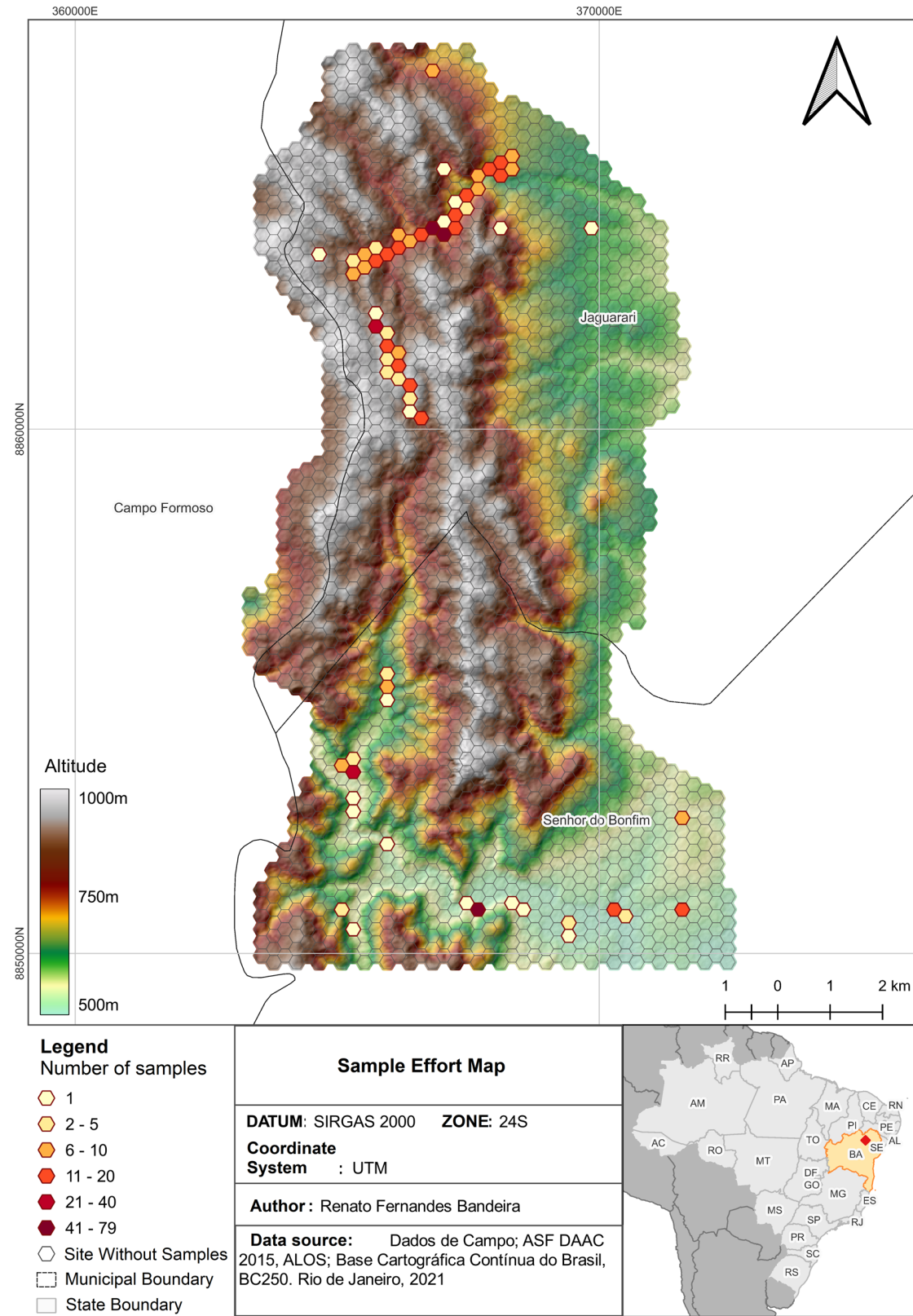


Figure 1 – Map of the locations of the collection sites and the elevation gradient in the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex), highlighting the number of samples collected at each site.

tree). The databases SpeciesLink (2025) and Re flora (2025) were used to check species records for the CPD. The species recorded in the study area were also classified according to degree of extinction risk, following ordinance No. 148 of the Brazilian Ministry of the Environment (MMA 2022).

Data Analysis

A data matrix was created with information on the presence or absence of species for each investigated vegetation type. The matrix was then subjected to a similarity analysis using the Jaccard index and the unweighted pair group method with arithmetic mean (UPGMA). Two dendrograms were generated, one with the natural vegetation types and one with the natural vegetation types and the anthropized vegetation types of Tropical Rainforest and Crystalline *Caatinga*. The dendrograms were generated using the `hclust` function of the R Package version 4.2.2 (R Core Team 2022) and the `fviz_dend` function of the `Factoextra` package of R Package version 1.0.7 (Kassambara & Mundt 2020). Descriptive statistics were used to compare anthropized and natural vegetation in terms of habit diversity as well as the richness of Brazilian endangered, native, or exotic species (both naturalized and cultivated), including those endemic to the CPD.

Results

A total of 428 species were collected, distributed among 85 families and 296 genera (Tab. S1, available on supplementary material <10.6084/m9.figshare.28800617>). Of all the species recorded, three were new occurrences for the CPD [*Lycianthes pauciflora* (Vahl) Bitter, *Blepharocalyx eggersii* (Kiaersk.) Landrum, *Maranta protracta* Miq.], according to the databases of Flora e Funga do Brasil 2025 (continuously updated), SpeciesLink (2025) and Re flora (2025).

Natural Crystalline *Caatinga* and natural Tropical Rainforest were the vegetation types with the highest observed richness in the study area with 191 and 129 species, respectively. These vegetation types were followed by anthropized Crystalline *Caatinga* (86 spp.), anthropized Aquatic Ecosystem (36), Rupestrian Grassland (30), Rocky Outcrop (28), and anthropized Tropical Rainforest (11 spp.).

The families with the highest species richness were Fabaceae, with 60 species, followed by Asteraceae (43), Rubiaceae (21), Malvaceae (19) and Euphorbiaceae (17), together representing 37.3% (160) of the total species found in the study area (Tab. S1, available on supplementary material <10.6084/m9.figshare.28800617>). *Mimosa* and *Senna* were the genera with the highest species richness with eight each. These genera were richest

in the natural Crystalline *Caatinga* vegetation type. The order of families and genera by decreasing species richness differed among the investigated vegetation types (Tabs. 1-2).

The habit with the greatest species richness was subshrub/shrub with 125 species, corresponding to 29.2%, followed by tree (100 spp., 23.3%), Herb (98 spp., 22.8%), Climber/Twiners/Vine (67 spp., 15.6%), epiphytes (13 spp., 3.1%), and palm (1 spp., 0.2%). Subshrub/shrub and Herb species (together) were predominant in natural Crystalline *Caatinga* (105 spp.), Rupestrian Grassland (20), Rocky Outcrop (20), and anthropized Tropical Rainforest (nine). Tree and subshrub/shrub species were prevalent in natural Tropical Rainforest (79), while Herb was predominant in Aquatic Ecosystem (25) (Fig. 3).

Out of the total species recorded in the study area, 376 are native to Brazil, 32 are naturalized, and nine are cultivated in the country (Tab. S1, available on supplementary material <10.6084/m9.figshare.28800617>). Twelve species were identified only to the genus or family level, and so were classified as “No information” for geographic origin and endemism for Brazil and/or CPD. The percentage of native Brazilian species within each natural vegetation type varied from 87.43% for Crystalline *Caatinga* to 96.67% for Rupestrian Grassland, while within anthropized vegetation types the percentage ranged from 72.73% for Tropical Rainforest to 91.67% for Aquatic Ecosystem (Fig. 4a). The percentage of native Brazilian species within anthropized Crystalline *Caatinga* was 76.74%, while within natural Tropical Rainforest it was 89.92%. Out of the total Brazilian native species recorded, 105 are endemic to the country, with 20 of those being endemic to the CPD (Fig. 4b). A total of 45 species are on the MMA (2022) list of endangered species, with 44 categorized as “Least Concern” (LC) and one, *Lafoensia glyptocarpa* Koehne, as “Endangered” (EN), the latter being recorded only in natural Tropical Rainforest. Natural Crystalline *Caatinga* and natural Tropical Rainforest were the vegetation types with the highest percentages of species in the LC category (Fig. 4b).

A total of 361 species had records exclusive to one vegetation type, which corresponds to 84.35% of the total richness of the study area. Rocky Outcrop and natural Tropical Rainforest had the highest percentages of exclusive species, considering only the studied natural vegetations, reaching 89.28% (25 spp.) and 83.72% (108 spp.) of total species richness in each, respectively. Anthropized Crystalline *Caatinga* and natural Crystalline *Caatinga* shared 47 species, corresponding to 16.64% of the species observed in at least one of these vegetation types. Anthropized Tropical Rainforest and natural Tropical Rainforest shared only one species, corresponding to 0.72% of the species observed in at least one

Table 1 – List of families with the greatest species richness in vegetation types of the *Caatinga* Phytogeographic Domain (*sensu* Queiroz *et al.* 2017) recorded in the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex). Captions: AEC = anthropized Aquatic Ecosystem; CCa = anthropized Crystalline *Caatinga*; CCn = natural Crystalline *Caatinga*; RG = Rupestrian Grassland; RO = Rocky Outcrop; TRFa = anthropized Tropical Rainforest; TRFn = natural Tropical Rain Forest. Gray shades indicate species richness: dark gray = highest; intermediate gray = second highest; light gray = third highest.

FAMILIES	AEC	CCa	CCn	RG	RO	TRFa	TRFn
Acanthaceae	2						
Amaranthaceae	2						
Asteraceae		20	26	4		2	17
Begoniaceae					2		
Bignoniaceae					3		
Bromeliaceae					4		
Cactaceae					3		
Cyperaceae	11						
Euphorbiaceae					2		
Fabaceae		9	41	5	2		
Malvaceae	2	6				2	
Myrtaceae							12
Nymphaeaceae	2						
Orchidaceae					3		
Piperaceae					2		
Poaceae	2						
Rubiaceae				3			14
Sapindaceae			12				
Verbenaceae						2	

of these vegetation types. The low Jaccard Index among the natural vegetation types confirms their floristic dissimilarity. Floristic dissimilarity was also confirmed between anthropized Crystalline *Caatinga* and natural Crystalline *Caatinga*, as well as between the natural Tropical Rainforest and anthropized Tropical Rainforest, with Jaccard Indexes below 0.2 (Fig. 5). Some species exclusive to each evaluated vegetation type are depicted in Figure 6.

Discussion

The number of species documented in the study area was high compared to other floristic surveys conducted in different vegetation types of the CPD (Costa *et al.* 2009; Ribeiro-Filho *et al.* 2009; Couto *et al.* 2011; Lima *et al.* 2012; Andrade *et al.*

2020; Sousa *et al.* 2021). The documented species represent 9.6% of the total species and 24.5% of the total genera of angiosperms in the CPD of the state of Bahia, according to the Flora e Funga do Brasil database (2025, continuously updated). Additionally, they represent 13.6% of the total species (3,150) and 31.1% of the genera (950) cited in the most recent checklist of CPD plants (Fernandes *et al.* 2020), developed from the compilation of floristic lists and online data repositories.

The richest families (Fabaceae, Asteraceae, Rubiaceae, Malvaceae, and Euphorbiaceae) and genera (*Croton*, *Mimosa*, and *Senna*) in the study area closely resemble those recorded in some studies covering different vegetation types of the CPD, though not necessarily in the same order of richness

Table 2 – List of genera with the greatest species richness in the vegetation types of the *Caatinga* Phytogeographic Domain (*sensu* Queiroz *et al.* 2017), recorded in the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex). Captions: AEC = anthropized Aquatic Ecosystem; CCa = anthropized Crystalline *Caatinga*; CCn = natural Crystalline *Caatinga*; RG = Rupestrian Grassland; RO = Rocky Outcrop; TRFn = natural Tropical Rainforest. Gray shades indicate species richness: dark gray = highest; intermediate gray = second highest; light gray = third highest.

GENERA	AEC	CCa	CCn	RG	RO	TRFn
<i>Astraea</i>					2	
<i>Begonia</i>					2	
<i>Croton</i>			5			
<i>Cyperus</i>	6					
<i>Cyrtocymura</i>		2				
<i>Euphorbia</i>		2				
<i>Heliotropium</i>		2				
<i>Jacaranda</i>					2	
<i>Lepidaploa</i>				2		
<i>Miconia</i>						3
<i>Mimosa</i>			7			
<i>Myrcia</i>						3
<i>Nymphaea</i>	2					
<i>Passiflora</i>						3
<i>Peperomia</i>					2	
<i>Periandra</i>				2		
<i>Rhynchospora</i>	2					
<i>Ruellia</i>		3				
<i>Senegalia</i>			6			
<i>Senna</i>			6			
<i>Sida</i>		2				
<i>Solanum</i>		3				
<i>Tillandsia</i>				2	2	
<i>Tithonia</i>		2				

(Costa *et al.* 2009, 2015; Ribeiro-Filho *et al.* 2009; Lima *et al.* 2012; Sousa *et al.* 2021). Fabaceae was also identified as the richest family in the current checklist of CPD plants (Fernandes *et al.* 2020). According to Fernandes & Queiroz (2018), Fabaceae is the most diverse family in the CPD due to their adaptations such as deciduousness, small leaves, and the presence of thorns. Various pollination and dispersal systems, as well as

phenological factors, with a large number of entomophilous, autogamous, and zoophilous species, along with the ability to colonize a wide variety of environments, have also been identified by many studies as reasons for this family being the richest in the CPD (Santos *et al.* 2005; Silva *et al.* 2006; Araújo *et al.* 2010; Borges 2010; Brito *et al.* 2010; Neves *et al.* 2011; Guedes *et al.* 2011; Calaça & Vieira 2012; Silva 2018).

Nonetheless, Fabaceae exhibits floristic particularities for the different vegetation types in the CPD (Moro *et al.* 2014; Queiroz *et al.* 2017). This is evidenced by the high percentage of species of Fabaceae that were recorded exclusively in one of the studied vegetation types (53 species or 83.33% of the richness within this family). Of these species with records exclusive to one vegetation type, the majority (35) occurred in natural Crystalline *Caatinga* or natural Tropical Rainforest. Physicochemical characteristics of the

soil are significant filters for plant community assembly, particularly for species of Fabaceae, in the different vegetation types of the CPD (Moro *et al.* 2015).

Research conducted in the Serra do Espinhaço, a mountain range extending from the state of Minas Gerais to the state of Bahia and comprising Savanna, Rupestrian Grassland, Tropical Rainforest, and Semi-Deciduous Forest, reported great species richness for Asteraceae (Zappi 2008; Amorim & Roque 2017; Bautista *et al.* 2017; Staudt *et al.* 2017; Staudt & Roque

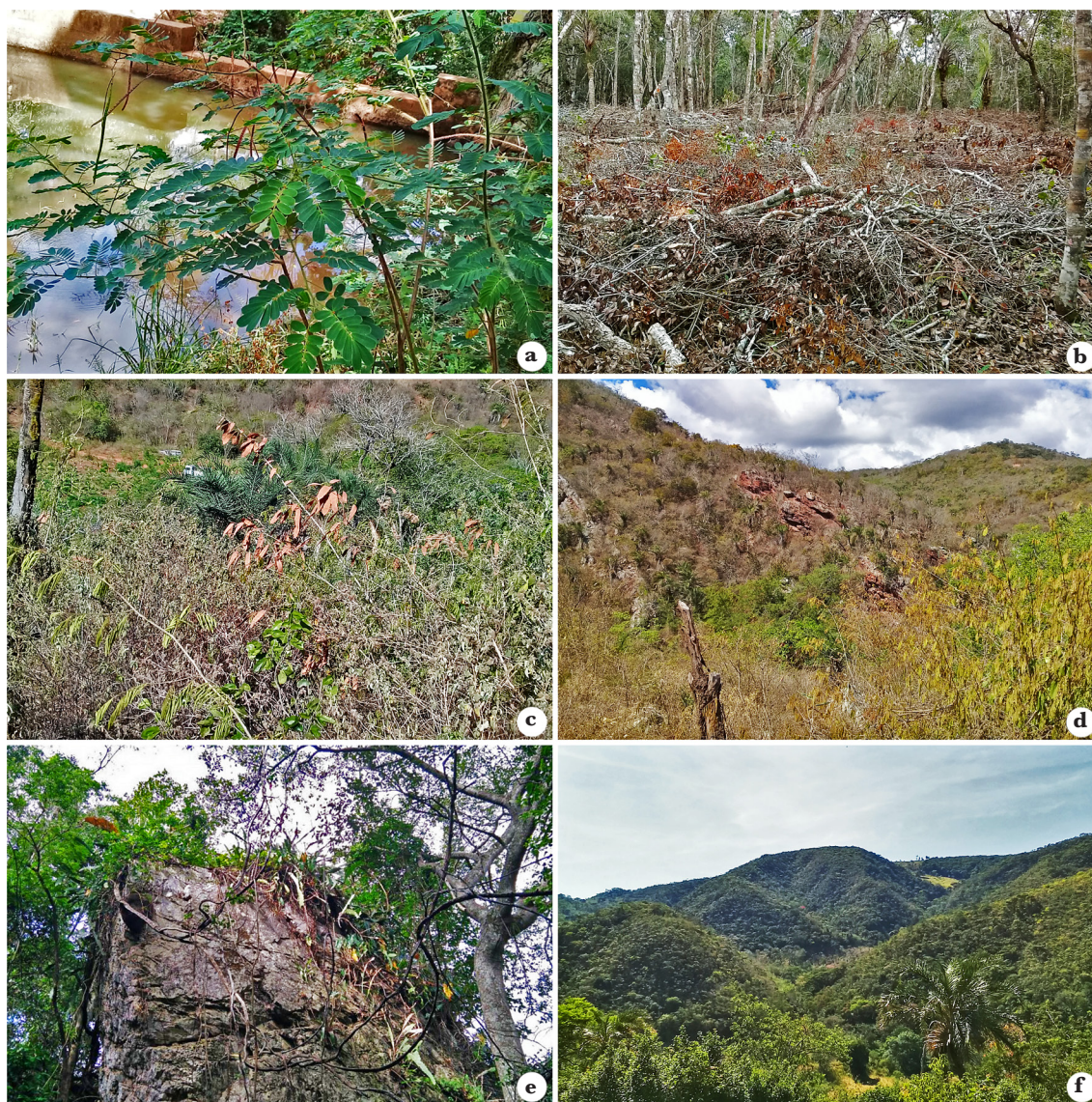


Figure 2 – a-f. Some of the vegetation types of the *Caatinga* Phytogeographic Domain (*sensu* Queiroz *et al.* 2017) recorded in the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex): a. anthropized Aquatic Ecosystem (AEC); b. anthropized Crystalline *Caatinga* (CCA); c. natural Crystalline *Caatinga* (CCn); d. Rupestrian Grassland (RG); e. Rocky Outcrop (RO); f. natural Tropical Rainforest (TRFn). Photographs: Alencar YO.

2020) with abundance being distributed similarly among these vegetation types. Asteraceae is the largest family of angiosperms with an estimated 24,000 to 30,000 species (Souza & Lorenzi 2012), and its radiation in mountainous areas is reflected in endemism within the phytogeographic domains of the *Caatinga* and *Cerrado* (Zappi 2008; Alves & Roque 2016; Staudt & Roque 2020).

The ecotonal character of the study area is evidenced by the variation in floristic composition among the evaluated vegetation types, especially of ubiquitous families of the domain, such as Fabaceae and Rubiaceae (Moreno *et al.* 2003; Lombardi & Gonçalves 2000; Carvalho *et al.* 2007; Pereira & Alves 2007; Joly *et al.* 2012). Thirty-nine species of Fabaceae [e.g., *Cenostigma pyramidale* (Tul.) E. Gagnon & G.P. Lewis and *Mimosa tenuiflora* (Willd.) Poir.] and Rubiaceae [e.g., *Hexasepalum teres* (Walter) J.H.Kirkbr. and *Staelia virgata* (Link ex Roem. & Schult.) K.Schum.] were recorded exclusively in natural Crystalline *Caatinga*, notably in lower regions of Chapada Diamantina. Twenty-nine exclusive species to one vegetation type were observed in regions of higher altitude in the study area, notably within Rupestrian Grassland, Rocky Outcrop, and Tropical Rainforest vegetation types, 15 of which belong to Fabaceae [e.g., *Andira fraxinifolia* Benth., *Anadenanthera colubrina* (Vell.) Brenan, *Inga capitata* Desv., *Periandra mediterranea* Taub., and *Senna splendida* (Vogel)

H.S.Irwin & Barneby.] and 14 to Rubiaceae [e.g., *Alseis floribunda* Schott, *Chiococca alba* (L.) Hitchc., and *Tocoyena formosa* (Cham. & Schltdl.) K. Schum.].

Some species documented in natural or anthropized Tropical Rainforest are notably frequent in various phytophysiognomies of the *Cerrado* Phytogeographic Domain (Marimon & Lima 2001; Silva *et al.* 2002; Sasaki & Silva 2008; Carielo *et al.* 2012), such as: *Achyrocline satureioides* (Lam.) DC., *Desmodium adscendens* (Sw.) DC., *Senna pendula* (Humb. & Bonpl. ex Willd.) H.S. Irwin & Barneby, *Galphimia brasiliensis* (L.) A. Juss., *Miconia rubiginosa* (Bonpl.) DC., *Pleroma heteromallum* (D. Don) D. Don, *Styrax camporum* Pohl, *Myrsine guianensis* (Aubl.) Kuntze, *Palicourea rigida* Kunth,

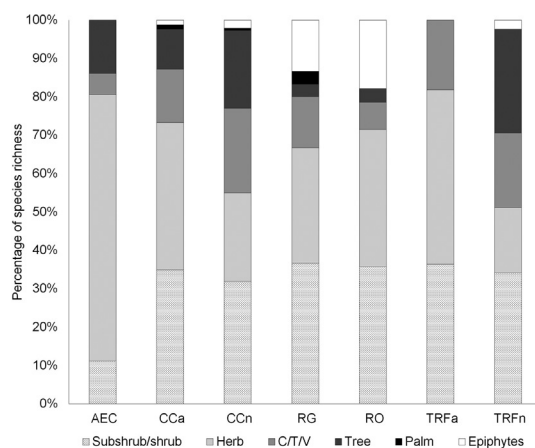


Figure 3 – Percentage of species richness by habit in the studied vegetation types of the *Caatinga* Phytogeographic Domain (*sensu* Queiroz *et al.* 2017) recorded in the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex). Captions: C/T/V = Climber/Twiners/Vine; AEC = anthropized Aquatic Ecosystem; CCa = anthropized Crystalline *Caatinga*; CCn = natural Crystalline *Caatinga*; RG = Rupestrian Grassland; RO = Rocky Outcrop; TRFa = anthropized Tropical Rainforest; TRFn = natural Tropical Rainforest.

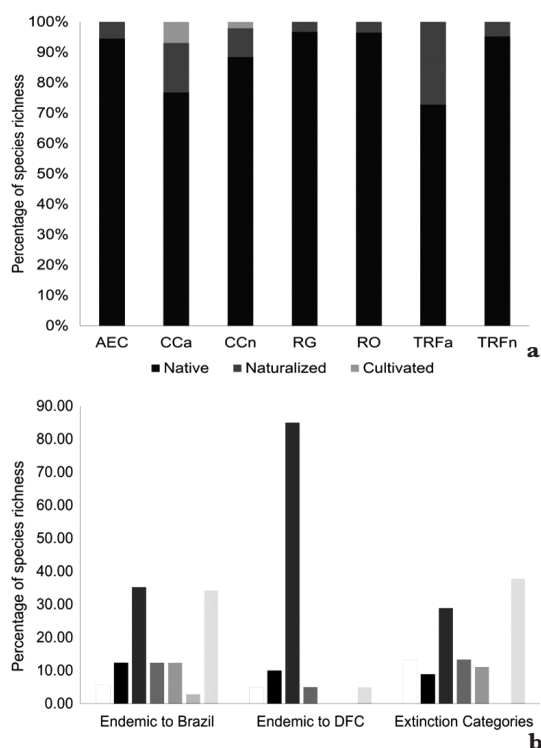


Figure 4 – a. Percentage of species richness by geographic origin (native, naturalized, or cultivated in Brazil) in the vegetation types of the *Caatinga* Phytogeographic Domain (*sensu* Queiroz *et al.* 2017) recorded within the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex); b. Percentage of species richness by endemism categories (Brazil and *Caatinga* Phytogeographic Domain), and by extinction categories in the vegetation types of the *Caatinga* Phytogeographic Domain (*sensu* Queiroz *et al.* 2017) recorded within the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex). Captions: AEC = anthropized Aquatic Ecosystem; CCa = anthropized Crystalline *Caatinga*; CCn = natural Crystalline *Caatinga*; RG = Rupestrian Grassland; RO = Rocky Outcrop; TRFa = anthropized Tropical Rainforest; TRFn = natural Tropical Rainforest.

Anacardium occidentale L., *Annona coriacea* Mart., *Duguetia furfuracea* (A.St.-Hil.) Saff., *Aspidosperma multiflorum* A.DC., *Myrcia tomentosa* (Aubl.) DC., and *Tocoyena formosa* (Cham. & Schltdl.) K. Schum. Therefore, the flora found in this vegetation type resembles that of different domains with notable bioclimatic seasonality (Silva 2008).

The Rocky Outcrop vegetation type in the study area showed great species richness of Orchidaceae, Bromeliaceae, and Cactaceae, which constitute taxonomic oligarchies adapted to rocky soils (Queiroz *et al.* 2017). Fabaceae and Asteraceae are ubiquitous families in patches of Rupestrian Grassland in different areas of the CPD (Conceição & Pirani 2005, 2007; Neves & Conceição 2010). The predominance of subshrub and Herb species in the studied Rupestrian Grassland and Rocky Outcrop sites was expected, as it is something already reported in the phytophysognomic description of the CPD and is notably linked to the grassland formation rather than the forest formation of these vegetation types (Queiroz *et al.* 2017).

The low number of species found in the

Rocky Outcrop and Rupestrian Grassland sites, especially of epiphytes, corroborates the results of other studies in Chapada Diamantina, as similarly low numbers or no species of this habit were found (Conceição & Pirani 2005, 2007; França *et al.* 2010; Ribeiro-Filho *et al.* 2009; Neves & Conceição 2010; Couto *et al.* 2011). The low species richness found for these vegetation types is mainly related to the difficulty of accessing these locations. Steep escarpments in privately owned areas with difficult access were indeed obstacles to a broader sweep of these two vegetation types. Furthermore, studies indicate that the low representativeness of epiphytes can be due to a low number of individuals of *Syagrus coronata* (a palm known as licuri), which is one of the main phorophytes in the wetter *Caatinga*, as it contains more humid microenvironments in the spaces between the leaf sheaths in the crown that are essential to species of this habit (Castro *et al.* 2016; Carvalho *et al.* 2020; Rebouças *et al.* 2021). Many individuals of *S. coronata* were felled in the study area to make way for pasture or banana (*Musa* sp.) plantations.

The greater number of species in natural Crystalline *Caatinga* vegetation, as well as the high richness of subshrub/shrub species of Fabaceae and the high percentage of native and endemic species (to Brazil and/or the *Caatinga*) in this vegetation, was not surprising. This vegetation type occupies the largest portion of the CPD (Moro *et al.* 2014; Fernandes *et al.* 2020), has the highest number of endemic species in the domain (Queiroz *et al.* 2017), and has a significant representation of subshrub/shrub species of Fabaceae in its total richness (Andrade *et al.* 2005; Costa *et al.* 2009, 2015; Ribeiro-Filho *et al.* 2009; Lima *et al.* 2012). The number of Climber/Twiners/Vine species recorded in Crystalline *Caatinga* is noteworthy. Some floristic studies indicate that the frequency of Climber/Twiners/Vine species in the CPD is related to the proximity of higher and more humid areas; this may explain the greater richness in these habits in ecotonal areas within the domain (Conceição & Pirani 2005, 2007; Ribeiro-Filho *et al.* 2009; França *et al.* 2010; Neves & Conceição 2010; Couto *et al.* 2011).

The families with the greatest representation in the richness of the studied natural and anthropized Aquatic Ecosystem vegetation are among the richest in the checklist of aquatic plants of Northeast Brazil (Moura-Júnior & Cotarelli 2019) and of the CPD (Cordova *et al.* 2022). Cyperaceae and Poaceae have vegetative propagation and fast-growing root systems (Souza & Lorenzi 2012), which may explain the strong representation of the former (especially *Cyperus*) in the studied anthropized Aquatic Ecosystem vegetation. Moreover, species of Cyperaceae adapt well to floodable areas or ecotones between terrestrial

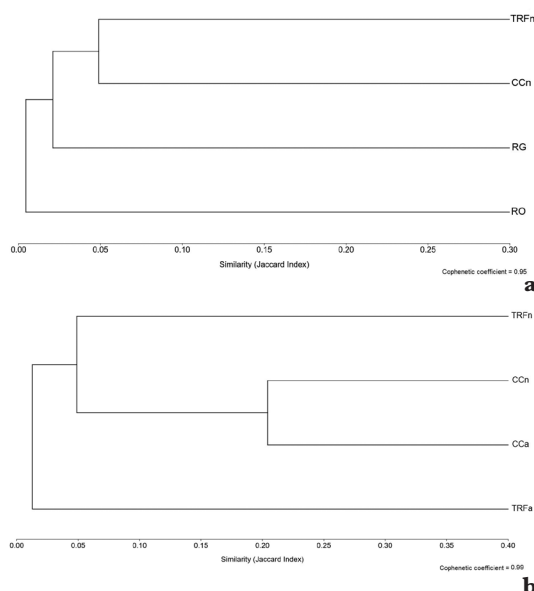


Figure 5 – a-b. Dendrograms of floristic similarity (computed with Jaccard index and UPGMA) between vegetation types of the *Caatinga* Phytogeographic Domain (*sensu* Queiroz *et al.* 2017) recorded in the study area (Serra de Santana, geo-environmental unit of the Chapada Diamantina complex) – a. dendrogram of floristic similarity generated with natural vegetation types; b. dendrogram of floristic similarity generated with natural vegetation types and anthropized Tropical Rainforest and Crystalline *Caatinga*. Captions: CCa = anthropized Crystalline *Caatinga*; CCn = natural Crystalline *Caatinga*; RG = Rupestrian Grassland; RO = Rocky Outcrop; TRFa = anthropized Tropical Rainforest; TRFn = natural Tropical Rainforest.



Figure 6 – a-k. Representatives of some botanical families recorded in the different vegetation types of the Caatinga Phytogeographic Domain found in the study area – a. anthropized Aquatic Ecosystem - *Costus spiralis*; b. anthropized Crystalline Caatinga - *Callianthe pickelii*; c. *Euphorbia comosa*; d. natural Crystalline Caatinga - *Jacquemontia nodiflora*; e. *Passiflora cincinnata*; f. Rupestrian Grassland - *Clidemia hirta*; g. *Perianthra mediterranea*; h. Rocky Outcrop - *Begonia grisea*; i. *Encyclia oncidoides*; j. *Centropogon cornutus*; k. natural Tropical Rainforest - *Habenaria rodeiensis*. Photographs: Alencar YO

and aquatic environments (Souza & Lorenzi 2012), which also explains the richness of the family in the of the studied Aquatic Ecosystem vegetation. The shallow depth, minimal wind influence, and long presence of water in the Aquatic/Terrestrial Transition Zone (ATTZ; Wantzen *et al.* 2008) make it more favorable to amphibious aquatic Herb plants (notably of Cyperaceae and Poaceae) in the Aquatic Ecosystem vegetation of the CPD (Moura-Júnior & Cotarelli 2019). Although less rich and frequent than Cyperaceae and Poaceae in the Aquatic Ecosystem vegetation of the CPD, Nymphaeaceae is a conspicuous family in this vegetation type, especially in temporary ponds (Queiroz *et al.* 2017), which is corroborated by the records in the study area.

Most of the species native or endemic to Brazil or the CPD observed in the studied area have been recorded in other floristic lists of the CPD, especially in natural Crystalline *Caatinga* (Andrade *et al.* 2005; Araújo *et al.* 2005; Costa *et al.* 2009, 2015; Neves & Conceição 2010; Lima *et al.* 2012; Lucena *et al.* 2015; Paulino *et al.* 2018; Sousa *et al.* 2021; Pifano *et al.* 2023). Of the recorded naturalized species, seven are listed in a set of studies compiled by Araújo (2021) for the CPD: *Amaranthus spinosus* L., *A. viridis* L., *Bidens pilosa* L., *Emilia fosbergii* Nicolson, *Commelina benghalensis* L., and *Desmodium adscendens* (Sw.) DC.

Among the endangered species recorded, *Lafoensia glyptocarpa* Koehne (Endangered) stood out, as it is very frequent in the *Cerrado* Phytogeographic Domain (*sensu* Flora e Funga do Brasil 2025, continuously updated), although it is less frequently noted in the Atlantic Forest Phytogeographic Domain or within the CPD, but not in the state of Bahia (SpeciesLink 2025). Most of the species categorized as Least Concern are notably frequent in the CPD, including within the state of Bahia (*sensu* Flora e Funga do Brasil 2025, continuously updated). This is reinforced by some floristic surveys conducted in other areas of the CPD, and include species such as the following: *Alternanthera tenella* Colla (Lima *et al.* 2012; Lucena *et al.* 2015), *Trichilia hirta* L., *Campomanesia eugenoides* (Cambess.) D.Legrand ex Landrum, *Sideroxylon obtusifolium* (Roem. & Schult.) T.D.Penn. (Costa *et al.* 2015), and *Paliavana tenuiflora* Mansf. (Pitrez 2006; Conceição & Pirani 2007; Ribeiro *et al.* 2009).

The new records of species for the CPD highlight the importance of the present floristic survey in expanding the known geographical distribution of plant taxa in the domain and demonstrating that there are still gaps in the ecological and biogeographical knowledge of these taxa, especially in ecotonal areas. Therefore, it is evident that the field efforts of the present study addressed the two main biodiversity shortfalls - Linnaean and Wallacean - in an extensive territory

of the CPD. These shortfalls represent a gap between current and actual knowledge, either about taxonomic diversity (Linnaean) or about the geographical distribution of species (Wallacean), mainly due to the human limitation of accessing certain habitats (Hortal *et al.* 2015).

In summary, the present study recorded many angiosperm species for the Northern Piedmont region of Chapada Diamantina, most of which are native to Brazil. The high number of species with records exclusive to one of the studied vegetation types highlights their distinctive compositions, as confirmed by similarity analysis. More sites of Crystalline *Caatinga* vegetation were recorded in the lower areas (500–700 meters), which had a flora rich in subshrub/shrub species of Fabaceae and Asteraceae, as well as high richness of species native and endemic to Brazil or the CPD, compared to the other studied vegetation types. Higher altitudes (above 700 meters) contained a conspicuous composition of Rupestrian Grassland (Fabaceae, Asteraceae and Rubiaceae) and Rocky Outcrop (*e.g.*, Bromeliaceae, Orchidaceae and Cactaceae) vegetation types rich in Herb, subshrub/shrub and epiphytes species, as well as Tropical Rainforest vegetation (*e.g.*, Asteraceae, Rubiaceae and Myrtaceae), notably tree or subshrub/shrub.

Results of surveys in extensive ecotonal areas, such as the Northern Piedmont region of Chapada Diamantina, are fundamental to addressing biodiversity shortfalls (mainly Linnaean, Wallacean) and supporting other studies with various approaches to biodiversity, especially in conservation biology. The strong anthropic pressure exerted in the low areas of *Caatinga* (Pifano *et al.* 2023) and the projections of biotic homogenization and mass extinction of plant species in the southern CPD, where Chapada Diamantina is located, by the end of this century (Moura *et al.* 2023), exemplify the importance of studies like the present one in the context of conservation biology. After all, decisions impacting the future of biodiversity cannot be made without understanding the biological communities of the past and how they are being transformed in the present.

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Data Availability Statement

In accordance with Open Science communication practices, the authors inform that all data used to prepare this manuscript are available in the Supplementary Material (Table S1, available on supplementary material <10.6084/m9.figshare.28800617>).

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