

## Original Paper

# Floristics, phytosociology and biogeography of capitinga vegetation in a white sand habitat in the Chapada Diamantina Mountains, Brazil

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### Abstract

Capitinga is poorly studied vegetation growing on small, scattered islands of fine, white sand surrounded by the latosol forests on the eastern flank of the Chapada Diamantina Mountains in northeastern Brazil. Our study characterized *capitinga* vegetation, its environmental features, and compared its flora with the vegetation mosaic within the Espinhaço and Chapada Diamantina ranges. Floristic data was collected from 1999-2006, and phytosociological surveys were undertaken in 2004-2005 and 2016-2017 within fifteen 50 x 2 m plots (100 m<sup>2</sup> each, 1500 m<sup>2</sup> in total). Multivariate grouping and ordination analysis were used to examine the floristic affinities of capitinga vegetation. Sixty different species from 36 families were recorded overall, while a total of 4945 individuals distributed among 25 families and 33 species were recorded in the plots. The richest families were Fabaceae (7) and Apocynaceae (5), while the most abundant families were Arecaceae (61.5% of all individuals) and Velloziaceae (18.4%), represented by *Syagrus harleyi* and *Vellozia dasypus* respectively. Capitinga represents a distinct habitat conditioned by edaphic features, and its flora is unlike other vegetations in the Espinhaço or Chapada Diamantina ranges, with several locally endemic species.

**Key words:** conservation, diversity, flora, northeastern Brazil.

### Resumo

Capitinga é uma vegetação pouco estudada que cresce em pequenas ilhas de areia branca e fina e cercadas por florestas de latossolo no lado leste das Montanhas da Chapada Diamantina, no nordeste do Brasil. Nosso estudo caracterizou a vegetação da capitinga, suas características ambientais e comparou sua flora com as faixas de mosaico da vegetação do Espinhaço e da Chapada Diamantina. Os dados florísticos foram coletados de 1999-2006 e os levantamentos fitossociológicos foram realizados em 2004-2005 e 2016-2017 em quinze parcelas de 50 x 2 m (100 m<sup>2</sup> cada, totalizando 1500 m<sup>2</sup>). O agrupamento multivariado e a análise de ordenação foram utilizados para examinar a similaridade florística da vegetação da capitinga. No total foram registradas sessenta espécies distribuídas em 36 famílias, enquanto nas parcelas foi registrado um total de 4945 indivíduos distribuídos em 25 famílias e 33 espécies. As famílias mais ricas foram Fabaceae (7) e Apocynaceae (5), enquanto as mais abundantes foram Arecaceae (61.5% de todos os indivíduos) e Velloziaceae (18.4%), representadas por *Syagrus harleyi* e *Vellozia dasypus* respectivamente. Capitinga representa um hábitat distinto condicionado por características edáficas e sua flora é diferente de outras vegetações nas áreas do Espinhaço e da Chapada Diamantina, com várias espécies endêmicas.

**Palavras-chave:** conservação, diversidade, flora, nordeste do Brasil.

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## Introduction

Brazil is known for its megadiversity, being the richest country in the world in terms of plant species (Forzza *et al.* 2010; BFG 2015), with plant diversity and endemism levels being especially high in the Espinhaço Range and Chapada Diamantina Mountains (Giulietti *et al.* 1997; Zappi *et al.* 2017). The Espinhaço Range and the Chapada Diamantina extend from the edge of the Cerrado (neotropical savanna) and Atlantic Forest phytogeographical domains in southeastern Brazil into the Caatinga (dry land vegetation) phytogeographical domain in the northeastern region of that country (Alkmim 2012; Zappi *et al.* 2017). The Chapada Diamantina highlands constitute the northernmost extent of the Espinhaço Range and is an ecoregion with its own endemism within the Caatinga domain (Veloso *et al.* 2002).

The Chapada Diamantina harbors different floras and vegetation types within its climatic and altitudinal gradients, including caatinga vegetation in the dry foothills, forests in the more humid sections of the range, and savannas and rupestrian grassland (*campos rupestres*) in the highest mountain areas (Harley 1995; Giulietti *et al.* 1997; Juncá *et al.* 2005; Moro *et al.* 2016; Zappi *et al.* 2017). In addition to those well-documented habitats, there is much less studied vegetation locally known as capitinga. Capitinga vegetation grows on small, scattered, and isolated “islands” of deep white quartzs and surrounded by tall latosol forests (Funch *et al.* 2009). Those small patches of nutrient-poor, sandy soils support plant communities with low, shrubby physiognomies embedded in extensive humid forests that develop on richer clayey soils. Capitinga vegetation is low and open, with many shrubs, acaulescent palms, as well as scattered and infrequent small trees and cacti (Funch *et al.* 2009).

Numerous studies have shown that plant species distributions are dominated by edaphic and topographic variability at different spatial scales (e.g. Bohlman *et al.* 2008; Damasco *et al.* 2013). In the Amazonian region, for example, structural variations of white-sand vegetation can be related to flooding gradients (Vicentini 2004), with forests being replaced by open vegetation as flooding frequencies increase or groundwater approaches the surface.

The forests on the eastern side of the Chapada Diamantina highlands are considered disjunct patches of Atlantic Forest (Oliveira-Filho

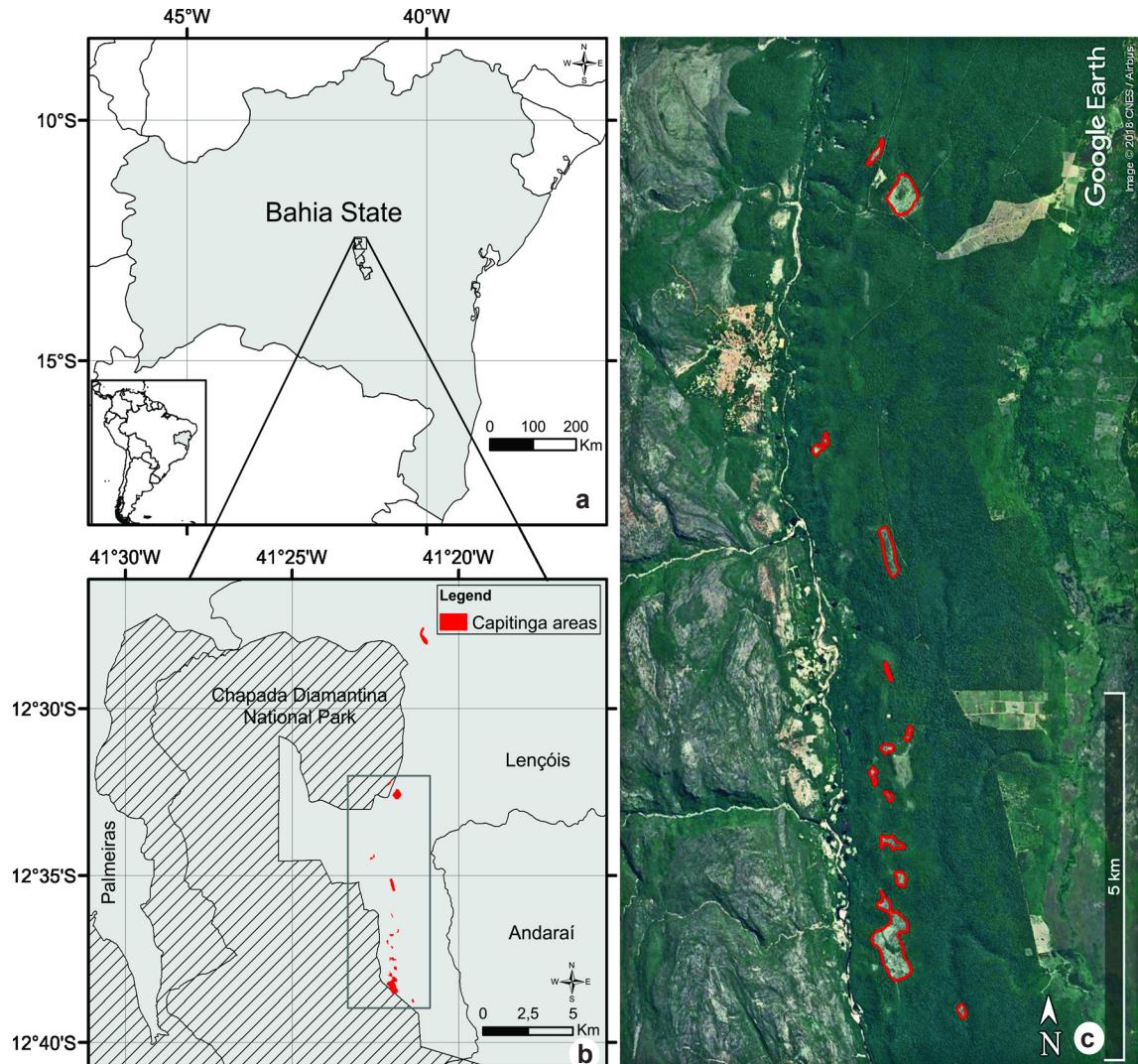
& Fontes 2000; Funch *et al.* 2008; Couto *et al.* 2011, 2015), but the sandy and shrubby capitinga ecosystems embedded in them have not yet been studied in terms of their structural, floristic, and biogeographical patterns. As relatively few biogeographic studies have focused on the floristic relationships of mountain vegetation (Vasconcelos & Rodrigues 2010; Ribeiro *et al.* 2012; Hughes *et al.* 2013; Barros *et al.* 2015; Silveira *et al.* 2016), we sought to characterize capitinga vegetation and its environmental features, record its floristic diversity, and compare the capitinga flora with the more typical vegetation mosaic (forest, caatinga, savanna, and rupestrian grasslands) within the Espinhaço and Chapada Diamantina ranges in a biogeographic analysis.

## Materials and Methods

### Study area

The Chapada Diamantina highlands consist of a series of mountains above 1,000 m a.s.l. within the Caatinga domain in northeastern Brazil. The Sincorá Range composes the eastern face of the Chapada Diamantina and extends approximately 200 km from north to south. The study areas are located in the municipality of Lençóis, Bahia State, Brazil (12°27'–12°38'S and 41°21'–41°22'W) at approximately 500 m a.s.l. in the Sincorá Range, along the eastern edge of the Chapada Diamantina National Park (Fig. 1). The Sincorá mountains are composed largely of fractured sandstones and quartzites of the Tombador Formation (CPRM 1994), with correspondingly nutrient-poor soils (Harley 1995). The predominant climates in the Caatinga domain are the semiarid BSh and Tropical AS (Alvares *et al.* 2013), both having reduced rainfall and very strong seasonality (Nimer 1972).

Although a semiarid climate predominates in the Caatinga, the Chapada Diamantina has a more heterogeneous rainfall gradient due orographic rains, with areas on the eastern (windward) faces of the mountains experiencing increased precipitation that allows seasonal and humid forests to flourish (Juncá *et al.* 2005; Moro *et al.* 2016) on the eastern slopes of the Sincorá Range on red-yellow and clayey latosols (Funch *et al.* 2008). Within that latosol matrix, however, are islands of fine, deep, well-drained white quartz sands (Funch *et al.* 2009). The capitinga sites studied are located along the eastern edge of the Chapada Diamantina National Park, and within the boundaries of the



**Figure 1** – a. Map of Bahia state, Brazil, showing the location of the Chapada Diamantina National Park. b. Chapada Diamantina National Park and the capitinga islands. c. Satellite image of capitinga patches within the evergreen broadleaf forest matrix (right half of the image) along the eastern edge of the Sincorá Range (left half of the image). Image source: Google Earth.

Marimbús/Iraquara Environmental Protection Area. The capitinga areas are traditionally used by local populations to collect wild *mangaba* fruits (*Hancornia speciosa* Gomes), but they have essentially no agricultural vocation. The regional climate is mesothermic, with a rainy season between November and April and a dry season of five months, usually between June and October (Nimer 1972). Mean monthly temperatures vary between 18 and 25 °C, and the mean annual rainfall is 1218 mm (data provided by the Brazilian Meteorological Institute).

### Sampling

The white sand capitinga vegetation sites correspond to a total area of 106 hectares in the region. Floristic data was collected in capitinga patches from 1999-2006, and phytosociological surveys were made in 2004-2005 and 2016-2017 in 15 randomly placed 50 × 2 m plots (100 m<sup>2</sup> each plot, 1500 m<sup>2</sup> total). The first sampling plot was selected at random, the rest defined at regular intervals (5 m) from the initial plot. All plant species (both herbaceous and woody) included in the plots were surveyed, and the numbers of individuals of

each species and their total percentage cover were recorded. In order to account for plants overlapping the plot lines, the following inclusion/exclusion criterion was used: individuals touching the upper or right-hand lines of the plots were included in the sample, while those touching the lower or left-hand lines were excluded. For counting plants showing difficulty of individualization (such as *Vellozia dasypus* Seub. and *Syagrus harleyi* Glassman),"clumps" were considered individuals, and the total numbers of clumps of each species were treated as populations. The species were also classified in the field according to their life forms, as: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes/geophytes, or terophytes (following Raunkiaer 1934).

Vegetation profile diagrams were elaborated according to Kershaw & Looney (1985), adapted to the study area, to obtain a structural image of the vegetation. The three randomly selected vegetation sampling lines took radial directions, 30 m long by 2 m wide, delimited by a track. All individuals were noted, as well as their heights. The transects were filmed to assist the elaboration of the schematic drawings and accurately depict canopy shapes. All species were identified, and vouchers deposited in the State University of Bahia at Feira de Santana herbarium (HUEFS). Identifications were made using the published literature, by expert consultations, and by comparisons with material available in the Brazilian virtual herbarium (<<http://www.splink.org.br/index?lang=pt>>). Botanical family circumscriptions follow the Angiosperm Phylogeny Group IV system (APG IV 2016); the spellings of all names were verified using the Flora do Brasil 2020 database (under construction) (<<http://floradobrasil.jbrj.gov.br/>>). Supplementary data associated with this article can be found at: <<https://doi.org/10.6084/m9.figshare.7822556>>.

### Data analyses

The following phytosociological parameters were calculated by location according to Mueller-Dombois and Ellenberg (2002): absolute density (AD), relative density (RD), absolute frequency (AF), and relative frequency (RF). Multivariate grouping and ordination analyses were used to compare the biogeographical floristic affinities of the capitinga with other vegetation types (Legendre & Legendre 2012) based on two recent biogeographical databases. Moro *et al.* (2016) developed a database of species occurrences in the

Caatinga domain and Zappi *et al.* (2017) elaborated a similar database for the Espinhaço Range and the Chapada Diamantina highlands. We extracted species occurrences in the main vegetation types of the region from those two databases: caatinga vegetation growing on crystalline terrains of the lowland Sertaneja Depression (caatinga *sensu stricto*); caatinga growing on lowland sandy terrains of sedimentary basins (sandy caatinga); and forest and open vegetation (rupestrian grasslands and savannas) in the Espinhaço Range and the Chapada Diamantina highlands growing on quartzite, canga (iron ore), and sandy substrates.

We thus selected the main habitat types of both the Espinhaço Range and the Chapada Diamantina highlands (Zappi *et al.* 2017) as well as the two main caatinga types in the surrounding semiarid lowlands (Moro *et al.* 2016) to compare them with the capitinga flora. We merged the selected sites of the two databases, added the capitinga list, and updated all species names using the Flora do Brasil 2020 database - <http://floradobrasil.jbrj.gov.br/> (BFG 2015) using the Plant Miner script - <<http://plantminer.com/>> (Carvalho *et al.* 2010), generating a database with species occurrences of the main vegetation types in the region (with updated nomenclatures). We then performed a UPGMA grouping analysis and NMDS ordination analysis using Bray-Curtis distances (Legendre & Legendre 2012). Multivariate analyses were performed using PAST software (Hammer *et al.* 2001) to compare the floristic links of the capitinga with other environments. We also created Venn diagrams to show the numbers of species shared between capitinga and the other environments.

### Results

Along the eastern border of the Chapada Diamantina, where this study was undertaken, capitinga vegetation is distributed in a patchy pattern on dystrophic sandy soils with rapid drainage under the influence of a moderately seasonal climate (3+ dry months). There is very little accumulated organic matter on the sandy soil surface, and the rhizosphere is a very dense entanglement, which favors capitinga establishment, as just a few meters from those white sand patches are dense humid forests (see the drone video in the supplementary data).

Capitinga vegetation demonstrates a physiognomy similar to coastal restinga scrub vegetation, with its planar relief and deep sandy soils (Fig. 2). The compact capitinga rhizosphere



**Figure 2 – a-c.** Physiognomy of the local vegetation, showing *Syagrus harleyi* Glassman, *Vellozia dasypus* Seub., and *Stephanocereus luetzelburgii* (Vaupel) N.P.Taylor & Eggli; **d.** soil profile; **e-f.** underground trees (*Andira humilis* Mart. ex Benth.) with golden leaves and green fruits.

that develops continuously below a thin layer of white sand (1–2 cm) is quite thick (30–40 cm). Figure 3 shows the clumped vegetation on the sandy soils surrounded by seasonal forests growing on deep clayey latosols. The capitinga vegetation is composed of scattered herbs and shrubs among dense clumps of *Syagrus harleyi*, *Calliandra linteae* Barneby, and *Stephanocereus luetzelburgii* (Vaupel) N.P.Taylor & Eggli (among others). The clumps are sometimes formed almost exclusively by *Vellozia dasypus*. Underground trees (*Anacardium humile* A.St.-Hil. and *Andira humilis* Mart. ex Benth.) occur sporadically. Figure 4 shows profile diagrams demonstrating the different physiognomies in the study sites, with sparse trees that can reach up to 7 m in height, such as *Hancornia speciosa* and *Humiria balsamifera* (Aubl.) A.St.-Hil.

### Floristic composition and vegetation structure

Our study recorded 60 species from 36 families (Tab. 1); three species could only be identified to the genus level. Twenty-four species were shrubs (43.7%), 15 herbaceous (23.4%), six sub-shrubs (9.3%), eight trees (12.5%), and seven vines (9%). Phanerophytes predominated (45 species; 76.5%), followed by hemicryptophytes (7; 10.9%), cryptophytes (4; 6.2%), terophytes (3; 4.6%), and chamaephytes (1; 1.5%). The richest families were Fabaceae (7 species), Apocynaceae (5), Asteraceae (3), Eriocaulaceae (3), Euphorbiaceae (3), and Rubiaceae (3). The sum of the richnesses of those six families represented 46.87% of all species surveyed. The remaining species were distributed in 30 families. The genus with the highest species richness was *Paepalanthus*, with three species; four genera were represented by two species, and 49 genera by only one.

A total of 4945 individuals of all habits were recorded in the 0.15 ha sample plots, distributed in 25 families, 32 genera and 33 species (Tab. 2). The most abundant families were Arecaceae (61.5% of all sampled individuals and represented by only one palm species: *Syagrus harleyi*), Velloziaceae (18.4% of all individuals, with only one species: *Vellozia dasypus*), Poaceae (4.9%, with two species: *Axonopus* sp. and *Renvoizea trinii* (Kunth) Zuloaga & Morrone), Fabaceae (4.1%, with two species: *Andira humilis* and *Calliandra linteae*), and Euphorbiaceae (1.8%, with two species: *Manihot jacobinensis* Müll.Arg. and *M. caeruleascens* Pohl). The five most important species (*Syagrus harleyi*,

*Vellozia dasypus*, *Axonopus* sp., *Calliandra linteae*, and *Stephanocereus luetzelburgii*) were responsible for 89.7% of the DA in the capitinga, occurring in all plots (93% - 100% FA) – and indicating that only a few species have high importance in terms of abundance in these sandy habitats. The highest density in the area was observed with the acaulescent palm, *Syagrus harleyi*, with D = 20287 ind.\*ha<sup>-1</sup>; followed by other herbaceous species (7), with D = 8354 ind.\*ha<sup>-1</sup>; the shrubby-arbooreal component (22 species) with D = 3713 ind.\*ha<sup>-1</sup>; the cactus *Stephanocereus luetzelburgii* (D = 307 ind.\*ha<sup>-1</sup>); and by vines (two species) with D = 247 ind.\*ha<sup>-1</sup>. The most abundant life forms were the cryptophytes *Syagrus harleyi*, *Hippeastrum glaucescens* (Mart.) Herb., and *Mandevilla tenuifolia* (J.C.Mikan) Woodson (D = 20967 ind.\*ha<sup>-1</sup>), chamaephytes *Vellozia dasypus* (D = 6067 ind.\*ha<sup>-1</sup>), phanerophytes with 25 species (D = 4020 ind.\*ha<sup>-1</sup>), the hemicryptophytes *Axonopus* sp., *Renvoizea trinii*, and *Paepalanthus bifidus* (Schrad.) Kunth (D = 1653 ind.\*ha<sup>-1</sup>), and two therophytes (D = 167 ind.\*ha<sup>-1</sup>).

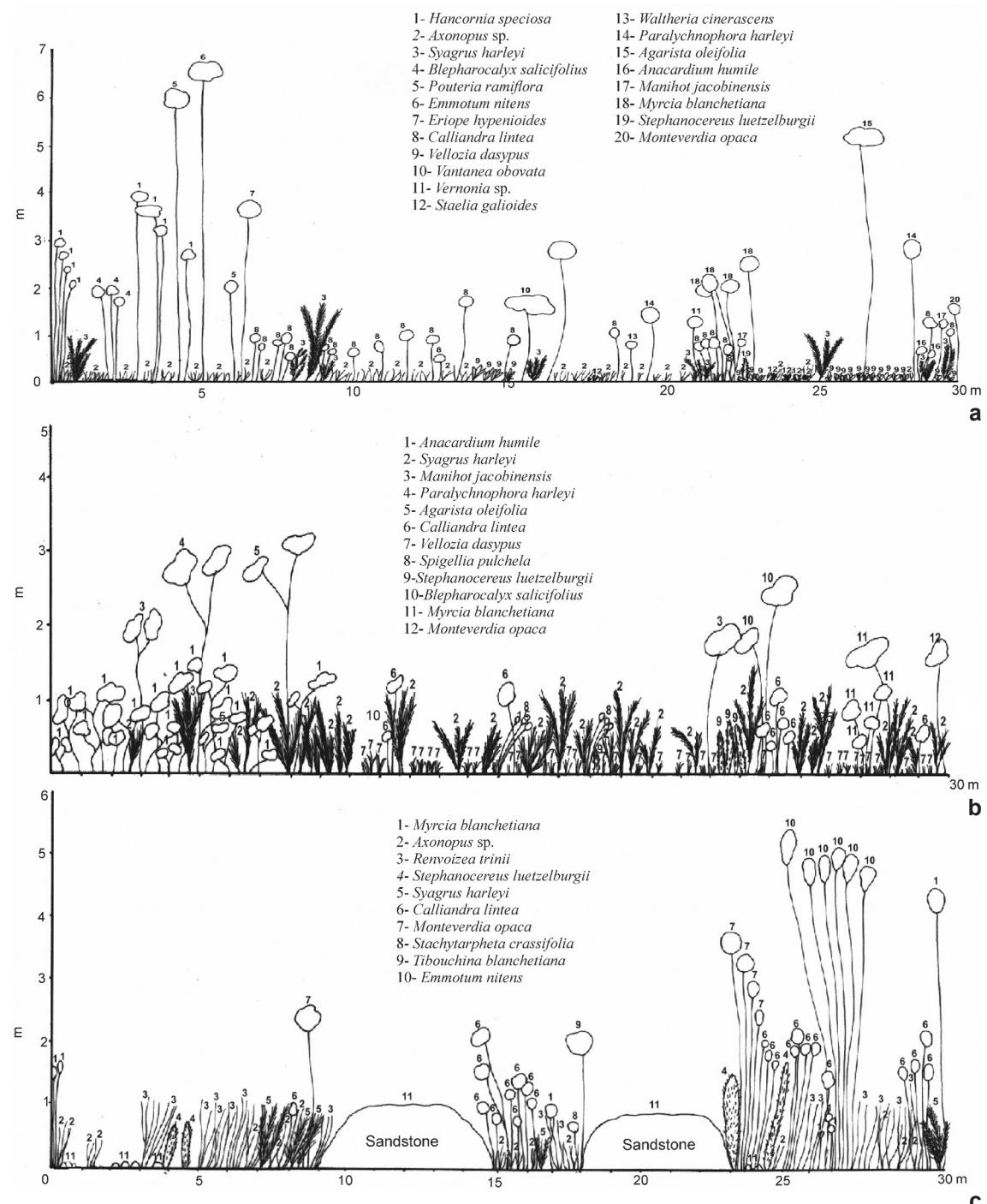
### Floristic relationships of capitinga on a biogeographic scale

Capitinga has a very distinctive flora when compared with other regional habitat types. It was positioned in a distinct position in the NMDS ordination when compared to other habitat types (Fig. 5), with few species in common between them. In the UPGMA group analysis (Fig. 6), the capitinga flora grouped with that of the Espinhaço Range and Chapada Diamantina but was still the most distinctive flora within the Espinhaço Range-Chapada Diamantina complex.

In group and ordination analyses (Figs 5; 6), an important influence of substrate on local floras can be seen. The substrates in the Espinhaço Range-Chapada Diamantina complex formed (with one exception) two groups: the flora on quartzite and the flora on canga (iron-rich substrates). The capitinga was grouped within this Espinhaço Range-Chapada Diamantina complex, but with a very distinctive flora that was more closely related to the vegetation on the quartzite substrate (the rupestrian grasslands) as they shared 41 species—but only 15 species with other geographically distant sandy sites in the Espinhaço Range (Fig. 7). Floristic links with the caatinga vegetation on the lowlands were found to be negligible (Fig. 7). Thus, although the capitinga is floristically related to the highlands, it harbors a very different species



**Figure 3** – Aerial photographs of the study site – a-b. distribution of *Syagrus harleyi* Glassman and *Vellozia dasypus* Seub.; c-f. contact area between sandy soil capitinga and evergreen forest on deep clayey soil; note in e that the more densely vegetated area in the center of the white sand site represents a rocky area from which the white capitinga sands are derived. An aerial video is provided in the Supplementary Data.



**Figure 4** – Profile diagram of three locations of capitinga vegetation in the Chapada Diamantina, Bahia state, Brazil – a. transition between the capitinga scrub and the surrounding forest; b-c. profile of typical capitinga vegetation.

**Table 1** – Floristic composition, habit, and life-forms of capitinga vegetation in the Chapada Diamantina Range, northeastern Brazil. Habits: Ca – Cactus, Hb – Herbs, Sb – Shrubs, Ss – Sub-shrubs, Te – Trees, Vi – Vines. Life forms: Ch – Chamaephytes, Cr – Cryptophytes, He – Hemicryptophytes, Ph – Phanerophytes, Th – Therophytes.

FAMILY/SPECIES	Habit	Life Form	Voucher (HUEFS)
<b>AMARANTHACEAE</b>			
<i>Gomphrena mollis</i> Mart.	Ss	Ph	44012
<b>AMARYLLIDACEAE</b>			
<i>Hippeastrum glaucescens</i> (Mart.) Herb.	Hb	Cr	35219
<b>ANACARDIACEAE</b>			
<i>Anacardium humile</i> A.St.-Hil.	Te	Ph	44046
<b>ANNONACEAE</b>			
<i>Annona coriacea</i> Mart.	Sb	Ph	44017
<b>APOCYNACEAE</b>			
<i>Ditassa retusa</i> Mart.	Vi	Ph	60525
<i>Hancornia speciosa</i> Gomes	Te	Ph	44041
<i>Himatanthus drasticus</i> (Mart.) Plumel	Te	Ph	44059
<i>Mandevilla bahiensis</i> (Woodson) M.F.Sales & Kin.-Gouv.	Vi	Ph	60524
<i>Mandevilla tenuifolia</i> (J.C.Mikan) Woodson	Ss	Cr	44011
<b>ARECACEAE</b>			
<i>Syagrus harleyi</i> Glassman	Hb	Cr	44038;44048;44064
<b>ASTERACEAE</b>			
<i>Acrithopappus confertus</i> (Gardner) R.M.King & H.Rob.	Sb	Ph	44031
<i>Paralychnophora harleyi</i> (H.Rob.) D.J.N.Hind	Sb	Ph	44040;60519
<i>Vernonia</i> sp.	Hb	Ph	51136
<b>CACTACEAE</b>			
<i>Stephanocereus luetzelburgii</i> (Vaupel) N.P.Taylor & Eggli	Ca	Ph	44045
<b>CELASTRACEAE</b>			
<i>Monteverdia opaca</i> (Reissek) Biral	Sb	Ph	44025;44035;44049
<b>COMMELINACEAE</b>			
<i>Commelina erecta</i> L.	Hb	Th	44044
<b>CYPERACEAE</b>			
<i>Bulbostylis capillaris</i> (L.) C.B.Clarke	Hb	He	44062
<b>ERICACEAE</b>			
<i>Agarista oleifolia</i> (Cham.) G.Don	Ss	Ph	44015
<b>ERIOCAULACEAE</b>			
<i>Paepalanthus bifidus</i> (Schrad.) Kunth	Hb	He	51138
<i>Paepalanthus manicatus</i> Poulsen ex Malme	Hb	He	51137
<i>Paepalanthus sessiliflorus</i> Mart. ex Körn.	Hb	He	51139
<b>EUPHORBIACEAE</b>			
<i>Manihot caerulescens</i> Pohl	Sb	Ph	44051;44054;64332
<i>Manihot jacobinensis</i> Müll.Arg.	Sb	Ph	44016;44066;47879
<i>Stillingia saxatilis</i> Müll.Arg.	Sb	Ph	60526
<b>FABACEAE</b>			
<i>Andira humilis</i> Mart. ex Benth.	Te	Ph	48615
<i>Calliandra lineata</i> Barneby	Sb	Ph	44047;44053;44065
<i>Cleobulia multiflora</i> Mart. ex Benth.	Vi	Ph	60522

FAMILY/SPECIES	Habit	Life Form	Voucher (HUEFS)
<i>Dioclea grandiflora</i> Mart. ex Benth.	Vi	Ph	60530
<i>Mimosa arenosa</i> (Willd.) Poir.	Te	Ph	60529
<i>Periandra coccinea</i> (Schrad.) Benth.	Vi	Ph	76382
<i>Swartzia bahiensis</i> R.S.Cowan	Te	Ph	145970
<b>HUMIRIACEAE</b>			
<i>Humiria balsamifera</i> (Aubl.) A.St.-Hil.	Te	Ph	44039
<i>Vantanea obovata</i> (Nees & Mart.) Benth.	Sb	Ph	44023;44034
<b>LAMIACEAE</b>			
<i>Eriope hypenoides</i> Mart. ex Benth.	Sb	Ph	44050
<b>LOGANIACEAE</b>			
<i>Spigelia pulchella</i> Mart.	Hb	Cr	44013;44058
<b>MALVACEAE</b>			
<i>Pavonia harleyi</i> Krapov.	Sb	Ph	44024;44042
<i>Pavonia cancellata</i> (L.) Cav.	Sb	Ph	60521
<i>Waltheria cinerascens</i> A.St.-Hil.	Sb	Ph	44021
<b>MELASTOMATACEAE</b>			
<i>Marctetia macrophylla</i> Wurdack	Sb	Ph	44022;44063
<i>Miconia holosericea</i> (L.) DC.	Sb	Ph	44060
<b>METTENIUSACEAE</b>			
<i>Emmotum harleyi</i> R.Duno	Sb	Ph	44027
<i>Emmotum nitens</i> (Benth.) Miers	Te	Ph	44026;44036
<b>MYRTACEAE</b>			
<i>Blepharocalyx salicifolius</i> (Kunth) O.Berg	Sb	Ph	44020;44033;44055
<i>Myrcia blanchetiana</i> (O.Berg) Mattos	Sb	Ph	44043;44056
<b>MOLLUGINACEAE</b>			
<i>Mollugo verticillata</i> L.	Hb	Th	44030
<b>PENTAPHYLLACEAE</b>			
<i>Ternstroemia brasiliensis</i> Cambess.	Sb	Ph	60527
<b>PLANTAGINACEAE</b>			
<i>Angelonia tomentosa</i> Moric. ex Benth.	Ss	Ph	51140
<b>PORTULACACEAE</b>			
<i>Portulaca hirsutissima</i> Cambess.	Hb	Th	44014
<b>POACEAE</b>			
<i>Axonopus</i> sp.	Hb	He	44019
<i>Renvoizea trinii</i> (Kunth) Zuloaga & Morrone	Hb	He	47886
<b>RUBIACEAE</b>			
<i>Mitracarpus salzmannianus</i> DC.	Ss	Ph	51135
<i>Chomelia parviflora</i> (Müell.Arg.) Müell.Arg.	Ss	Ph	34590
<i>Staelia galiooides</i> DC.	Hb	Ph	44029
<b>RUTACEAE</b>			
<i>Dictyoloma vandellianum</i> A.Juss.	Sb	Ph	60523
<b>SAPINDACEAE</b>			
<i>Serjania lethalis</i> A.St.-Hil.	Vi	Ph	44052
<b>SAPOTACEAE</b>			
<i>Pouteria ramiflora</i> (Mart.) Radlk.	Te	Ph	44061

FAMILY/SPECIES	Habit	Life Form	Voucher (HUEFS)
<b>SMILACACEAE</b>			
<i>Smilax</i> sp.	Vi	Ph	51141
<b>SOLANACEAE</b>			
<i>Solanum thomasiifolium</i> Sendtn.	Sb	Ph	60528
<b>VELLOZIACEAE</b>			
<i>Vellozia dasypus</i> Seub.	Hb	Ch	44032;44037;44057
<b>VERBENACEAE</b>			
<i>Stachytarpheta crassifolia</i> Schrad.	Sb	Ph	44018

pool within the Espinhaço Range-Diamantina complex.

The highland flora is also very different from the caatinga vegetation of the semiarid lowlands surrounding the Chapada Diamantina. The caatinga vegetation on crystalline terrain and the caatinga vegetation on sandy terrain formed different subgroups – but both joined together on a broader scale as a larger group representing the flora of the semiarid lowlands of the Caatinga domain (Fig. 5; 6). The capitinga was positioned midway between both groups in the NMDS analysis, with a larger floristic bond with the highland flora, but still floristically distinct.

## Discussion

Even after 30 years of modern studies of the floristic diversity in the Espinhaço Range/Chapada Diamantina highlands (Harley & Simmons 1986; Harley 1995; Giulietti *et al.* 1997; Funch *et al.* 2009; Zappi *et al.* 2017), floristic, phytosociological, and biogeographic evidence demonstrates that the capitinga is a distinct vegetation type. Capitinga is defined by edaphic features, associated with sandy dystrophic soils with rapid drainage embedded within a latosol matrix occupied by humid forests on the eastern flank of the Chapada Diamantina Mountains (Funch *et al.* 2008; Couto *et al.* 2011, 2015) under a seasonal climate, and numerous studies have demonstrated that plant species' distributions can be associated with edaphic variability at different spatial scales (*e.g.*, Bredenkamp *et al.* 2002; Bohlman *et al.* 2008; Damasco *et al.* 2013; Silva *et al.* 2016).

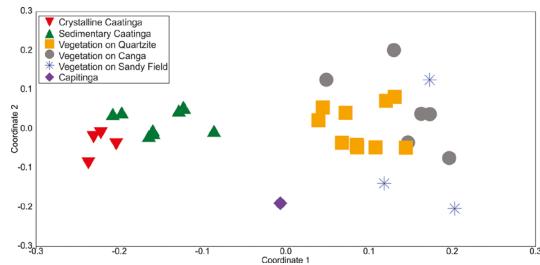
Those sandy vegetation patches physiognomically resemble coastal restinga vegetation (Veloso *et al.* 1991; Martins *et al.* 2008; Scarano 2009; Oliveira-Filho 2009), with

a continuous rhizosphere below the clumped vegetation. Communities result from the interactions of abiotic and biotic filters that select species capable of colonizing a given habitat and maintaining their populations (Lortie *et al.* 2004). White sand vegetations (like capitinga) reflect the interactions between soil characteristics and species attributes of nutrient and water absorption that play important roles in mitigating the effects of water stress (Damasco *et al.* 2013; Fort *et al.* 2016).

The herbaceous-shrub capitinga vegetation is dominated by dense clumps of *Syagrus harleyi* and *Vellozia dasypus* (80 % of all individuals), with cryptophytes and chamaephytes therefore representing the most abundant life forms (density = 27034 ind.\*ha<sup>-1</sup>). Similarly, the high importance of cryptophytes in restinga vegetation is evidenced by the abundance of Arecaceae species, such as *Allagoptera arenaria* (Gomes) Kuntze (Pereira *et al.* 2004) adapted to the seasonal stress imposed by drought as well as nutrient deficiency conditions (Sarmiento & Monasterio 1983). Phanerophytes are important in the capitinga flora in terms of their high numbers of species, in spite of their low abundances. The under-representation of therophytes in capitinga vegetation shows that herbaceous species (annual plants) do not develop abundantly in those sandy sites (Sarmiento & Monasterio 1983). Therophytes growing on poor soils must obtain new compliments of scarce nutrients each year in order to grow, which is problematic on poor soils like those in the Chapada Diamantina and Espinhaço Range. Therophytes are richer in the shallow and nutrient-rich semiarid caatinga soils derived from crystalline basement formations (Queiroz *et al.* 2015; Moro *et al.* 2016), but much less prominent components in caatinga floras growing on sandy sites in sedimentary basins (Moro *et al.* 2016) – reinforcing the idea

**Table 2.**—Structural parameters of the species found in capitinga vegetation plots in the Chapada Diamantina Range, northeastern Brazil. N – Number of individuals of the species, AD – Absolute Density, RD – Relative Density, AF – Absolute Frequency, RF – Relative Frequency, Pi – Number of parcels in which the species occurred.

Species	N	AD	RD	pi	AF	RF
<i>Syagrus harleyi</i>	3043	20287	63,40	15	100	1,35
<i>Vellozia dasypus</i>	910	6067	18,96	15	100	1,35
<i>Axonopus</i> sp.	235	1567	4,90	14	93	1,26
<i>Calliandra linteae</i>	202	1347	4,21	14	93	1,26
<i>Manihot jacobinensis</i>	69	460	1,44	10	67	0,90
<i>Hippeastrum glaucescens</i>	66	440	1,38	3	20	0,27
<i>Agarista oleifolia</i>	48	320	1,00	12	80	1,08
<i>Stephanocereus luetzelburgii</i>	46	307	0,96	14	93	1,26
<i>Myrcia blanchetiana</i>	43	287	0,90	7	47	0,63
<i>Spigelia pulchella</i>	42	280	0,88	11	73	0,99
<i>Mandevilla tenuifolia</i>	36	240	0,75	9	60	0,81
<i>Blepharocalyx salicifolius</i>	27	180	0,56	7	47	0,63
<i>Waltheria cinerascens</i>	27	180	0,56	6	40	0,54
<i>Portulaca hirsutissima</i>	24	160	0,50	9	60	0,81
<i>Manihot caerulescens</i>	20	133	0,42	4	27	0,36
<i>Stachytarpheta crassifolia</i>	20	133	0,42	3	20	0,27
<i>Emmotum nitens</i>	14	93	0,29	6	40	0,54
<i>Hancornia speciosa</i>	12	80	0,25	10	67	0,90
<i>Marctetia macrophylla</i>	11	73	0,20	5	33	0,45
<i>Pouteria ramiflora</i>	9	60	0,19	3	20	0,27
<i>Renvoizea trinii</i>	8	53	0,17	4	27	0,36
<i>Himatanthus drasticus</i>	6	40	0,13	4	27	0,36
<i>Mitracarpus salzmannianus</i>	6	40	0,13	2	13	0,18
<i>Paepalanthus bifidus</i>	5	33	0,10	2	13	0,18
<i>Staelia galiooides</i>	4	27	0,08	2	13	0,18
<i>Andira humilis</i>	3	20	0,06	2	13	0,18
<i>Humiria balsamifera</i>	2	13	0,04	2	13	0,18
<i>Monteverdia opaca</i>	2	13	0,04	2	13	0,18
<i>Commelina erecta</i>	1	7	0,02	1	7	0,09
<i>Miconia holosericea</i>	1	7	0,02	1	7	0,09
<i>Pavonia harleyi</i>	1	7	0,02	1	7	0,09
<i>Serjania lethalis</i>	1	7	0,02	1	7	0,09
<i>Vantanea obovata</i>	1	7	0,02	1	7	0,09

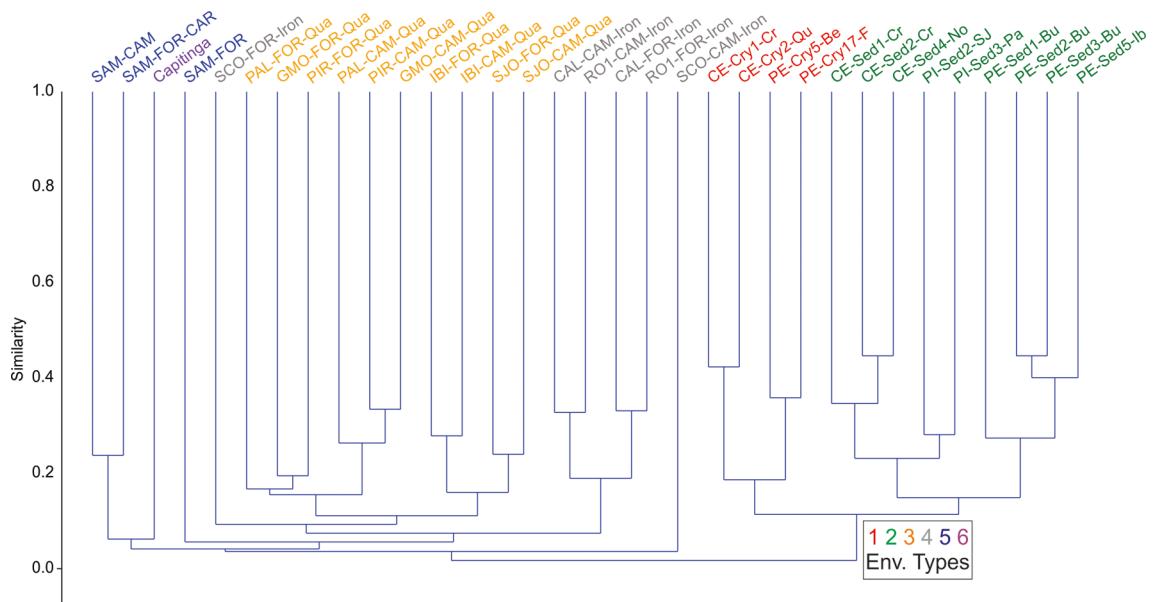


**Figure 5** – NMDS comparison of the capitinga flora with the flora of other important habitats in the region: caatinga on crystalline lowland substrates; caatinga of sandy sedimentary basins; open highland vegetation on quartzite substrates; forests on quartzite substrates in the highlands; open vegetation on canga substrates in the highlands; and forests on canga substrates in the highlands. Stress of the two dimensional solution in the NMDS: 0.1931.

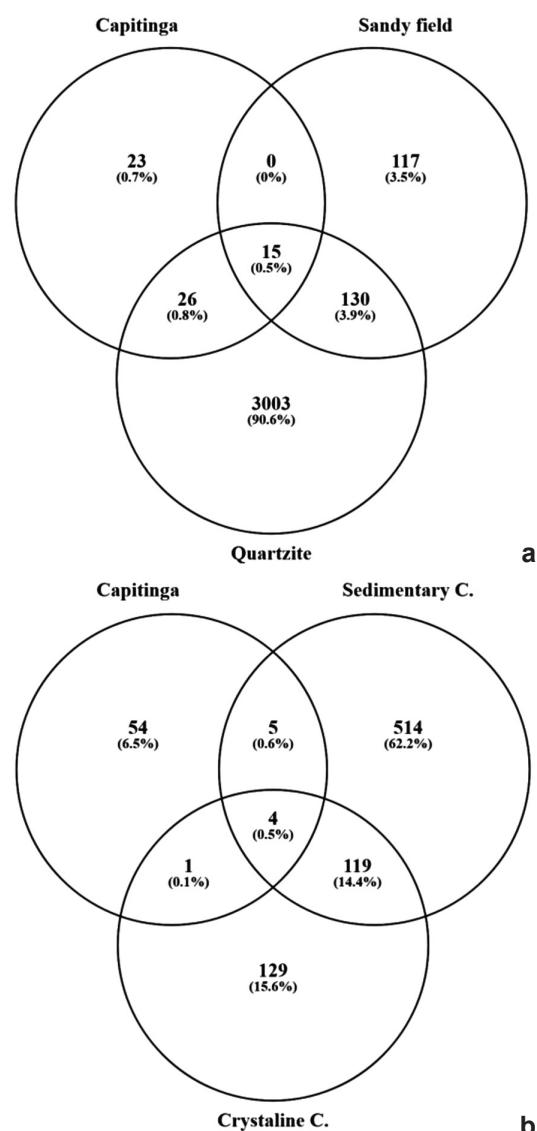
that very poor sandy soils represent a challenging environment for annual plants.

The most important families in the capitinga vegetation (Fabaceae, Apocynaceae, Asteraceae, Eriocaulaceae, Euphorbiaceae, and Rubiaceae – which represented almost 50% of the total

species surveyed in this study) likewise stand out in floristic surveys throughout the Espinhaço Range, in different order of species richness (Stannard 1995; Giulietti *et al.* 1997; Guedes & Orge 1998). In general the species found in the study area show wide geographical distributions, such as *Blepharocalyx salicifolius* (Kunth) O.Berg, *Emmotum nitens* (Benth.) Miers, *Miconia holosericea* (L.) DC., and *Pouteria ramiflora* (Mart.) Radlk., and are found in the seasonal forests growing on red-yellow latosols surrounding the capitinga sites (Funch *et al.* 2008; Couto *et al.* 2011, 2015); most capitinga species also occurs in forests and in rupestrian grasslands on the quartzite substrates of the Espinhaço Range. Notably, the most abundant capitinga species show endemic distribution patterns, such as *Syagrus harleyi* (restricted to the Chapada Diamantina, Bahia), *Vellozia dasypus* (occurring in the Chapada Diamantina and the coastal restinga in Sergipe), and *Calliandra lineata* (restricted to the Chapada Diamantina, Bahia). Some species occur in both the Chapada Diamantina and in coastal scrub (restinga) vegetation, such as *Mandevilla tenuifolia* and *Mollugo verticillata* L. (Oliveira-Filho & Carvalho 1993; Pereira & Assis 2000; Alves *et al.* 2007).



**Figure 6** – UPGMA group analysis comparing the capitinga flora with the flora of other important habitats in the region: 1 (red)- caatinga on crystalline lowland substrates; 2 (green)- caatinga of sandy sedimentary basins; 3 (orange)- highland vegetation on quartzite substrates; 4 (grey)- highland vegetation on canga substrates; 5 (blue)- highland vegetation on sandy areas; 6 (purple)- capitinga. Cophenetic correlation of the UPGMA: 0.91.



**Figure 7 – a.** Venn diagram showing the floristic relationships between capitinga, other sandy areas, and quartzite site vegetation; **b.** Venn diagram showing the floristic relationships between capitinga, sedimentary caatinga, and crystalline caatinga.

Although floristically more related to the quartzite substrate vegetation of the Espinhaço and Chapada Diamantina ranges, capitinga vegetation (and other sandy patches, such as the carrasco vegetation of Ambrósio Range, Minas Gerais state) (Pirani *et al.* 1994) harbored the most distinct species pool within the Espinhaço Range-Diamantina complex. The flora of the Espinhaço-Chapada Diamantina complex is

likewise completely distinct from the surrounding caatinga vegetation growing on both crystalline and sandy substrates. But the level of Bray-Curtis similarity between the capitinga and other habitats in the Espinhaço and Chapada Diamantina ranges was also very low. Other sites on sandy patches had low levels of similarity with both capitinga and quartzite vegetation, constituting a fragile group in the UPGMA analyses, and did not form a clear pattern on the NMDS ordination. The stress for the two dimensional solution of the NMDS was 0.1931, which is an acceptable value, while the cophenetic correlation for the UPGMA was high (0.91). Both results reinforce the evidence that despite the enormous diversity of Brazilian biomes, our grouping and ordination analyses were able to reveal floristic groups consistent with the major environment types. Both stress and cophenetic values presented an adequate representation of the data.

Zappi *et al.* (2017) evaluated the biogeography of plant communities growing on quartzite and canga substrates along the Espinhaço Range and found that the substrate category was an important feature in determining floristic groups (although exceptions were also detected, such as the canga sites in Condado Range) (Pifano *et al.* 2010). In Zappi's study and here, those canga sites did not group with other such sites, as most canga sites are located in the Quadrilátero Ferrífero, a huge iron-ore deposit in southern Minas Gerais state, distant from Condado Range.

We found here that geographically distant sandy patches demonstrated only very low levels of similarity. Although disjunct and geographically distant, sandy sedimentary caatinga vegetations had strong floristic links and grouped together, forming groups distinct from other habitats. The much smaller sandy patches along the Espinhaço Range do not constitute a single floristic group. Nevertheless, it is notable that the capitinga had a number of species endemic to the Chapada Diamantina, such as *Syagrus harleyi* and *Calliandra linnea*.

We present here a comprehensive record of the structure and floristics of capitinga vegetation in the Chapada Diamantina. Capitinga sites are located in the more humid regions of the Chapada Diamantina, but while the surrounding areas are covered by evergreen forests, capitinga is conditioned by the edaphic features of its deep sandy soils that prevent forest development – and its flora is not similar to other forest or rupestrian

grasslands areas in the Espinhaço or Chapada Diamantina ranges. While the capitinga does share species with vegetations growing on quartzite and other sandy patches of the Espinhaço Range, the beta similarity between those sites is very low; likewise, the sandy sites of Minas Gerais State do not constitute a floristic group with capitinga. Capitinga also harbors a number of locally endemic species (such as *Syagrus harleyi*) that are not shared with other habitats in the Espinhaço Range. Although not very diverse when compared to the forest and rupestrian grasslands of the Espinhaço Range, capitinga does harbor endemic species and represents a distinct habitat – and it would be interesting to extend the limits of the Chapada Diamantina National Park to include at least some of those patches.

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