

A Phytogeographical Metaanalysis of the Semi-arid Caatinga Domain in Brazil

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Abstract Seasonally Dry Tropical Plant Formations (SDTFs) are among the most threatened biomes worldwide. Nevertheless, they have received less scientific attention than rainforests or savannas. One such SDTF, the Caatinga Phytogeographic Domain (CPD), is the largest semi-arid tropical ecoregion in South America. Earlier floristic studies of the Caatinga flora discerned two floristic groups in the CPD, in terrains of crystalline and sedimentary origin respectively. We compiled and analysed the most comprehensive dataset on CPD plant distributions to produce a general biogeographical synthesis for Caatinga, including inselbergs, riverine forests and ecotonal areas. Not only are crystalline and sedimentary caatingas clearly distinct, but inselbergs collectively form a third floristic group in the CPD. Non-woody plants, omitted from many studies, are a major component of Caatinga diversity, comprising more than 60 % of species in some local communities. Raunkiaerian life-form spectra of Caatinga sites show that Caatinga vegetation differs in life-form spectra from those of major world biomes, supporting recognition of SDTFs as a discrete world biome.

Resumo Formações Tropicais Sazonalmente Secas (SDTFs) estão entre os biomas mais ameaçados do planeta e, ainda assim, recebem menos atenção científica que florestas úmidas e savanas. O Domínio Fitogeográfico da Caatinga (CPD) é a maior ecorregião semiárida tropical da América do Sul. É uma região de grande heterogeneidade e estudos fitogeográficos mostraram que a flora presente nas superfícies sedimentares é diferente daquela presente na Depressão Sertaneja. Nós compilamos e analisamos um banco de dados de ocorrência de plantas no CPD e produzimos uma síntese fitogeográfica para a Caatinga, analisando as afinidades florísticas entre seus ecossistemas, incluindo inselbergs, florestas ripárias e áreas ecotonais. Nós mostramos que as floras das superfícies cristalinas, sedimentares e de inselbergs formaram grupos distintos. Além disso, plantas herbáceas, muitas vezes ignoradas em levantamentos florísticos, corresponderam a uma grande proporção da biodiversidade vegetal do CPD, correspondendo a mais de 60 % das espécies de

algumas áreas. Os espectros de formas de vida de Raunkiaer no DFC também diferem dos espectros dos grandes biomas do mundo, sugerindo que as SDTF podem ser reconhecidas como um bioma particular.

Keywords Biogeography · Seasonally Dry Tropical Forests · Semi-arid vegetation · Biomes · Brazil

Introduction

South America has a very diversified set of vegetation and phytogeographical domains (Cabrera & Willink, 1973; Ab'Sáber, 1977; Olson et al., 2001; Eva et al., 2002). South American environments vary from very dry deserts, on the Pacific coast, to very wet rainforests, especially in the Amazon basin. Climates range from hot-humid equatorial in the Amazon region to cold-dry temperate in the Patagonian region, not forgetting arid and semiarid ecosystems (Cabrera & Willink, 1973; Ab'Sáber, 1977). Most of South America is under tropical and subtropical climate, but even within tropical areas we find a diversified range of climatic conditions. Among the many ecoregions/provinces of the American continent (Cabrera & Willink, 1973; Morrone, 2001, 2014; Olson et al., 2001) there is a group of vegetational formations exposed annually to a long dry season lasting more than 5 months. These disjunct areas vary in physiognomy and geographical location but have some similar ecological constraints. They share common disjunct species and genera and undergo a long shortage of rainfall every year (Sarmiento, 1975; Prado & Gibbs, 1993; Prado, 2000; Pennington et al., 2000; Oliveira et al., 2013; Mogni et al., 2015). One of the largest tropical semiarid areas in the world, with an extent of more than 800,000 km², is the Caatinga Phytogeographical Domain (CPD), located in Northeastern Brazil. The CPD has a strong seasonality, with the dry season lasting 6–11 months each year and most areas typically receiving less than 1,000 mm of annual rainfall, with some areas receiving less than 500 mm annually (IBGE, 2002; Nimer, 1989, 1972).

Rainforests are probably the vegetation type most commonly associated with South America in people's minds. Because of this focus on rainforests, other biomes such as semiarid formations were often neglected both from the point of view of conservation strategies and from that of scientific research (Castelletti et al., 2003; Moro et al., 2015a; Prado, 2000; Santos et al., 2011). An increased focus on the biodiversity of tropical non-rainforest vegetation in South America has increased awareness of the existence of a group of disjunct plant formations annually exposed to a harsh dry season. These formations are distributed over many different regions of the continent (Fig. 1) and vary in structure from dense to open dry scrublands, woodlands and forests. They are physiognomically diverse and have been treated in the literature under a range of different names, including Dry Plant Formations of South America (Sarmiento, 1975), Tropical Dry Forests (Murphy & Lugo, 1986), Dry Seasonal Forests of South America (Prado & Gibbs, 1993) and Seasonally Dry Tropical Forests (Prado, 2000; Pennington et al., 2000).

The idea that these distantly located areas of dry vegetation could be considered a single phytogeographical group, a disjunct biome, arose from the occurrence of species with disjunct distributions, with subpopulations occurring in dry areas separated by significant geographical distances. Such disjunct species include representatives of



Fig. 1 Distribution of the disjunct seasonally dry tropical plant formations of South America (also called Seasonally Dry Tropical Forests - SDTF). The map shows the ecoregions of South America (as mapped by Olson et al., 2001) which are classified by Pennington et al. (2000) as SDTF. Cerrado and Chaco are also shown because enclaves of SDTF (Cerro Leon in Paraguay and “Matas Secas” in the Brazilian Cerrado) are reported to occur within their boundaries. The Bahia interior forests and Alto Paraná forests are usually considered part of the Atlantic Forest Domain, but they have more seasonal climates than the coastal, ombrophilous Atlantic forests and are considered by Pennington et al. (2000) as part of the SDTF biome. Map design: M.F. Moró

Fabaceae, Euphorbiaceae and Cactaceae (Lewis et al., 2006; Oliveira et al., 2013; Prado & Gibbs, 1993; Taylor & Zappi, 2004).

These seasonally dry areas also share some ecological features, including low annual rainfall amounts (very often below 1000 mm), a long dry season (normally over five and sometimes up to 11 dry months annually in some areas of Caatinga), erratic rainfall with unpredictable timing of precipitation and periodic droughts. SDTFs usually have fertile soils and are home to plants lacking adaptation to survive wildfires, as well as a wealth of succulent plant taxa, such as Cactaceae (Bullock et al., 1995; Sampaio, 1995; Pennington et al., 2000, 2006; Oliveira-Filho et al., 2013). The features uniting these disjunct vegetation formations were discussed in two seminal papers published by Sarmiento (1972, 1975), reviewed by Murphy and Lugo (1986) and analysed from a biogeographical perspective by Prado and Gibbs (1993). But since the beginning of the 21st century an increased effort has been made to survey SDTF biodiversity, assess the threats to its conservation, evaluate its geographical extent and provide biogeographical analyses with a view to understanding its biodiversity patterns (Pennington et al., 2000; Sampaio et al., 2002; Castelletti et al., 2003; Giulietti et al., 2006; Miles et al., 2006; Linares-Palomino et al., 2011; Särkinen et al., 2011; Santos et al., 2012; Moro et al., 2014a, 2015c).

Of the many areas indicated by Pennington et al. (2000) as part of the disjunct biome of the Seasonally Dry Tropical Forests (SDTF), one of the largest is the semiarid Caatinga Phytogeographical Domain (CPD), located in Northeastern Brazil (Figs. 1 and 2). The harsh climatic conditions of the CPD were already noted by 19th century naturalists. Carl Friedrich Philipp von Martius, the first editor of the *Flora Brasiliensis*, travelled great distances in Brazil to make collections and almost died while crossing the semiarid Caatinga (Henriques, 2008). Martius would later remember the caatinga vegetation as a “*silva horrida*” and in the first phytogeographical scheme of Brazil, proposed by him, the semiarid Caatinga was deemed to merit clear recognition as one of the country’s distinctive phytogeographical domains (von Martius, 1824, 1906). This first map was the basis for the other phytogeographical systems developed later in Brazil (IBGE, 2012; Romariz, 1964) and the CPD has since been recognized as a distinct natural region of Brazil (Ab’Sáber, 2003; IBGE, 2004).

Despite being recognized as a distinct natural region, the Caatinga Domain was regarded by some influential 20th century biologists as poor in species richness and endemism (Rizzini, 1963; Vanzolini, 1974). It was also understudied by biologists when compared with the Cerrado and Atlantic Forest Domains, because of a prejudice, which regarded the CPD as less important biologically than these other Brazilian biomes (Moro et al., 2015a; Santos et al., 2011). These attitudes were also reflected in the conservation policies towards Caatinga. Although it is now recognized as one of the most threatened Brazilian natural regions (Castelletti et al., 2003; Miles et al., 2006), the Caatinga has a relatively small fraction of its extent within fully protected nature reserves (*Unidades de Conservação de Proteção Integral*), as the focus on nature reserves establishment was usually directed to other vegetation types (Castelletti et al., 2003; Menezes et al., 2010; Brazil, 2015). Starting in the 1990s, but increasing in the early 21st century, interest in Caatinga conservation and biodiversity has intensified (Moro et al., 2015a). A number of assessments of the threats faced by the CPD, its remaining area covered by native vegetation, protection policies, estimation of species numbers and endemism levels, sample coverage, biogeographical analysis, geographical mapping (Sampaio et al.,

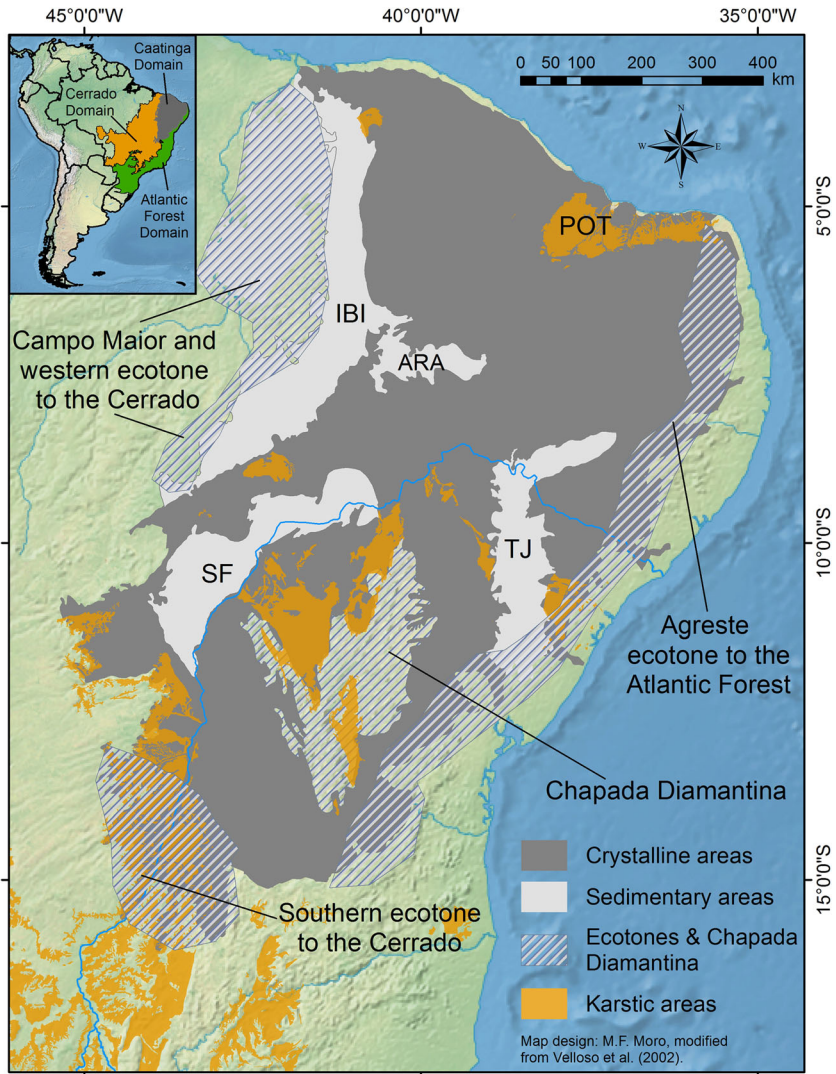


Fig. 2 Geographical location of the Caatinga Phylogeographical Domain (CPD) in northeastern Brazil. The CPD is surrounded by the Atlantic Forest Domain to the east and the Cerrado Domain to the west. The areas within the CPD with predominantly crystalline geology are represented in dark gray, whereas areas where the predominant geology is sedimentary are represented in light gray. The enclaves of karstic terrains (brown areas) within and around the CPD are also shown. The main ecotonal areas of the CPD are hatched, as is the Chapada Diamantina highland in the middle of the CPD, where caatinga, cerrado and campos rupestre (rocky grasslands) vegetation mix. The main sedimentary areas within the CPD are: *TJ* Tucano-Jatobá sedimentary basin; *IBI* Ibiapaba sedimentary basin; *ARA* Araripe sedimentary basin; *SF* São Francisco Continental Dunes; *POT* Potiguar sedimentary basin, a basin with abundance of karstic deposits. The CPD map is modified from Velloso et al. (2002). Map design: M.F. Moro

2002; Velloso et al., 2002; Castelletti et al., 2003; Araújo et al., 2005; Giulietti et al., 2006; Queiroz, 2006, 2009; Forzza et al., 2010; Menezes et al., 2010; Beuchle et al., 2015) and a new set of recent floristic studies (Moro et al., 2014a, 2015a) have been published in recent years.

Objectives of the Study

In this study we build on the recent acceleration in the development and publication of floristic and phytosociological studies for the Caatinga Domain to provide: 1) a brief overview of the main geographical and biological features of the Brazilian semiarid; 2) a metaanalysis of plant biogeography of Caatinga, exploring phylogeographical patterns based on the Caatinga database developed by Moro et al. (2014a, 2015a); 3) an evaluation of the relative role of woody versus non woody species for the plant biodiversity in Caatinga; and 4) an evaluation of the Raunkiaerian life-forms spectra reported in the literature for the CPD.

The Caatinga database was built upon an extensive survey of previously published floristic and phytosociological papers (Moro et al., 2014a, 2015a) and has comprehensive coverage of published floristic studies regarding both woody and non woody plants up to 2011. We use this database to investigate phylogeographical patterns and specifically to analyse the patterns of relative importance of woody versus non woody plants in the CPD. We present here habit and life-form spectra for the CPD to show the importance of non woody plants to the biodiversity of semiarid areas and also to understand how the relative importance of woody and non woody plants varies between the main habitat types in a biogeographical context.

A Brief Overview of the Caatinga Phylogeographical Domain

Geographical Characterization

The Caatinga Phylogeographical Domain (CPD) is one of the broad Brazilian natural regions (Ab'Sáber, 2003; IBGE, 2004) located in the northeastern corner of the South America continent (Figs. 1 and 2). It is bounded to the north by the Atlantic Ocean, on its eastern and southeastern limits by the Atlantic Forest Phylogeographical Domain (AFPD) and on its western and southwestern limits by the Cerrado Phylogeographical Domain (CERPD). The CPD is the main phylogeographical domain of the Northeastern region of Brazil and is comprised of a set of different environment types, floristic groups and physiognomies. The main vegetation type of the CPD is the caatinga *sensu stricto*, which occurs on the extensive crystalline peneplains that dominate the region, but large areas of sedimentary terrains also occur in the region (Fig. 2). The CPD occupies an area over 800,000 km² (according to IBGE 2004 its area is 844,453 km²) in the states of Bahia, Sergipe, Alagoas, Pernambuco, Paraíba, Rio Grande do Norte, Ceará, Piauí, a small area of Maranhão and northern Minas Gerais. This makes the CPD one of the largest semiarid regions in the world and it is recognized as one of the world's ecoregions in its own right (Ab'Sáber, 1977; Olson et al., 2001).

The name of the Caatinga Domain is derived from the caatinga vegetation, a deciduous, thorny and succulent biome that is widespread in the region. The word caatinga probably means “white forest” in the indian Tupi language, probably a reference to the open and grey aspect of the vegetation during the dry season, when almost all trees and shrubs shed their leaves. Martius, in his phylogeographical treatment of Brazil, named the CPD as *Hamadryades*, comparing it to Greek nymphs who were mortal, making a reference to the fact that during the dry season the plants appear to be dead (Fernandes & Bezerra, 1990; von Martius, 1906, 1824).

The CPD is notably characterized by its semiarid climate, which is unusual for a tropical region. Occupying the same latitude as the Amazon and Atlantic Forest Domains (Fig. 2) the CPD receives much less rainfall than the surrounding regions. The Brazilian semiarid is approximately delimited by the 1,000 mm isohyet, which closely matches the delimitation of the CPD (IBGE, 2004; Nimer, 1972). The annual rainfall amount in the region is very heterogeneous and varies considerably between consecutive years and across the territory. Annual rainfall can reach 1,000 mm or more in the transition zone to the AFPD or on the windward faces of mountains in the region or less than 500 mm in the driest sites (Nimer, 1972, 1989). Amplifying the impact of low annual rainfall, the region is exposed to strong solar radiation and the potential evapotranspiration in the CPD is much greater than the rainfall. Due to its megathermic climate, with vast areas presenting mean annual temperatures above 24 °C, and maximum day temperatures easily exceeding 30°, sometimes reaching 36° or even 40 °C (Nimer, 1972), the potential evapotranspiration in the region reaches 1,500 or even 2,000 mm annually (Nimer, 1972, 1989; Velloso et al., 2002), far surpassing rainfall amounts.

Low rainfall volumes and high evapotranspiration alone are not sufficient to characterize the climate of the CPD. Another key factor is that the rains are unpredictable in timing (erratic) and strongly concentrated in time and space, with the number of dry months varying from six up to an astonishing 11 months annually depending on the region (IBGE, 2002; Nimer, 1972). These erratic rains mean that in a given year the rainy season may begin in a certain month, while being delayed by several months in the following year. Droughts occur when rainfall is negligible for one or more consecutive years. The volume of precipitation also varies greatly from one year to the next and one year can see floods followed by consecutive years of droughts (Nimer, 1972). Thus, plant communities must be prepared to deal with years of abundance of resources (or even catastrophic floods) and years with scarce rains.

The pedology of the CPD is very complex and a high number of soil types can be found in the region (Marques et al., 2014), with changes from one soil type to another often occurring within a few meters (Ab'Sáber, 1977; Sampaio, 1995; Velloso et al., 2002). However, geologically speaking we can separate the CPD in two large geological environments. The first and most widespread is the crystalline and the second the sedimentary environments (Ab'Sáber, 1974; Brito, 1976; Velloso et al., 2002). Scattered within the CPD we can also find enclaves of karstic terrains, adding to the regional heterogeneity (Fig. 2).

Crystalline Environments. The largest geological environment in the Brazilian semiarid is composed of the widespread crystalline peneplains regionally called *Depressão Sertaneja* (Ab'Sáber, 1974). The *Depressão Sertaneja* is usually flat or slightly hilly and has nutrient rich, but shallow and stony soils. According to Ab'Sáber (1974) a strong erosional process took place in the region during the Tertiary period, exposing the pre-cambrian granitic and gneissic basement of the region and resulting in a degraded (geologically speaking) landscape composed mostly of areas of low altitude. The *Depressão Sertaneja* usually has heights between 300 and 500 m, but some highlands, such as the Chapada Diamantina, Borborema and smaller mountains (*serras*) scattered throughout the CPD can reach over 1,000 m. In sites where the bedrock is more resistant than the bedrocks of the surrounding terrains, mountains or highlands (*serras*) would remain as isolated, elevated areas within the landscapes. These mountains add

extra heterogeneity to the region, because some are high enough to promote orographic rains on their windward slopes and rain shadows, with reduced precipitation, on their leeward slopes. Wetter sites will usually have more developed soils where taller dry forests can occur. And where rainfall is sufficiently high, windward sides of mountains can harbor 'islands' of wet or subhumid forests surrounded by dry caatinga vegetation. These wet areas surrounded by semiarid climate can harbor wet forests which are floristically more related to the Atlantic Forests than to the drier caatinga vegetation surrounding them (de Oliveira & de Araújo, 2007; Porto et al., 2004; Rodal et al., 2008). On the other hand, on the leeward slopes of these same mountains, rain shadows can result in the existence of very dry sites, harboring caatinga. Examples include the Borborema range, stretching from Rio Grande do Norte to Alagoas states and the Chapada Diamantina range, in the center of Bahia state (Velloso et al., 2002).

Besides the typical areas of the Depressão Sertaneja, with fertile, but rocky and shallow soils, and the highlands, in many places the rocky basement is completely exposed with no soil or very poorly developed litholic neosols. These sites can be located on the top of mountains or as large exposed rocks that rise steeply in the midst of the landscape (commonly termed inselbergs) or as flat rocky surfaces where the bedrock is exposed (locally called *lagedos*). Inselbergs are an important environment within the CPD. They are widespread in the crystalline terrains of the Depressão Sertaneja and provide an important habitat for rupicolous plants. In some areas a great number of inselbergs are found in a single region, where they constitute the inselberg fields (*campos de inselberg*). Famous of such areas are the Milagres region, in Bahia, and Quixadá, in Ceará.

Sedimentary Environments. The second main "geological environment" of the CPD are the sedimentary areas. Most of these areas are Mesozoic sedimentary basins, many formed by rifting when Africa and South America separated. These basins were filled by sedimentary material, which accumulated over millions of years and were subsequently lifted due to isostatic equilibrium, raising higher than the surrounding crystalline landscapes around. The most important of these basins are the Tucano-Jatobá basin, stretching from Bahia to Pernambuco; the Araripe basin, separating Pernambuco and Ceará; and the Ibiapaba basin, occupying most of the state of Piauí (Fig. 2) (Brito, 1976; Carvalho & Melo, 2012; Velloso et al., 2002). These areas can be important paleontological sites for the study of Mesozoic biota, as exemplified by the large fossil deposits found in the Araripe basin (Martill et al., 2011). Besides these large sedimentary basins, one can also find many smaller basins scattered over the region, such as the Rio do Peixe, Sousas, Iguatu, Lavras da Mangabeira and Mirandiba basins (Carvalho & Melo, 2012).

Another extensive sedimentary area is represented by the São Francisco dunes. This large system of paleodunes represents old fields of dunes covered by caatinga (Velloso et al., 2002; Rocha et al., 2004). This area is not a sedimentary basin, having been formed much more recently but it has sandy quartzarenic soils (Rocha et al., 2004) similar to those found in other small and large basins (Pinheiro et al., 2010; Araújo et al., 2011).

While soils in crystalline areas are usually shallow, rocky and nutrient rich, soils in the sedimentary basins can be deeper, constituting in some places sandy soils or deep and nutrient-poor latosols, or Quartzarenic Neosols (Pinheiro et al., 2010; Araújo et al., 2011; Marques et al., 2014). Because soils in sedimentary basins are deeper, it is possible that they may have a greater capacity to retain edaphic water than the usually shallow soils of crystalline environment.

Although sedimentary basins generally have nutrient poor soils, in many areas of the CPD we can find karstic deposits, which represent an exception to this rule (Fig. 2). Karstic deposits render the soils of certain areas the richest in the region, as exemplified by Cambisols (Marques et al., 2014). Plant communities occurring in these areas are presumably different to those of other sedimentary areas. One such area is the Potiguar basin, which is a medium sized, karstic sedimentary basin located between Ceará and Rio Grande do Norte states (Hasui, 2012; Sallun Filho & Karmann, 2012). The Potiguar karstic areas also result in the presence of many caves in the region, some of which are protected by the small Furna Feia National Park. Karstic enclaves in the CPD also occur in other sites, especially in Bahia and northern Minas Gerais (Sallun Filho & Karmann, 2012).

In summary, sedimentary areas usually have deeper soils than crystalline sites, but have relatively nutrient poor soils. Nevertheless, sedimentary areas with karstic deposits have eutrophic soils and may represent a very different edaphic environment for plants when compared with oligotrophic sandy soils of the typical basins.

The Chapada Diamantina. The Chapada Diamantina is a mountain range rising at the heart of the Brazilian semiarid (Fig. 2). It is an area of complex geology (Alkmim, 2012) and phytogeography where one can find a mixture of crystalline caatinga, wet and subhumid forests (probably floristically related to the Atlantic Forest), campos rupestres (rocky grasslands) and cerrado savannas (Conceição et al., 2007; Juncá et al., 2005; Neves & Conceição, 2007). The complex intermix of geologies, soils, rainfall and temperature at different sites within this range depends on the altitude, location and aspect of each place in the mountains and makes the vegetation of the Chapada Diamantina hard to map and interpret. We discuss here only the areas within the Chapada Diamantina mountains that harbor caatinga vegetation, but it is important to know that this is an area of great phytogeographical complexity within the Brazilian semiarid. The Chapada Diamantina range itself is part of a much larger mountain chain called the Espinhaço range (Alkmim, 2012). The southern part of the Espinhaço range extends to Minas Gerais state at the boundary of the Atlantic Forest and the Cerrado domains, while the northern part (discussed here) is located in Bahia state and is contained within the CPD (Velloso et al., 2002; Juncá et al., 2005; Alkmim, 2012). As a whole the Espinhaço range is extremely rich in species and in endemism, especially in the campo rupestre vegetation of the mountain tops.

Ecotones of the CPD with Surrounding Domains. The interface of the CPD with the Cerrado and Atlantic Forest Phytogeographical Domains is characterized by ecotonal zones, where the features of each domain can be intermediate and/or interdigitated with the other. As noted by the geographer Ab'Saber (1974, 2003), each geographical domain has a core zone, where the full set of the most characteristic features of that domain is expressed, and transitional zones where the typical features of each domain are seen in combination with those of the neighboring domain. Based on this reasoning Ab'Saber proposed his map of the Brazilian “geomorphological domains” (Ab'Sáber, 1974, 1977, 2003) without precise borders, but instead having a central “nuclear” areas surrounded by bands of ecotonal zones. The most noticeable ecotones of the CPD are the ecotonal belts between the CPD and the Cerrado Phytogeographical domain (CERPD) and the Atlantic Forest Phytogeographical Domain (AFPD) (see Fig. 2).

The CERPD borders the western and part of the southern limits of the CPD. A considerable part of Piauí state is covered by cerrado vegetation and much of the “Campo Maior” subregion of the CPD (as mapped by Velloso et al., 2002 - see Fig. 2) is actually a large ecotonal transition presenting a mixture of caatinga and cerrado vegetation (Barros & Castro, 2006; de Farias & Castro, 2004).

To the east, the CPD has an ecotonal belt with the AFPD, regionally known as *agreste* (Fig. 2). The AFPD is known mostly for its once extensive tracts of rainforests (ombrophilous forests) located close to the coast (and thus receiving more rain from the ocean). But moving inland from the coast westward, the rainfall amount decreases and seasonality increases (Oliveira-Filho & Fontes, 2000), allowing the existence of tracts of semideciduous and deciduous forests in the *agreste*, most of which have now been destroyed. *Agreste* is characterized by rainfall amounts intermediate between those of the very dry caatinga *sensu stricto* and the very wet ombrophilous atlantic forest.

To the very south of the CPD, in southern Bahia and northern Minas Gerais states, there are further transitional areas of cerrado and caatinga. This region is more complex because of the presence of calcareous enclaves (Fig. 2) and the mixed floristic influence of caatinga, cerrado and seasonal atlantic forest vegetation. In the southern part of the CPD, the less arid conditions and nutrient rich calcareous soils allow the caatinga vegetation to reach an arboreal physiognomy which is termed arboreal caatinga (Apgaua et al., 2014a; dos Santos et al., 2007, 2011).

Vegetation Types Within the Caatinga Phytogeographical Domain

Differences in environment (soil type, geology, etc.) and rainfall regime have long been recognized as important factors responsible for structuring plant communities (Buck, 1964; Balvanera et al., 2011; Neri et al., 2012). Thus, within a large and heterogeneous domain/ecoregion such as the Caatinga (Andrade-Lima, 1981; Ab’Sáber, 2003) one would expect to have different plant communities associated with different geological terrains, environment types and rainfall gradients.

Following differences in geology, soils and rainfall gradients, a set of different ecosystems and plant communities are distinguishable within the CPD (Velloso et al., 2002; Giulietti et al., 2006; Santos et al., 2012; Moro et al., 2014a). The most common ecosystem type within this domain is the caatinga *sensu stricto* vegetation, which occurs in the widespread peneplains of northeastern Brazil (*Depressão Sertaneja*), in areas over the crystalline bedrock (Figs. 2 and 3) (these communities are hereafter referred to as *crystalline caatinga*). These areas usually have shallow, nutrient rich soils (Sampaio, 1995; Velloso et al., 2002). Besides the crystalline caatinga, another large ecosystem type within the CPD is the deciduous vegetation growing on the sedimentary basins and dune systems where terrains of sedimentary origin are available for plant communities to colonize (Figs. 2 and 4). These sedimentary areas differ in edaphic conditions from crystalline terrains: the soils are much deeper and poorer in nutrients, including quartzarenic neosols and latosols (Velloso et al., 2002; Sampaio, 2010; Marques et al., 2014) and harbor a different type of caatinga, the *sedimentary caatinga*.

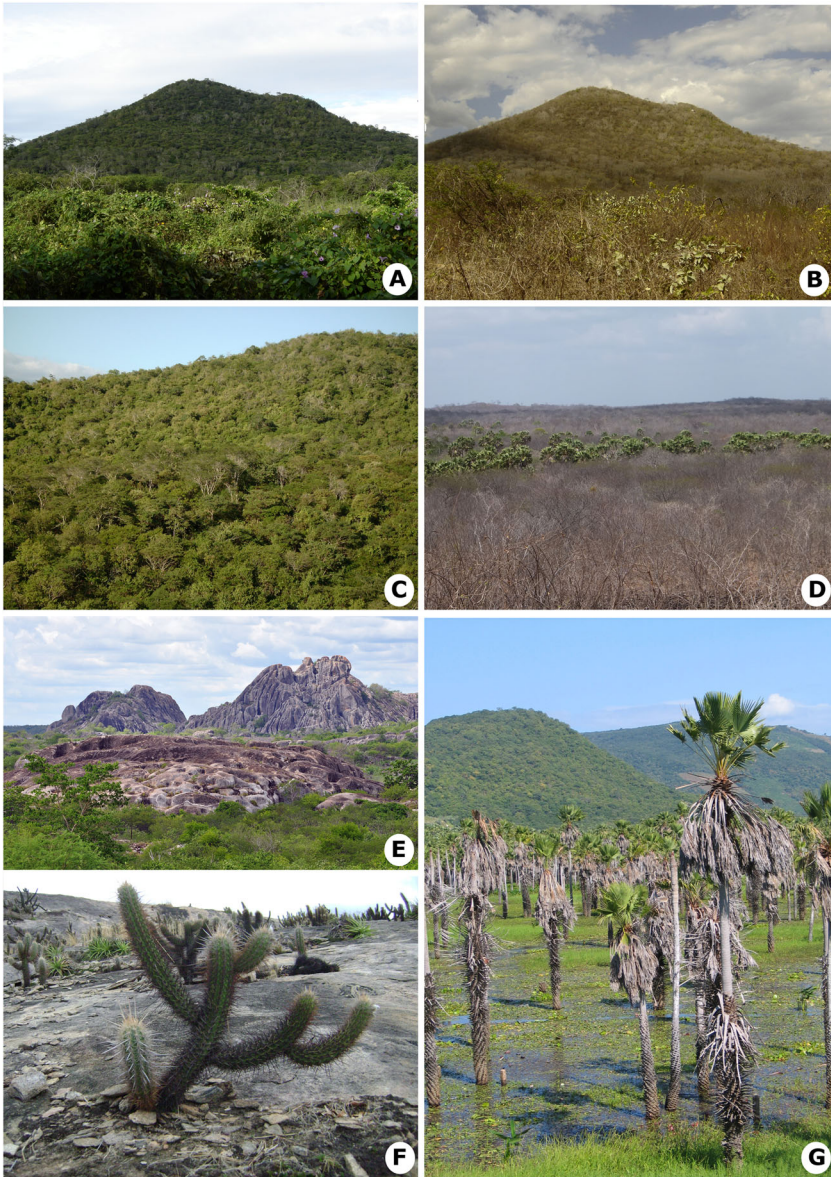


Fig. 3 Some of the main habitats in the *Depressão Sertaneja* crystalline lowlands. **a–b** a hill covered by crystalline caatinga (caatinga *sensu stricto*) during the rainy (*left*) and dry (*right*) season in General Sampaio municipality, Ceará State; **c** a well developed crystalline caatinga featuring a forest or woodland physiognomy during the rainy season in General Sampaio, Ceará; **d** a dense shrubby crystalline caatinga during the dry season in Pentecoste municipality in Ceará State showing how most plants are deciduous. The row of green palms in the middle of the photo is a carnaubal (riverine community dominated by the endemic palm *Copernicia prunifera*) following a small river; **e** Inselbergs rising abruptly from the plain in Quixadá, Ceará; **f** the vegetation growing in the rupicolous habitats of an inselberg in Ceará. The cactus in the foreground is the endemic *Pilosocereus gounellei*; **g** a carnaubal in Caucaia municipality, Ceará State. Both riverine forests and swamped areas where the endemic carnauba palm (*Copernicia prunifera*) is conspicuous are termed ‘carnaubais’. Photos credits: A,B: M.O. Teles de Menezes; C,D,F: M.F. Moro; E,G: A.S.F. Castro

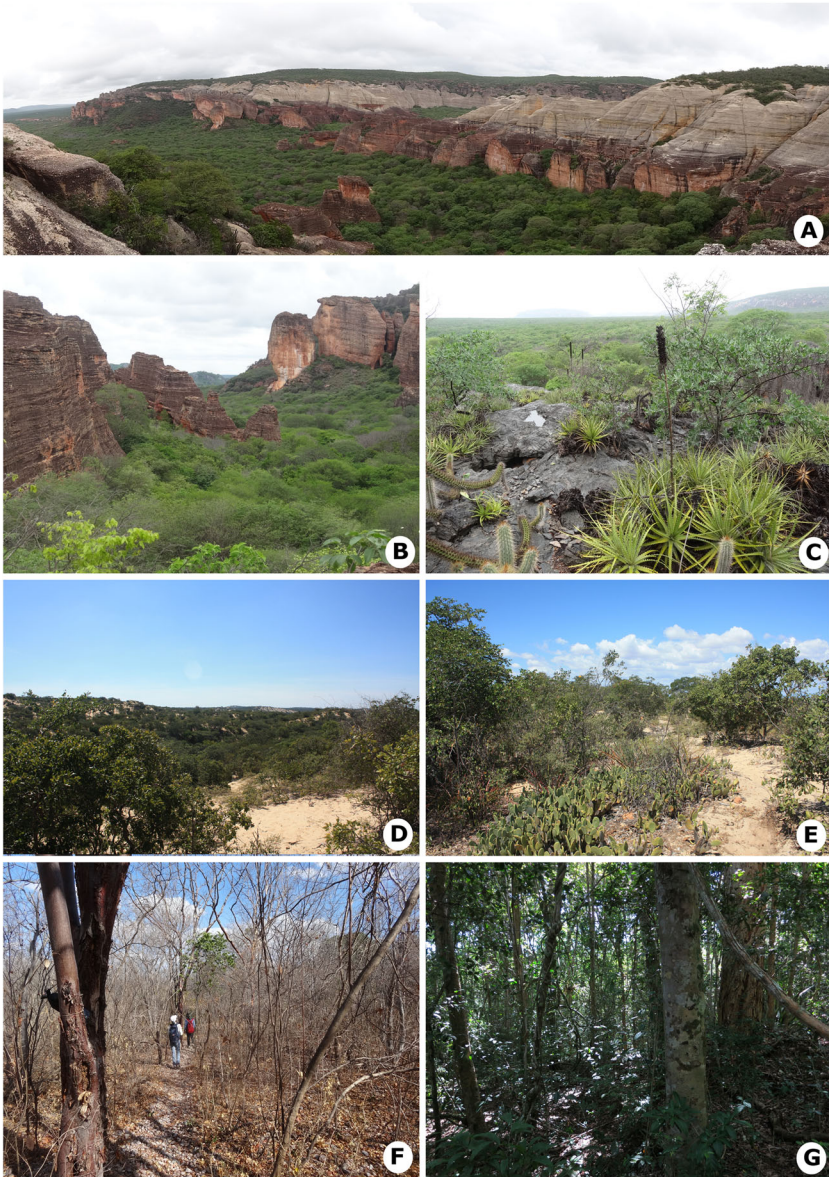


Fig. 4 Some of the main sedimentary habitats in Caatinga. **a–b** Sedimentary cliffs in Serra da Capivara National Park, Piauí State, with sedimentary caatinga formations on top and at their base; **c** A rupicolous habitat in the sedimentary rocks of Serra da Capivara National Park. During the compilation of our floristic database we could not find any study of the flora of these sedimentary rupicolous environments; **d–e** Sedimentary caatinga in the continental São Francisco dunes in Bahia State; **f** Shrubby caatinga during the dry season in the Potiguar sedimentary basin in Açú municipality, Rio Grande do Norte State; **g** Arboreal caatinga in northern Minas Gerais State. In this region of Caatinga the relatively nutrient-rich soils derived from karstic rocks together with greater rainfall, allow Caatinga vegetation to grow higher than in other regions. Photo credits: **a, b, c, f** M.F. Moro; **d, e** Domingos Cardoso; **g** L.P. Queiroz

The idea that the flora occupying the sedimentary terrains might differ from the flora of crystalline areas was the subject of biogeographical discussions since the 1990s (Araújo & Martins, 1999; Araújo et al., 1999). However, up to the end of the 20th century the CPD was very poorly sampled and only a very limited amount of data was available for comparative studies (Moro et al., 2015a). Over the last 20 years the number of floristic and phytosociological studies in the CPD has increased, especially in the last decade (Moro et al., 2015a). Based on the growing number of floristic surveys available in the literature, some biogeographical studies have shown that the CPD has at least two floristic groups: one located in the crystalline peneplains of the Depressão Sertaneja and the other in the sedimentary basins (Araújo et al., 1999; Queiroz, 2006; Gomes et al., 2006; Cardoso & Queiroz, 2007; Santos et al., 2012; Costa et al., 2015).

Apart from these two principal environment types, other, fine scaled ecosystem types also occur within the CPD. These include plant communities in *inselbergs* and *riverine forests*, completing the picture of terrestrial ecosystems for the CPD.

Enclaves of Other Vegetation Within the CPD. Within the core region of a particular domain one can usually find enclaves of conditions typical of the surrounding domains (Ab'Sáber, 2003). The CPD is no exception to this generalization as, within the delimitation of the CPD proposed by IBGE (2004) and Velloso et al. (2002) one can find enclaves of vegetation floristically or ecologically similar to other domains. The most important are the enclaves of *campos rupestres* in the Chapada Diamantina; enclaves of the cerrado *sensu stricto* and *cerradão* (which are vegetation typical of the CERPD); and enclaves of wet and subhumid forests (related to a great extent with the flora of the AFPD).

The cerrado enclaves within the CPD are found mainly in the Chapada Diamantina highlands (Fig. 2) and in the Araripe plateau, on the border between Ceará and Pernambuco states (da Costa et al., 2004; Juncá et al., 2005; Moro et al., 2015b), although other small patches can be found, like those in the south of Ceará state, Serra das Flores or in the coastal region (Moro et al., 2011, 2015b; de Oliveira et al., 2012; Oliveira-Filho et al., 2013). They represent areas of savanna vegetation floristically and physiognomically related to the cerrados of central Brazil.

Ombrophilous and subhumid forest enclaves are also found within the CPD, and are locally known as *brejos de altitude*. These wet forests usually occur on the windward faces of small mountains of the CPD. Due to the orographic rains these “islands of humidity” in the semiarid harbor forests that, in wetter sites, are floristically more related to the AFPD than to the CPD (Porto et al., 2004; de Oliveira & de Araújo, 2007; Rodal et al., 2008; Moro et al., 2015b).

The third very important vegetational enclave occurring within the CPD is the *campos rupestres* (rocky grasslands). This vegetation is typical of the rocky mountain tops of Brazilian ranges and occurs over different mountain ranges in the country. In the context of the CPD, the *campos rupestres* are associated with the Chapada Diamantina mountains at the center of the Brazilian semiarid. The *campos rupestres* are a very distinctive type of vegetation with grassland or scrubland physiognomy adapted to rocky soils and extremely rich in species and endemism (Conceição et al., 2007; Juncá et al., 2005; Neves & Conceição, 2007).

Also of note is the fact that the Brazilian semiarid has a wealth of temporary and a few permanent aquatic bodies that allow aquatic and marsh plants to survive in this dry region (França et al., 2003; Tabosa et al., 2012; Moro et al., 2014b, 2015b). These plants thrive during the rainy season when ponds and temporary rivers rise and these aquatic ecosystems can have a considerable number of aquatic species adapted to grow fast and complete their lifecycles during the annual rainy season (França et al., 2003; Tabosa et al., 2012; Moro et al., 2014b).

Conversely, enclaves of deciduous forest, similar in ecology and floristic composition to the caatinga, occur within other domains (Oliveira-Filho et al., 2013; Neves et al., 2015). The driest sites of the interior of the AFPD for example, are considered by some authors (Pennington et al., 2000) to belong to the biome of the Seasonally Dry Tropical Forests (SDTF – Fig. 1) and in the middle of the CERPD we can find the so-called “calcareous deciduous forests” (Ribeiro & Walter, 2008) growing in karstic areas (on limestone) where one can find a dry forest with the presence of species very characteristic of the caatinga vegetation (Felfili et al., 2007; Carvalho & Felfili, 2011; Arruda et al., 2013; Neves et al., 2015).

In this paper we present a general biogeographical synthesis for the CPD, evaluating the biogeographical patterns of both the woody and non woody components. We also produced habit spectra for plant communities included in our database and extracted Raunkiaerian life-form spectra, in order to evaluate what proportion of plant species is concentrated in the usually neglected non-woody component.

Phytogeographical Comparisons of the Caatinga Plant Communities

Procedures

Database Compilation

This study is based on the largest available dataset on floristic data for the Caatinga Phytogeographical Domain (Moro et al., 2014a). The dataset was assembled by Moro et al. (2014a, 2015a) while preparing a general synthesis for the semiarid Caatinga ecoregion, in which 131 floristic lists were compiled from published papers. This initial database resulted in 8,076 records of over 1700 species (Moro et al., 2014a). We took this database as a starting point and excluded exotic species, surveys in degraded areas (especially surveys in areas impacted by agriculture) and surveys that reported fewer than 20 species, retaining 74 sites (Fig. 5; Appendix 1), which represented 5471 records of 1586 species (Appendix 3).

To understand the floristic relationships between the many ecosystem types within the CPD we gathered floristic and phytosociological papers surveyed within the borders of the CPD (as geographically delimited by Velloso et al., 2002). We considered any floristic studies dealing with terrestrial ecosystems inside the CPD, excluding only surveys of enclaves of wet forest, cerrado savannas and rocky grasslands (*campos rupestres*), because these vegetation formations are floristically related to the surrounding biomes, not to Caatinga itself. We then classified each compiled survey in one of the ecosystem types defined below (Fig. 5).

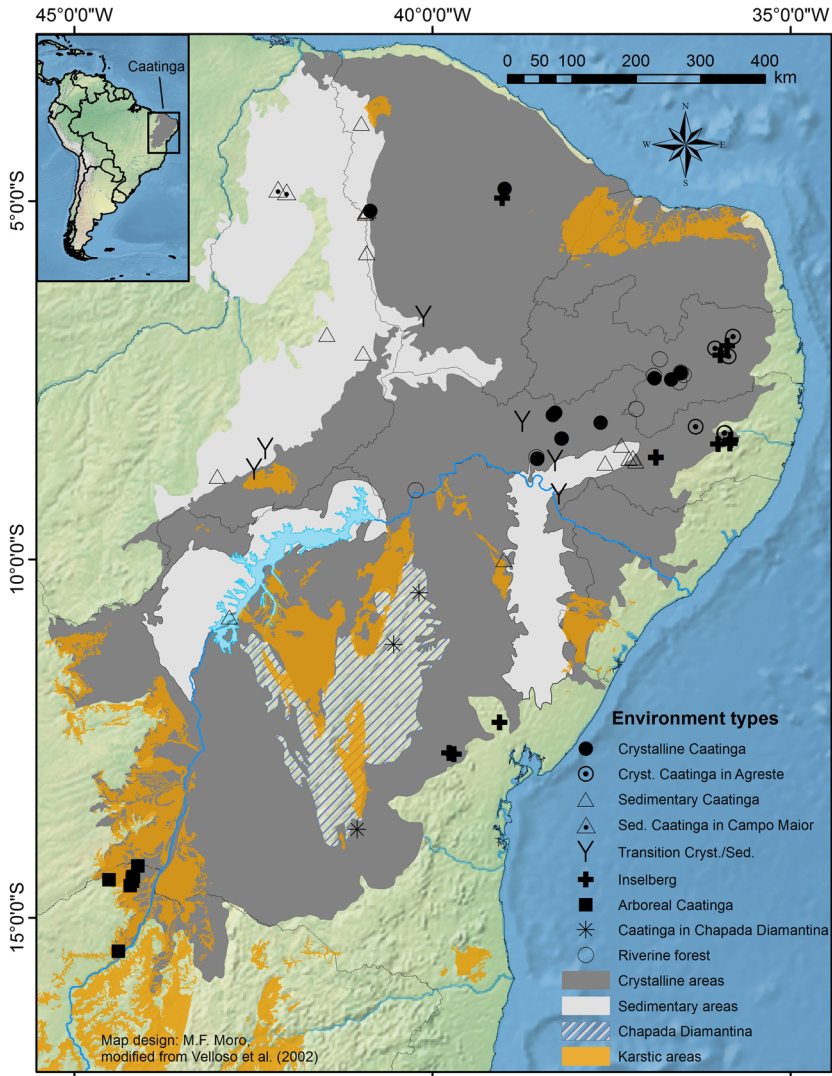


Fig. 5 Geographical location of the 74 surveys compiled within the Caatinga Phytogeographical Domain, NE Brazil, and the environment type of each study. *Dark gray* areas represent terrains over crystalline bedrocks (*Depressão Sertaneja*), *light gray* areas represent the large sedimentary basins and dune systems within the CPD and *brown* areas represent karstic enclaves within and around the CPD. The *hatched* area represent the Chapada Diamantina highlands, where caatinga, cerrado, wet forests and rocky grasslands mix. Map design: M.F. Moro

Vegetational Categories Used in this Study

Crystalline caatinga: typical caatinga of the crystalline peneplains that occupy most of the area of the CPD, being CPD’s most widespread environment type (see Fig. 5).

Sedimentary caatinga: A type of vegetation occurring on sedimentary basins and continental dune systems within Caatinga. Some small patches of sedimentary terrains also occur within mainly crystalline landscapes.

Transition crystalline/sedimentary: sites located in transitional regions between crystalline and sedimentary landscapes.

Inselbergs: scattered within the CPD there are many sites where extremely shallow soils occur and the rocky basement is apparent. These rupicolous environments, where crystalline rock outcrops rise above the Depressão Sertaneja lowlands represent the inselberg environment. Rupicolous environment also occur in sedimentary landscapes, but we could not locate any published floristic study surveying the flora of rupicolous sedimentary areas and thus only the crystalline rupicolous vegetation of inselbergs are considered here.

Riverine Forests: within the CPD there are riverine forests following the riverbeds, where soils are deeper and edaphic water supply larger. Some species in this environment are evergreen (e.g. *Ziziphus joazeiro*, *Licania rigida*), while most species in the typical crystalline caatinga are deciduous.

Caatinga in Agreste: the transitional areas between the CPD and the Atlantic Forest Domain are known as *agreste*. Although under semiarid climate, the Agreste is less seasonal and usually has more rainfall than the typical CPD, mixing floristic elements of the CPD and the Atlantic forest.

Arboreal caatinga: In the southernmost part of the CPD, where a transition to the Cerrado savannas occurs (northern Minas Gerais state) there is a taller subtype of caatinga known as “arboreal caatinga”. These represent areas with larger rainfall than core Caatinga sites.

Caatinga in the Chapada Diamantina: In the very center of the CPD (see Fig. 5) exists a range of highlands called Chapada Diamantina. In these areas rocky grasslands (campos rupestres), cerrado savannas and caatinga vegetation mix. We selected for our biogeographical analysis only surveys in the caatinga vegetation of Chapada Diamantina, excluding studies in the cerrados, campos rupestres and wet forests.

Caatinga in Campo Maior: Campo Maior region represents a transition between the CPD and the cerrado areas of Piauí state. While agreste represents the easternmost ecotonal areas (to the Atlantic Forest) and arboreal caatinga represents the southernmost ecotone (to the Cerrado), Campo Maior represents the westernmost ecotone of the CPD. We selected from the literature surveys in the caatingas of Campo Maior, excluding studies in the cerrados.

Biogeographical Analysis

To compare the floristic resemblance between plant communities in each site, we created a presence/absence matrix (incidence matrix). Each site was classified in one of the “environment types” described above and all species reported at each site were entered in a database. We updated the species names following the *Lista de Espécies da Flora do Brasil* (Forzza et al., 2011) and excluded from our database exotic species and records not identified to species level (i.e. records assigned only to genus or family level). We classified each species with respect to general plant habit: woody and non woody plants. We considered shrubs, trees, lianas (woody climbers) and palms as woody plants, while herbs, tender climbers and subshrubs were classified as non woody plants. Epiphytes and hemiparasites were excluded from the biogeographical matrices. We then created a matrix showing the presence of 1) all woody plants in all areas and 2) all non woody plants in all areas. Most of the studies in our sample focused only on

woody plants, while a few focused only on non woody plants. But 31 studies reported data about the general flora of the study site, recording both woody and non woody plants. We used group and ordination techniques to evaluate these three datasets (woody only, non woody only and general flora). We then compared the floristic resemblance among sites considering the dataset of woody plants, of non woody plants and of general flora (woody and non woody plants at the same site) with multivariate analysis.

Using the presence-absence matrices we calculated Sorensen (Bray-Curtis) distances among sites. We then used the distance matrix to analyse the floristic resemblance among sites using group analysis with the UPGMA algorithm (Unweighted Pair-Group Method using Arithmetic Averages), and ordination analysis using NMS (Non Metric Multidimensional Scaling) (Legendre & Legendre, 2012; McCune & Grace, 2002). The results are presented as UPGMA dendrograms and as bidimensional NMS plots. These methods show the floristic similarity among sites based on the number of species they share. The largest the number of shared species, the closer they will be positioned in the graphs.

Results of the Phylogeographical Comparisons

Database Compilation

Excluding the surveys which we could not assign to any ecosystem type (poorly documented studies), studies in agricultural landscapes and poorly sampled studies (i.e. less than 20 species reported), we retained in our database 74 surveys (Table 1; Fig. 5; Appendix 1) from the original 131 sites reported by Moro et al. (2014a). Of these 74 surveys, 31 sampled the general flora of the study site (both woody and non woody plants reported by the study), 39 sampled only the woody plants and five sampled only the non woody plants (Table 1). The sedimentary caatinga environment had the largest number of surveys in our dataset, with 18 sites, followed by the

Table 1 Number of selected surveys (complete dataset presented in Moro et al., 2014a, 2015a) for each environment type and floristic component sampled for each site

Environment type	General flora (woody + non woody)	Woody only	Non woody only	Total
Sedimentary Caatinga	11	7	0	18
Crystalline Caatinga	4	6	2	12
Inselberg	10	0	0	10
Arboreal Caatinga	0	9	0	9
Riverine forest	1	7	0	8
Caatinga in Agreste (Ecotone to the Atlantic Forest)	2	3	1	6
Transition crystalline/sedimentary	3	2	1	6
Caatinga in the Chapada Diamantina	0	3	0	3
Caatinga in Campo Maior (Ecotone to the Cerrado)	0	2	0	2
Total	31	39	4	74

crystalline caatinga (12 sites), inselberg communities (10), arboreal caatinga (9), riverine forest (8), caatinga in the agreste ecotone (6), the transition between crystalline and sedimentary sites (6), the caatinga in the Chapada Diamantina highlands (3) and the caatinga in the campo maior ecotone (2) (Table 1; Fig. 5).

Biogeographical Analysis

Both the group and the ordination analyses showed a clear floristic differentiation between the flora of crystalline and sedimentary environments. All sedimentary caatingas, including the Campo Maior ecotone to the Cerrado (also a sedimentary landscape), formed a group which is quite separate from the crystalline caatinga sites (Fig. 6). This grouping of Sedimentary caatingas and the caatinga of Campo Maior was evident from the analysis of both the general flora and that restricted to woody plants (Figs. 6 and 7). However, when only the non woody component was evaluated, sedimentary sites formed two groups (Fig. 8). As a whole, the sedimentary caatinga environment, though dispersed in disjunct areas at considerable geographical distances from each other (Fig. 5), had a congruent grouping of species, sharing a clear floristic affinity between all sedimentary sites, especially regarding the woody component (Fig. 9).

Crystalline caatinga, the most widespread environment type, had a more heterogeneous, but still individualized flora when compared to the sedimentary caatinga (Figs. 6, 7, 8, and 9). Minor environments embedded within the crystalline terrains

UPGMA of sites (n= 31) with data on general flora (woody + non woody plants)

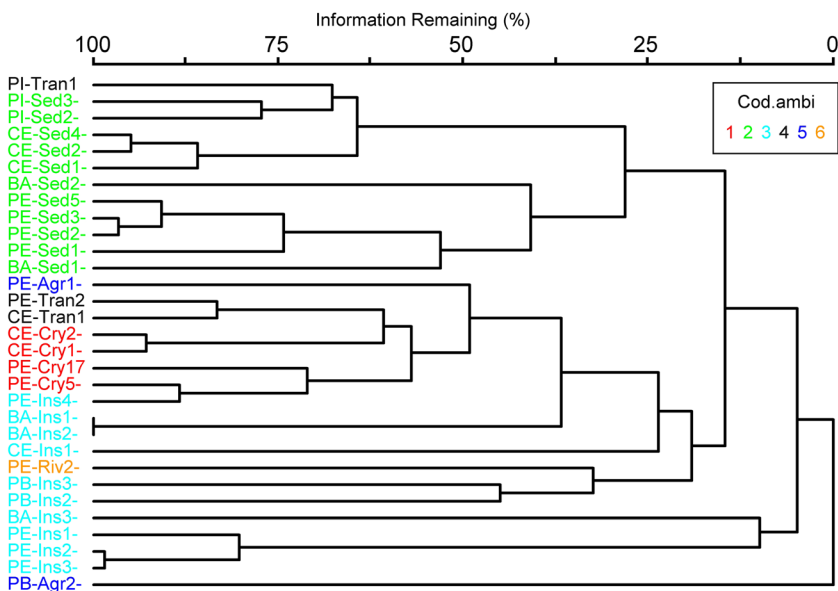


Fig. 6 UPGMA group analysis for the 31 sites with data on general flora (woody and non woody plants) showing the floristic relationships between the different areas based on the complete list of species for each site. Environment types: 1- crystalline caatinga (red); 2- sedimentary caatinga (light green); 3- inselbergs (light blue); 4- transition crystalline and sedimentary sites (black); 5- Caatinga in the Agreste Ecotone (dark blue); 6- Riverine forests (orange)

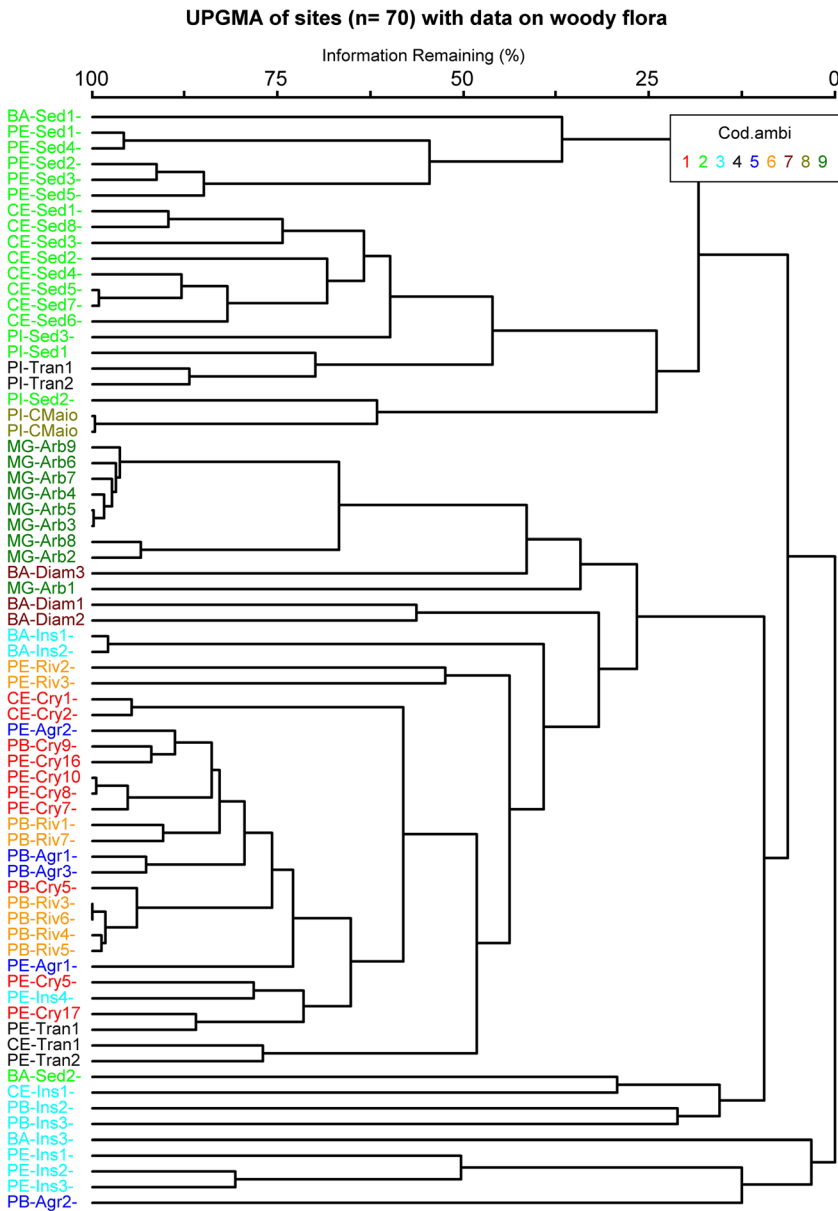


Fig. 7 UPGMA group analysis for the 70 sites with data on woody plants, showing the floristic relationships between the different areas based only on the woody plants reported in each site. Environment types: 1- crystalline caatinga (red); 2- sedimentary caatinga (light green); 3- inselbergs (light blue); 4- transition crystalline and sedimentary sites (black); 5- Caatinga in the Agreste Ecotone (dark blue); 6- Riverine forests (orange); 7- Caatinga in the Chapada Diamantina (brown); 8- Caatinga in Campo Maior Ecotone (yellow); 9- Arboreal Caatinga of northern Minas Gerais (dark green)

(i.e. Riverine forests and the Agreste ecotone) were represented as floristic subtypes of crystalline caatingas (Figs. 6, 7, 8, and 9). Unfortunately, no site-based floristic study on the typical crystalline caatingas of the vast areas of Bahia state was available for

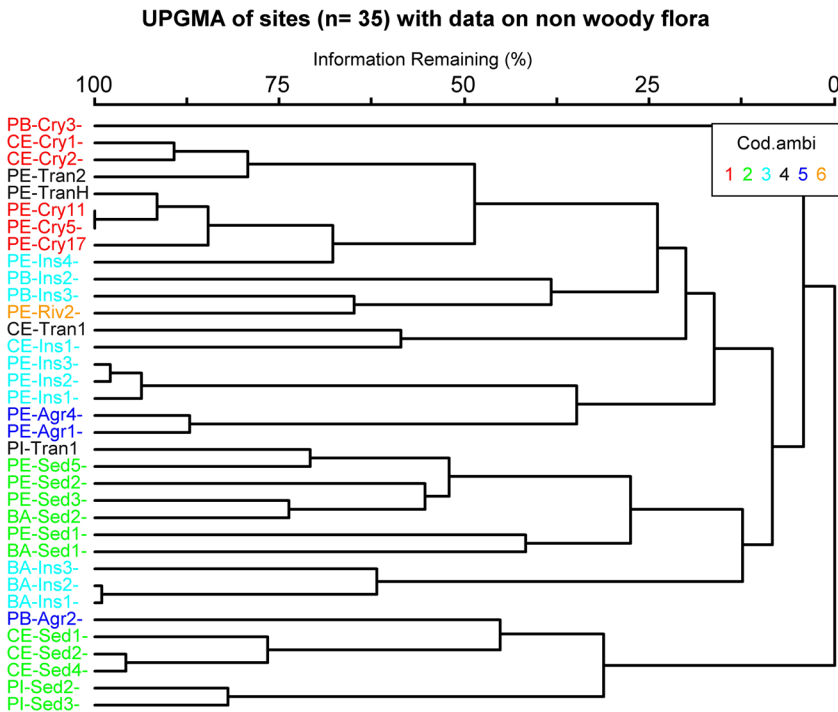


Fig. 8 UPGMA group analysis for the 35 sites with data on non woody plants, showing the floristic relationships between the different areas based only on the non woody plants reported in each site. Environmental types: 1- crystalline caatinga (red); 2- sedimentary caatinga (light green); 3- inselbergs (light blue); 4- transition crystalline and sedimentary sites (black); 5- Caatinga in the Agreste Ecotone (dark blue); 6- Riverine forests (orange)

comparison, but it seems that crystalline sites form a latitudinal gradient of which the caatingas of Chapada Diamantina and arboreal caatingas of northern Minas Gerais state represent the southernmost extreme. Both arboreal and Chapada Diamantina caatingas grouped within the crystalline caatinga in the UPGMA analysis, but assumed a peripheral position on the two dimensional NSM plot (Figs. 6, 7, and 9), where the arboreal caatinga of northern Minas Gerais had a cohesive flora. The sites in the Chapada Diamantina were geographically located midway from the northernmost crystalline caatingas and the southernmost arboreal caatingas and, accordingly, had a flora intermediate between the northernmost crystalline caatinga and the southernmost arboreal caatinga.

Inselberg sites showed a more complex distribution pattern. Analysing the general flora and woody flora (Fig. 9a–b), we can distinguish a long gradient which seems to be related to rainfall. Inselbergs located in dryer areas had a flora very similar to the flora of crystalline caatinga, while inselbergs of wetter areas had a flora that gradually became more and more distinct from crystalline caatinga sites. Regarding the non woody component, the inselberg plant communities were represented in the NMS as somewhat similar to those of the crystalline caatinga, grouping with them in both group and ordination analyses (Figs. 8 and 9c). But the non woody flora of inselbergs from the Bahia agreste ecotone (wetter areas) had a flora similar to the floras of the sedimentary Tucano-Jatobá basin, a pattern that should be of interest to explore in further studies.

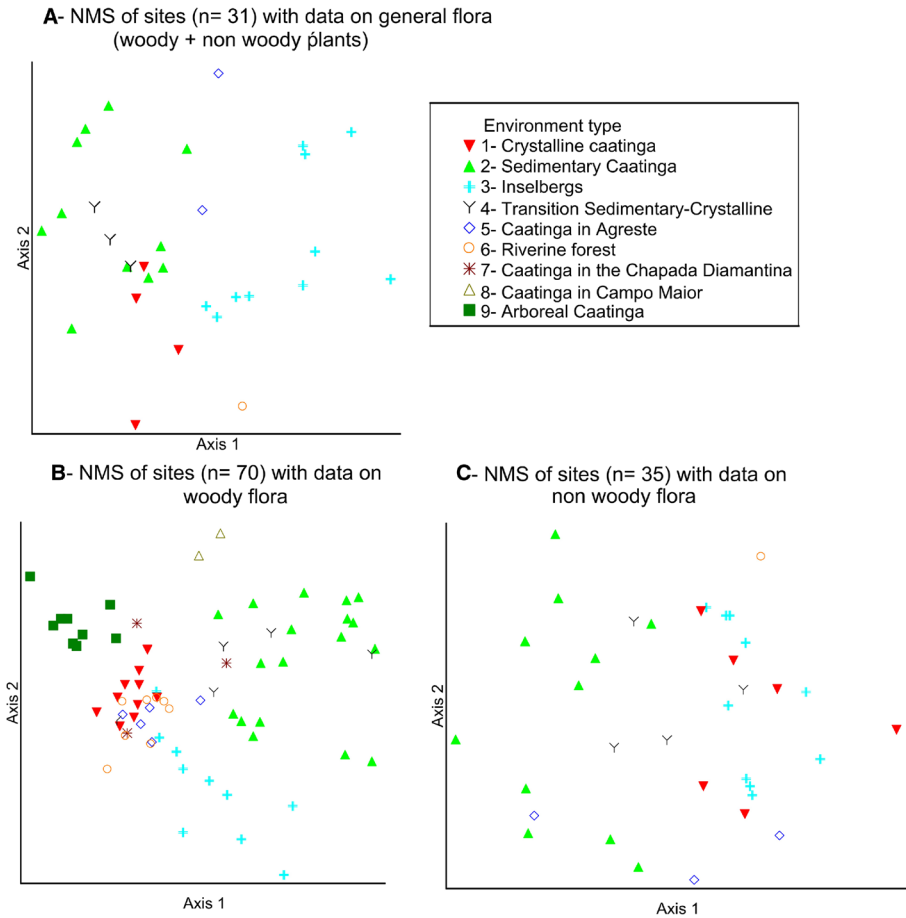


Fig. 9 NMS ordination of the sites, showing the floristic relationships in the Caatinga Phytogeographical Domain for the three subsets of our data (**a** only sites where we had data on general flora; **b** sites where we had data on woody plants; **c** sites where we had data on non woody plants). Environmental types: 1- crystalline caatinga; 2- sedimentary caatinga; 3- inselbergs; 4- transition crystalline and sedimentary sites; 5- Caatinga in the Agreste Ecotone; 6- Riverine forests; 7- Caatinga in the Chapada Diamantina; 8- Caatinga in Campo Maior Ecotone; 9- Arboreal Caatinga of northern Minas Gerais. NMS calculated with Sorensen distance

Habit Spectra in the Caatinga Phytogeographical Domain: Evaluating the Relative Importance of Woody Versus Non Woody Species

Procedures

Habit Spectra Construction

To evaluate the relative importance of woody versus non woody species in the CPD we classified each of the 1586 species present in our dataset in one of the following standardized habits: “woody plants” for trees and shrubs; “climber woody plants” for woody lianas (i.e. those with diameter usually over 2 cm); “non woody plants” for herbs and subshrubs; “climber non woody plants” for tender climbers (i.e. herbaceous

climbers and lianas with diameter usually below 2 cm); “parasites/hemiparasites” for mistletoes and fully parasitic plants; and “epiphytes”. Species were classified based on our field experience, consultation of botanical literature or personal communications with taxonomists. We then produced a general habit spectrum for the whole Caatinga counting the number of species with a given habit considering all 1586 species reported in the 74 surveys. We also produced a habit spectrum for each of the 31 study sites with published data on general flora (both woody and non woody species).

Comparing the Richness of Woody and Non Woody Plants in the CPD: Using Interpolation, Extrapolation and Richness Estimation to Evaluate the Number of Species

As the literature includes more floristic data for woody than non woody plants it is expected that a higher number of woody species could be reported simply because a larger dataset is available for this plant assemblage. To deal with this bias we built an extrapolated species accumulation curve showing the expected number of woody and non woody species if each assemblage was sampled in 100 sites. To do so we considered each floristic list a sampling unit and split our dataset into two matrices: one recording the presence-absence of woody plants and other with data on non woody plants. We then used rarefaction (interpolation) and extrapolation to build the species accumulation curve for each plant assemblage with 95 % confidence intervals using EstimateS software (Chao et al., 2014; Colwell, 2009; Colwell et al., 2012, 2004; Gotelli & Colwell, 2011). We also computed with EstimateS the total number of species expected for each assemblage using non parametric species richness estimators Chao 2, ICE, Jackknife 1 and Jackknife 2.

Results of the Habit Spectra Analysis

From the total dataset (see Appendix 3) with 1586 species reported from 74 sites we recorded 727 non-woody plants (604 non-climbing, 123 climbing non-woody plants), which represented 45.8 % of the total species complement, versus 823 woody plants (710 non-climbing, 113 climbing woody plants), which represented 51.9 % of the species. Only 25 species of epiphytes and 11 species of hemiparasites were reported (Table 2; Fig. 10).

Table 2 Number and proportion of species with each habit in the semiarid Caatinga Phytogeographical Domain (based on the combined data from 74 sites)

	Non woody	Climber non woody	Climber woody	Woody	Epiphytes	Parasites and hemiparasites	Total
Number of species reported with each habit	604	123	113	710	25	11	1586
Percentage of species reported with each habit	38.1 %	7.8 %	7.1 %	44.8 %	1.6 %	0.7 %	100.0 %

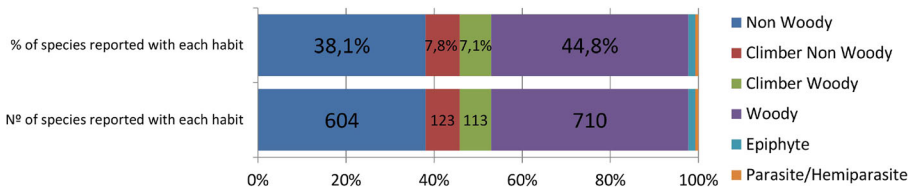


Fig. 10 General habit spectra in the semi-arid Caatinga Phytogeographical Domain as represented in our database (70 sites with data for woody plants and 35 sites with data for non woody plants)

Although the recorded number of woody species (both climbing and non climbing) was slightly larger than the number of non woody species in our dataset the volume of data for woody plants was much greater. When we evaluated the expected richness extrapolated to 100 sites we could see that the expected number of non woody plants in Caatinga is slightly, but significantly, higher than the richness expected for woody plants if both assemblages had been sampled with the same intensity. For 100 sites sampled, the extrapolated species accumulation curve reports $938,2 \pm 19,33$ woody plants and $1098,67 \pm 41,04$ non woody plants (Fig. 11; Table 3). The total richness estimated by non parametric species richness estimators was approximately the same for both components, but since the amount of data available for calculating the non parametric estimators was much smaller for non woody plants the expected total richness of this component may have been more strongly under-estimated than that of woody plants (Table 3). As estimators tend to underestimate the true richness (Brose et al., 2003), this picture is likely to be conservative and the true richness of the Caatinga flora, especially the non-woody flora, is expected to be much higher than that estimated here.

Plotting the habit spectrum of each individual site we can see a large variation in the relative share of woody and non woody plant species reported at each site (Fig. 12). In almost all sites each component represented at least 20 % of the total reported richness,

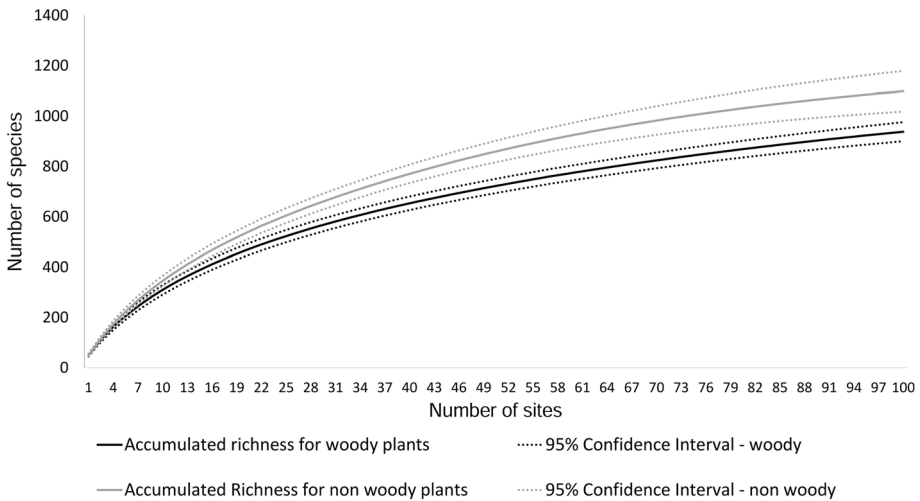


Fig. 11 Extrapolated species accumulation curves showing the expected number of woody and non woody species based in our dataset if each plant assemblage had been sampled in 100 sites. Solid lines represent the extrapolated mean values expected for each assemblage and dotted lines represent the 95 % confidence interval for the data

Table 3 The recorded number of woody species in 70 sites and the recorded number of non woody species in 35 sites as we compiled in our dataset, and the expected extrapolated richness for 100 sites (\pm standard deviation), as well as the total, asymptotic richness estimated by Chao 2, Jackknife 1, Jackknife 2 and ICE estimators

Actual number of species recorded (in 70 sites for woody and 35 for non woody plants)	Number of species expected by the extrapolation to 100 sites	Number of species estimated by Chao 2	Number of species estimated by Jackknife 1	Number of species estimated by Jackknife 2	Number of species estimated by ICE
Data for woody plants (based on 823 70 sites with data on woody plants)	938.2 \pm 19.3	1192	1140.4	1320.1	1189.8
Data for non woody plants (based on 727 ^a 35 sites with data on non woody plants)	1098.7 \pm 41.0	1238.9	1078.5	1309.2	1270.9

^a This represents the total number of non woody species in our full dataset. When preparing the matrices for multivariate analyses, estimation of richness and extrapolation, we excluded from the matrices sites with fewer than 10 species with a given habit reported for that particular site, resulting in a matrix with 721 non woody species in the analyses, from an initial dataset with the full 727 species. Epiphytes and hemiparasites were not included in this analysis

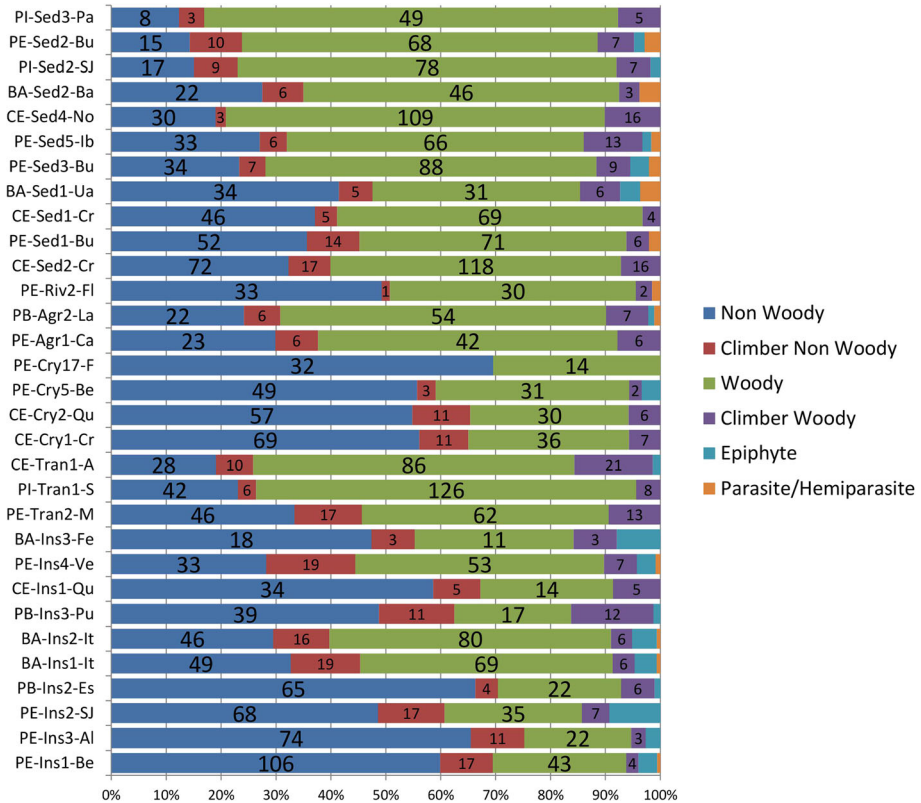


Fig. 12 Habit spectra showing the proportion and number of species with a given habit in each of the 31 sites with data for general flora (both woody and non woody species reported) in the semiarid Caatinga Phytogeographical Domain

with some sites having non woody plants contributing the most to the reported species richness (sometimes over 60 % of the reported local diversity) and other sites having proportionally more woody plant species (Table 4; Fig. 12). In general, inselbergs and crystalline caatingas were the habitats where non woody assemblages showed the largest proportional richness while in sedimentary habitats or transitional sites between the crystalline and the sedimentary woody plants tended to contribute more to the total reported richness (Table 4; Fig. 12).

Raunkiaerian Life-Forms in the Caatinga Phytogeographical Domain: How Do Life-Form Spectra Vary Among Edaphic Environments and How Does the Structure of Caatinga Compare with Other World Biomes?

Procedures

We compiled from the literature up to 2011 all floristic surveys in the CPD which reported Raunkiaerian life-forms for the species sampled. We considered only surveys which reported the life-forms for the general flora (i.e. we did not include papers

Table 4 Number of species in each of the 31 sites with data for general flora (both woody and non woody species reported) used to build the habit spectra in the semiarid Caatinga Phytogeographical Domain

Environment type	Site Code	Number of species reported						Total
		Non Woody	Climber non woody	Woody	Climber woody	Epiphyte	Parasite/Hemiparasite	
Inselberg	PE-Ins1-Be	106	17	43	4	6	1	177
Inselberg	PE-Ins3-AI	74	11	22	3	3		113
Inselberg	PE-Ins2-SJ	68	17	35	7	13		140
Inselberg	PB-Ins2-Es	65	4	22	6	1		98
Inselberg	BA-Ins1-It	49	19	69	6	6	1	150
Inselberg	BA-Ins2-It	46	16	80	6	7	1	156
Inselberg	PB-Ins3-Pu	39	11	17	12	1		80
Inselberg	CE-Ins1-Qu	34	5	14	5			58
Inselberg	PE-Ins4-Ve	33	19	53	7	4	1	117
Inselberg	BA-Ins3-Fe	18	3	11	3	3		38
Transition crystalline/sedimentary	PE-Tran2-M	46	17	62	13			138
Transition crystalline/sedimentary	PI-Tran1-S	42	6	126	8			182
Transition crystalline/sedimentary	CE-Tran1-A	28	10	86	21	2		147
Crystalline	CE-Cry1-Cr	69	11	36	7			123
Crystalline	CE-Cry2-Qu	57	11	30	6			104
Crystalline	PE-Cry5-Be	49	3	31	2	3		88
Crystalline	PE-Cry17-F	32		14				46
Crystalline	PE-Agr1-Ca	23	6	42	6			77
Crystalline	PB-Agr2-La	22	6	54	7	1	1	91
Riverine forest	PE-Riv2-FI	33	1	30	2		1	67
Sedimentary	CE-Sed2-Cr	72	17	118	16			223
Sedimentary	PE-Sed1-Bu	52	14	71	6		3	146
Sedimentary	CE-Sed1-Cr	46	5	69	4			124
Sedimentary	BA-Sed1-Ua	34	5	31	6	3	3	82
Sedimentary	PE-Sed3-Bu	34	7	88	9	5	3	146
Sedimentary	PE-Sed5-Ib	33	6	66	13	2	2	122
Sedimentary	CE-Sed4-No	30	3	109	16			158
Sedimentary	BA-Sed2-Ba	22	6	46	3		3	80
Sedimentary	PI-Sed2-SJ	17	9	78	7	2		113
Sedimentary	PE-Sed2-Bu	15	10	68	7	2	3	105
Sedimentary	PI-Sed3-Pa	8	3	49	5			65

addressing only woody or only herbaceous plants). We considered only the life-form categories originally proposed by Raunkiaer: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes. When a different life-form was reported for a species, we translated it back to Raunkiaer's original system: aerophytes, epiphytes and hemiparasites were considered phanerophytes; cacti and succulent plants were considered phanerophytes or chamaephytes, depending on the size of the adult plant; climbers were reclassified as phanerophytes, chamaephytes, or therophytes, depending on their ability to survive the dry season. Sometimes the authors of the original papers did not classify a given species into any category. In those cases we attributed it a life-form based on our knowledge or after consulting other botanists.

Differences in Life-Form Spectra Among Habitats Types in Caatinga

We classified each survey we located in one of three environment categories: (1) crystalline caatinga; (2) sedimentary caatinga; and (3) inselbergs. The inselbergs were further divided in two subcategories as follows. Four of our inselbergs (França et al., 2005; Gomes & Alves, 2010; Porto et al., 2008) occurred in the agreste ecotone and were termed *inselbergs in the agreste*. One inselberg was located within an area of typical crystalline semiarid caatinga (Araújo et al., 2008) and was termed *inselberg in caatinga*. We then built a table showing the Raunkiaerian life-form spectrum for each site and ordered the life-form spectra among the sites using a Nonmetric Multidimensional Scaling Analysis (NMS) with Euclidean distances (Legendre & Legendre, 2012; McCune & Grace, 2002). We performed the NMS with PC-ORD 6.0 (McCune & Mefford, 2011) and chose two axes to represent the data (because two axes was the best solution after pilot tests using the autopilot mode of the software and 250 runs).

Differences in Life-Form Spectra Between the Caatinga and Other World Biomes

To address our last question we used the biological spectra of the main world biomes compiled from Batalha and Martins (2002) and compared them with the biological spectra of crystalline caatingas, sedimentary caatingas and inselbergs (the complete matrix used in our analysis is available in Appendix 2). We then analysed the biological spectra of all sites with a NMS and Euclidean distance in PC-ORD 6.0 (McCune & Mefford, 2011) in order to evaluate whether the biological spectrum of Caatinga differed from those documented for the main world biomes (a two dimensional solution was used after pilot tests using autopilot mode in PC-ORD software and 250 runs).

Results of the Raunkiaerian Life-Form Analysis

A thorough literature search yielded data on Raunkiaer's life-form spectra for 13 sites within the CPD, of which five were in crystalline caatinga, three in sedimentary caatinga, one on an inselberg in caatinga and four on inselbergs in the agreste (Table 5). In all crystalline caatingas and on the inselberg in caatinga, therophytes were the main life-form, whereas the sedimentary caatinga had spectra dominated by the phanerophytic life-form (Table 5; Appendix 2). Inselbergs in agreste, exposed to a milder rain seasonality than the inselberg in caatinga, had biological spectra between those of crystalline and sedimentary sites.

The NMS of the life-form spectra of the caatingas and inselbergs formed three groups (Fig. 13). One group comprised all crystalline caatingas and the inselberg in caatinga and was characterized by the predominance of therophytes (Table 5; Fig. 13). A second group encompassed all the sedimentary caatingas and one inselberg in agreste and was characterized by an overrepresentation of phanerophytes (Table 5; Fig. 13), indicating that the differences between crystalline and sedimentary caatingas are not only floristic, but also functional and physiognomic. The third group comprised the remaining inselbergs in agreste which had a high proportion of phanerophytes, but also a high proportion of therophytes (Table 5; Fig. 13).

Even under the same regional macroclimate, the life-form spectra of crystalline and sedimentary caatinga were markedly distinct and clearly separate in the NMS ordination (Fig. 13). But considered in a broader context the CPD had a set of spectra that were distinguishable from those of the major world biomes. CPD shows a range of spectra between those of deserts and rainforests, with the crystalline caatingas structurally closer to the hot steppes and deserts due to the overrepresentation of therophytes, and sedimentary caatingas closer to the tropical forests due to their higher proportion of phanerophytes (Fig. 14).

Table 5 Biological spectra in the Caatinga Domain in Brazil, with reclassified life-forms to match the original Raunkiaerian categories

Caatinga subtype	Site code	Life-form class (%)					Reference
		Ph	Ch	He	Cr	Th	
Crystalline Caatinga							
Crateús, Ceará	Cry-caa1	28.5	19.0	5.1	1.5	46.0	Araújo et al. (2011)
Quixadá, Ceará	Cry-caa3	26.3	15.8	12.8	2.3	42.9	Costa et al. (2007)
Floresta/Betânia 1, Pernambuco	Cry-caa2	28.7	21.8	12.9	1.0	35.6	Costa et al. (2009)
Floresta/Betânia 2, Pernambuco	Cry-caa4	26.1	19.6	15.2	2.2	37.0	Rodal et al. (2005)
Floresta, Pernambuco	Cry-caa5	23.4	16.9	16.9	2.6	40.3	Rodal et al. (2005)
Sedimentary Caatinga							
Crateús 1, Ceará	Sed-caa1	57.4	19.1	3.7	2.9	16.9	Araújo et al. (2011)
Crateús 2, Ceará	Sed-caa2	58.0	23.2	2.4	3.2	13.2	Araújo et al. (2011)
S. José do Piauí, Piauí	Sed-caa3	71.3	12.5	8.1	3.7	4.4	Mendes and Castro (2010)
Inselberg in the Caatinga							
Quixadá, Ceará	Ins-caa	26.0	14.3	13.0	2.6	44.2	Araújo et al. (2008)
Inselberg in the Agreste							
S. Joaquim do Monte, Pernambuco	Ins-agr1	49.4	6.5	4.5	11.7	27.9	Gomes and Alves (2010)
Altinho/Agrestina, Pernambuco	Ins-agr2	35.2	5.6	3.2	11.2	44.8	Gomes and Alves (2010)
Esperança, Paraíba	Ins-agr3	39.7	12.7	4.8	0.8	42.1	Porto et al. (2008)
Feira de Santana, Bahia	Ins-agr4	60.4	18.8	8.3	6.3	6.3	França et al. (2005)

Ph phanerophyte, *Ch* chamaephyte, *He* hemicryptophyte, *Cr* cryptophyte, *Th* therophyte

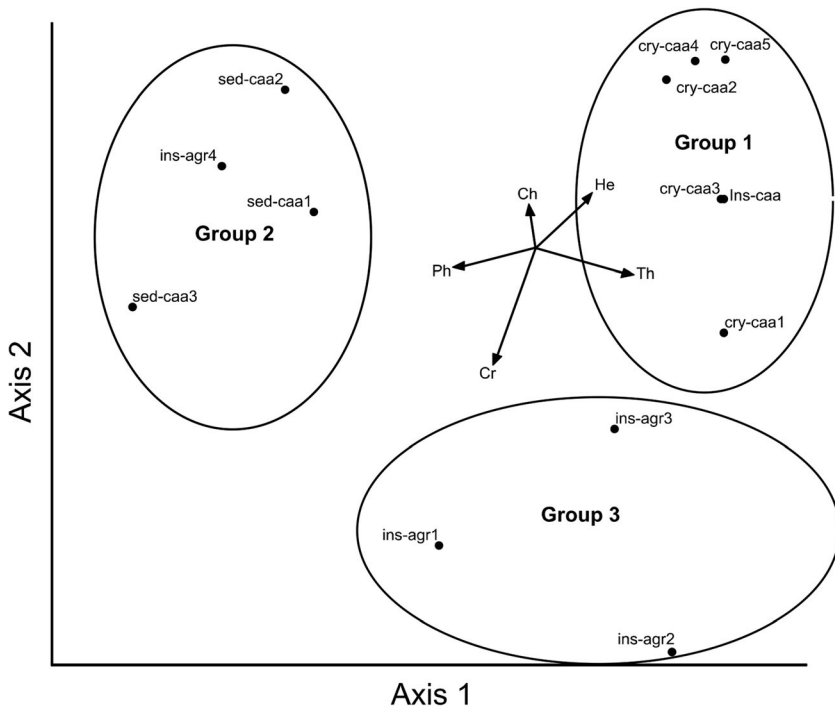


Fig. 13 Nonmetric Multidimensional Scaling analysis of the biological spectra of 13 sites in the Caatinga. The best solution was a two dimensional configuration: final stress for 2-dimensional solution = 1.09675. Cry-caa and sed-caa refer to crystalline and sedimentary sites, respectively. Ins-caa and ins-agr refer to inselbergs in the Caatinga and Agreste region, respectively. Raunkiaer's life-forms: *Ph* phanerophyte; *He* hemicryptophyte; *Cr* cryptophyte; *Ch* chamaephyte; *Th* therophyte

Discussion

Data Availability and Bias

Caatinga was historically one of the least studied phytogeographical domains in Brazil (Santos et al. 2011), but fortunately the number of published floristic and phytosociological studies is increasing each year (Moro et al., 2015a). Nevertheless there are important biases in the available data. Although the crystalline caatinga is by far the most widespread ecosystem type in the CPD it is by no means the best studied, and most of the surveys in crystalline caatingas are concerned only with woody plants, ignoring the species rich, non woody component (Table 1; Moro et al., 2014a). We show here that the non woody component represents a high proportion of the plant species richness of the CPD as a whole and that this is particularly true of the crystalline caatinga. It seems ironic that crystalline caatinga, which is so very rich in herbaceous plants (Costa et al., 2007; Table 4; Fig. 12) should be precisely the environment where botanists have most often overlooked the non woody component (Table 1). Moreover, when the geographical distribution of studies in crystalline caatingas is considered (Fig. 5), striking gaps in the sampling coverage become evident. The typical crystalline caatingas of Bahia, for example, were not

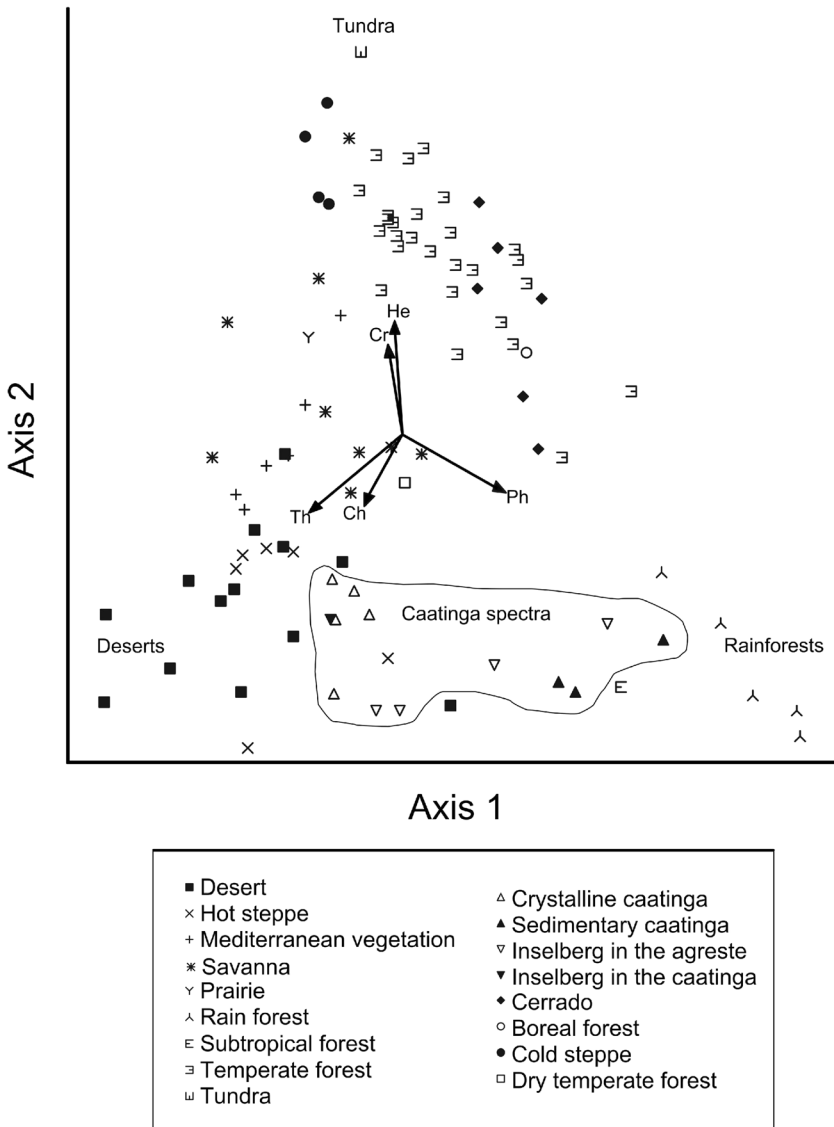


Fig. 14 Nonmetric Multidimensional Scaling analysis of Raunkiaer’s life-form spectra of the Caatinga and major world biomes. The best solution was a two dimensional configuration: final stress for 2-dimensional solution = 7.63037. Raunkiaer’s life-forms: *Ph* phanerophyte; *He* hemicryptophyte; *Cr* cryptophyte; *Ch* chamaephyte; *Th* therophyte. The spectrum of each site plotted in this NMS graph is presented in Appendix 2

represented by any study published up to 2011, the endpoint for inclusion of studies in our dataset (but see the more recent study of Costa et al., 2015).

Similar sampling biases are clear with regard to other environment types. All surveys in riverine forests and rupicolous vegetation were undertaken within crystalline landscapes, and most of the inselbergs were surveyed in the *agreste* ecotonal areas, not in typical semiarid crystalline sites. These biases must be acknowledged when interpreting the biogeography of the domain and they reveal gaps to be addressed by

further studies. Nevertheless, despite these gaps a clear biogeographical pattern could be observed regarding the plant communities present in the CPD as discussed below.

Phytogeography of Plant Communities in Different Habitat Types

The CPD has long been recognized as a domain of high environmental heterogeneity (Ab'Sáber, 1974, 2003; Andrade-Lima, 1981), which is reflected in the flora of the region, recently shown to present high beta diversity (Apgaua et al., 2014b). Multivariate analyses evaluating the phytogeography of the Domain were undertaken in the 1990s (Araújo et al., 1999), but it was only with the availability of more data from the 2000s onward that studies began to show clearly the biogeographical differences between the flora of crystalline and sedimentary terrains (Cardoso & Queiroz, 2007; Gomes et al., 2006). Although those studies were based on a much more restricted datasets (smaller number of sites and comparisons of legume species only respectively) our data generally agree with their findings, as sedimentary caatingas formed clear groups, distinguishable from the crystalline flora. Although the sedimentary sites evaluated here were disjunct and located at significant distances from each other (Ibiapaba-Araripe basin, Tucano-Jatobá basin and São Francisco Dunes – see Fig. 5), they were floristically more similar to each other than to the crystalline caatingas in their immediate vicinity (Figs. 6, 7, 8, and 9).

The caatinga sites in Campo Maior (an ecotone between sedimentary caatingas and the cerrados) formed a peripheral subgroup of sedimentary caatingas, nested within the range of sedimentary caatingas, but somewhat dissimilar to the main sedimentary sites (Figs. 7 and 9). As these are transitional areas (Castro & Martins, 1999; de Farias & Castro, 2004; Ratter et al., 2003) one could expect elements of the cerrados (savannas) to mix with typical caatinga species. This was the case here, with cerrado species such as *Anacardium occidentale* and *Curatella americana* forming part of the plant assemblages (de Farias & Castro, 2004).

Crystalline caatingas had a more complex pattern, which presented interpretation challenges. Excluding a few outliers (e.g. Pb-Agr2 – See Fig. 6), it seems that the flora of crystalline caatingas, riverine forests, the agreste ecotone and some of the inselbergs constitute a second floristic group (Figs. 6, 7, 8, and 9), separate from sedimentary sites. Although riverine forests in the CPD do have a group of characteristic species (e.g. *Ziziphus joazeiro* and *Licania rigida*), these were not sufficient in number to make the whole flora very distinct from typical crystalline caatinga sites. This could, to a certain degree, be attributable to the fact that some of the studies included in our analyses (Appendix 1) sampled relatively large areas, rather than more geographically restricted and well defined riverine forests. The need for more focused studies of riverine vegetation within the CPD is further illustrated by the fact that we could find no published studies of carnauba palm riverine forests (*carnaubais*) despite the fact that this forest type is common and very characteristic of the CPD (Andrade-Lima, 1981; Moro et al., 2015b). In summary, the riverine forest floras included in our study are not representative of those of the CPD as a whole, as all occur within crystalline landscapes and do not cover many of the important river systems in the CPD (as the São Francisco and Jaguaribe). The

data available to date about these riverine forests within crystalline landscapes show that their flora is closer to the surrounding crystalline caatingas than to other environments.

In contrast, arboreal caatingas of Minas Gerais are positioned in a peripheral position to crystalline caatinga sites, in a similar fashion to the relationship observed between the Campo Maior ecotone and the sedimentary caatingas. It seems that the arboreal caatinga is an extreme of a latitudinal gradient of crystalline caatinga flora (Figs. 7 and 9). The arboreal caatinga might therefore most appropriately be treated as a peripheral subgroup within the crystalline caatinga flora or, as suggested by Santos et al. (2012), as a distinct floristic group within the CPD. The latter option might be appropriate, as the arboreal caatingas are located on a large karstic region with different pedological features when compared with the typical crystalline caatingas (Fig. 5). Both the arboreal caatingas and the deciduous dry forest enclaves within the CERPD have floristic links with the CPD and other SDTF of the South American continent (Arruda et al., 2013; Neves et al., 2015).

Considered as a whole, the crystalline landscapes seems to present a latitudinal gradient of species turnover beginning in the northern crystalline caatinga sites and ending in the caatingas of Chapada Diamantina and the arboreal caatingas of Minas Gerais discussed above (Figs. 7 and 9). This gradient reveals both the floristic particularities (peripheral position of arboreal and Chapada Diamantina caatingas in the NMS) and the floristic bounds (floristic connection with crystalline sites in the UPGMA) of the arboreal and crystalline caatingas. Santos et al. (2012) showed arboreal caatinga in an intermediate position between the typical crystalline caatingas and the deciduous forests of the Cerrado Domain, as would be expected in a gradient of species turnover, a result also supported by Neves et al. (2015). When floristic studies of crystalline caatingas in Bahia state become available, it will be possible to evaluate to what extent the crystalline caatingas of southern Bahia resemble the distant crystalline caatingas of Pernambuco and Ceará or the geographically closer caatingas of Chapada Diamantina and arboreal caatingas of Minas Gerais. Unfortunately, all available studies of the caatinga of Chapada Diamantina and arboreal caatinga focused only on woody plants (Table 1; Appendix 1), with no data on the non woody component. There is a clear need for new and more inclusive studies which also sample the non woody components of the flora to provide a more complete picture of the biodiversity of these environments.

Inselberg sites provide a harsh environment for organisms, with shallow soils and little edaphic water supply (Porembski, 2007). These conditions can be expected to influence the composition of flora, with a set of drought tolerant plants occupying this environment type (Porembski & Barthlott, 2000; Porembski, 2007). The inselberg flora formed another gradient, distinct from the crystalline caatingas gradient. Multivariate analyses of both the general flora and the woody flora recovered the inselbergs as a separate group (Fig. 9a and b), but analyses based on the non woody component showed similarities with the flora of crystalline caatinga sites (Fig. 9c). The non woody flora of a few inselbergs (the wettest ones, in Bahia state) grouped with sedimentary sites of the Tucano-Jatobá sedimentary basin and Dunas do São Francisco (Fig. 8), perhaps reflecting the geographical proximity of these areas. Although some inselbergs were floristically closer to the crystalline caatingas and a few outlier inselbergs emerged closer to the sedimentary caatingas (Figs. 6, 7, 8, and 9), as a whole inselbergs

constituted a floristic group to a large extent distinct from both crystalline and sedimentary floras (Fig. 9). This pattern may be attributable to the rainfall gradient across the different areas, with the inselbergs located in drier areas having a flora very similar to the crystalline caatingas while wetter sites present progressively more different floras (Figs. 6, 7, and 9).

As a whole we found in our analyses three broad, well defined floristic groups within the CPD related to substrate: sedimentary caatingas and their ecotonal sites (Campo Maior); crystalline caatingas and their associated ecosystems and ecotonal sites (agreste, riverine forests, Chapada Diamantina and arboreal caatinga); and inselbergs. Thus, it seems that the main factor determining plant communities within the CPD is the substrate, which is recognized to influence plant communities in both broad and fine scales (Balvanera et al., 2011; Santos et al., 2012; Arruda et al., 2013; Neves et al., 2015). But even if the edaphic environment is the main factor determining the flora of each site, within a given environment type we also recognize the relevance of gradients (Santos et al., 2012). Both crystalline caatinga and inselberg floras seem to be influenced by latitudinal and rainfall gradients, a result comparable to that found by Neves et al. (2015) studying SDTF on a continental scale.

It is important to note that the sites here referred to as “sedimentary caatingas” are plant communities generally located on oligotrophic sedimentary soils such as quartzarenic neosols and latosols (Velloso et al., 2002; Marques et al., 2014) while both in Chapada Diamantina and northern Minas Gerais there are eutrophic soils derived from calcareous areas (Arruda et al., 2013). We did not have access to a detailed geological mapping of the CPD, but it seems that eutrophic calcareous terrains support a flora more similar to the crystalline caatingas. This is consistent with the existence of many dry forest enclaves (calcareous deciduous forests) inside the Cerrado Domain which share species with both the arboreal and crystalline caatinga (e.g. *Aspidosperma pyriformium*, *Commiphora leptophloeos* and *Cavanillesia arborea*) (dos Santos et al., 2007; Felfili et al., 2007; Carvalho & Felfili, 2011; Oliveira-Filho et al., 2013; Neves et al., 2015).

Habit Spectra in the Caatinga Phytogeographical Domain

Phanerophytes are the most prominent element in most vegetation and because of that woody plants receive much more attention from botanists collecting not only in wet forests, but also in more open vegetation such as savannas, woodlands and scrublands. The effect of this focus over many years is evident in Table 1 where a large number of surveys focused only on the woody component. As a consequence, our knowledge of the woody component is more comprehensive than our knowledge of the non woody plants, resulting in macroecological and biogeographical studies that confine their analyses to tree and shrub species distributions when seeking to discern biogeographical patterns (Oliveira-Filho & Fontes, 2000; Ratter et al., 2003; Santos et al., 2012; Eisenlohr & Oliveira-Filho, 2015; Neves et al., 2015). This approach is particularly problematic in the case of seasonal ecosystems such as the savannas and dry forests which are very rich in non woody plants (Batalha & Martins, 2002; Costa et al., 2007; Sano et al., 2008) and this component has been largely overlooked (Table 1), even in semiarid ecosystems, where non woody plants constitute a large proportion of the local biodiversity (Table 2; Table 3).

The habit spectrum we built for our whole dataset (Table 2; Fig. 10) shows the importance of non woody plants in the CPD. In our dataset non woody plants (summing both climbing and non climbing) represented 45.9 % of the species, while woody plants represented 51.9 %. But this result should be considered in light of the fact that the floristic data available to date is strongly skewed towards woody plants. Our analysis included 70 studies with data on woody plants and only 35 studies with data on non woody plants and, despite this bias, yielded a very even distribution in the species richness between the two plant assemblages. If more studies reporting non woody plants are published, especially in the crystalline caatinga, we would expect the number of non woody species to equal or surpass the number of woody plants. This expectation is supported by the higher richness of non woody plants estimated with extrapolation methods and also by the similar total number of species estimated for each assemblage by the non parametric richness estimators (Table 3; Fig. 11). This also gives support to the idea that semiarid ecosystems are functionally intermediate between rain forests, where the woody component dominates, and deserts, where annual herbs dominate, an idea reinforced by the life-form spectra compiled, which were ordered in an intermediate position between rainforests and deserts by the NMS ordination (Fig. 14).

Epiphytes and parasites/hemiparasites are both a minor component of the Caatinga flora (Table 2), a pattern also found in floras of dry vegetation in general (Medina, 1995). But while parasites and hemiparasites are commonly a minor component in other vegetation, epiphytes are an extremely rich component in some rainforests, such as the Atlantic Forest adjacent to the Caatinga (Stehmann et al., 2009; Zappi et al., 2015). Due to water restriction, only a few epiphytes can survive in dry forests (Medina, 1995) and in fact we found very few epiphytic species, usually in the families Orchidaceae and Bromeliaceae (genus *Tillandsia*) (see Appendix 3 and Moro et al., 2014a). Woody and non woody climbers had in general a similar proportion of species in the CPD (Fig. 10), collectively comprising 15 % of the reported species.

Therophytic herbs are expected to thrive in unpredictable habitats, especially in arid or semiarid ecosystems where rainfall timing and amount is uncertain (Raunkiaer, 1934). Due to its semiarid climate, with unpredictable rainfall, short rainy season and periodical strong droughts (Nimer, 1972, 1989) the Caatinga is one such habitat, and studies evaluating Raunkiaerian life-forms in Caatinga have shown a large proportion of therophytes in the local plant communities (Costa et al., 2007, 2009; Araújo et al., 2011). We show here that non woody plants are a major component of the CPD flora as a whole (Table 2; Fig. 10), rarely constituting less than 20 % and usually constituting more than 40 % of the species diversity of local plant communities (Table 4, Fig. 12). In many inselbergs and crystalline caatingas non woody plants represented over 60 % of the recorded species (see also Queiroz et al., 2015).

Crystalline caatingas usually have shallow, but nutrient-rich soils (Sampaio, 1995, 2010; Velloso et al., 2002) while inselbergs have extremely shallow soils or none. It seems that these conditions are more conducive to the establishment and survival of non woody plants than of woody plants. Inselbergs may present particularly acute challenges for woody plants because it is difficult for them to establish on bare rocks and to survive water restrictions after the rainy season. In our study, the inselbergs with the largest proportion of woody plants are those in Bahia, located in the wetter transition of caatinga to the Atlantic Forest at the very edge of the Brazilian semiarid, in a much wetter location than the others (Moro pers. obs.).

Although crystalline caatingas have shallow soils, presumably retaining edaphic water for a short time after the rainfall has ended, the fact that they have nutrient rich soils should facilitate rapid nutrient uptake and regrowth of therophytes and the aerial parts of geophytes, chamaephytes and hemicryptophytes once the rainy season returns. Sedimentary sites, in contrast, generally have much deeper and nutrient-poor soils (Sampaio, 1995, 2010; Velloso et al., 2002; Marques et al., 2014). These oligotrophic soils likely make life difficult for annual plants which have a narrow window of opportunity for nutrient uptake each year. These same conditions would allow woody plants with well developed root systems to reach edaphic water for a longer time after rainfall ends. This may explain why most sedimentary sites, sites in the wetter Agreste ecotone and the wetter inselbergs from Bahia have a predominance of woody plants, while crystalline caatingas and inselbergs in dryer sites have a predominance of non woody plants (Table 4; Fig. 12).

Raunkiaerian Life-Forms in the Caatinga Phytogeographical Domain

Differences in Life-Form Spectra Between the Crystalline, Sedimentary and Inselberg Environments

Our results showed a significant floristic distinction between crystalline and sedimentary caatingas in the life-form spectra. This suggests that the differences between crystalline, sedimentary and inselberg environments are not restricted to species composition, but are reflected also in the structure of vegetation in each habitat and even in the phylogenetic structure of the plant communities occupying each habitat (Moro et al., 2015c). We show here that crystalline caatingas are rich in therophytes, whereas sedimentary caatingas are dominated by phanerophytes and this is the first time that life-form spectra are compared for the whole Caatinga.

Although all sites are exposed to a strong precipitation seasonality and high potential evapotranspiration (Nimer, 1972), crystalline sites have generally shallow, stony soils, whereas sedimentary sites have deep soils (Sampaio, 1995, 2010; Queiroz, 2006; Marques et al., 2014). Thus, therophytes thrive in the harsh, but nutrient-rich, environment of the crystalline caatinga, completing their life cycle in one rainy season. Living in a nutrient rich environment would allow therophytes to germinate in the beginning of the rainy season, absorb the necessary minerals from the soil and complete their life-cycles, dying when the rainy season ends.

On the other hand, phanerophytes predominate in sedimentary soils that are poorer in nutrients, but can potentially retain water for a long time after the end of the rains (Marques et al., 2014; Sampaio, 1995, 2010). Since phanerophytes are perennial plants, they can store nutrients in vegetative organs and have a root system that allows them to access water at greater depths. Thus, it seems that phanerophytes are functionally more efficient in the Caatinga's deep, nutrient-poor sedimentary soils because they can retain in their vegetative organs nutrients from one year to the other and access edaphic water for a longer timeframe than therophytes.

While different edaphic environments are known to influence species composition elsewhere (McAuliffe, 1994; Balvanera et al., 2011), our conclusions highlight a second aspect of this edaphic influence: the differences were not restricted to species composition but were also reflected in the functional attributes of vegetation (i.e. life-

forms). While crystalline and sedimentary caatingas had clearly distinct biological spectra, inselbergs constituted a functional gradient between them. Located in a drier climate, the inselberg in caatinga (Ins-caa) had the greatest proportion of therophytes, with a life form spectrum and a flora similar to that of crystalline caatingas. On the other hand the inselberg exposed to the mildest climate (Ins-agr4) had the greatest proportion of phanerophytes, approaching the spectra of sedimentary caatingas (although with a different flora), whereas the other inselbergs in agreste had intermediate spectra, consistent with their intermediate climatic conditions (Fig. 13; Table 5).

In dry formations, edaphic related factors have been shown to drive important floristic and functional differences on a regional scale (Balvanera & Aguirre, 2006; Balvanera et al., 2011; Buck, 1964; Moro et al., 2015c; Santos et al., 2012). Thus, although climate is recognized as the main factor governing biome distribution on a world scale, communities on a regional scale may be more influenced by substrate differences than by climate gradients (Moro et al., 2015c). Thus, we infer that the functional structure of each community is more related to substrate than to climatic here and this may be explained by differences in nutrient and water availability in the soil between sedimentary and crystalline areas. Inselberg communities showed a more complex pattern, with drier inselbergs more similar to the crystalline caatinga and wetter inselbergs progressively different from both crystalline and sedimentary caatingas, apparently following a climatic gradient within this environment type.

Differences in Life-Form Spectra Between the Caatinga and Other Biomes

We found that the Raunkiaerian life-form spectrum of Caatinga is distinct when compared to the main world biomes. It seems that the long dry season in the CPD resulted in plant communities with spectra which are intermediate between those of rain forests and deserts (Fig. 14). Although different edaphic environments resulted in different spectra on a regional scale (Fig. 13), when these spectra are considered in a global context they represent a single group (Fig. 14), filling the “structural” gap between deserts and rainforests in the world spectra. This is the first time we are aware that this pattern has been shown on a subcontinental scale for a SDTF.

SDTFs were defined in the literature based on floristic and ecological features (Pennington et al., 2000, 2009; Prado, 2000). Now we also show that differences to other world biomes also hold for functional, physiognomic features like the life-form spectrum. Moreover, Caatinga was physiognomically different not only from other large South American biomes (Cerrado and Rainforests), but also from all other world biomes we compared. Collation of life-form spectra from other dry formations (in America, Africa, Asia and Oceania) would represent an interesting further step to test whether the spectra of other semiarid formations are congruent with those of Caatinga.

Key Questions and Directions for Future Research

This review has presented a series of synthetic analyses of the floristic and phytosociological data published for Caatinga up to and including 2011. Our work to collate, analyse and

interpret these data has brought into sharp focus the various limitations of the data currently available. Here we propose a set of key actions and future research directions which we consider important in increasing knowledge of the Caatinga and helping to ensure its future by documenting and mapping its diversity and improving its management.

Further site based floristic studies are urgently required to increase coverage, especially in poorly known areas of the CPD such as the sedimentary caatingas of the São Francisco's dunes and the crystalline caatingas of southern Bahia. Editors of scientific journals are urged to facilitate publication of such studies which are increasingly dismissed as 'natural history'. The synthetic approaches adopted by the current study and by other recent authors (Cardoso & Queiroz, 2007; Gomes et al., 2006; Moro et al., 2015c; Santos et al., 2012) are only possible because they are built on a foundation of many individual, careful site-based studies, requiring months or years of collecting and identifying plant material.

Ecologists and botanists undertaking floristic surveys in the CPD are encouraged to include non woody plants in their data capture plans, as this very important component of the flora has often been overlooked in studies of this kind.

Macroecological studies will play an important role in investigating how the environment shapes plant communities within Caatinga and how woody and non woody plants respond to different environmental conditions. Community phylogenetic approaches such as those adopted by Oliveira-Filho et al. (2013) and Moro et al. (2015c) have the potential to contribute significantly to our understanding of how ecology shapes phylogeny in both woody and non woody guilds in the semi-arid.

New cartographic studies are required to delineate more precisely the limits of the CPD and propose a new geographical classification for the entire region, supported by high resolution maps. There is a particularly pressing need for updated maps of vegetation coverage, showing where native vegetation survives in relatively intact form and how much has been altered or lost. The current 5 to 6 year delay in revising and publishing such remotely sensed data for Caatinga (and all other extra Amazonian biomes, as reported in Brazil's 5th National Report to the Convention on Biological Diversity) is not consistent with the urgency of the challenges faced in characterizing and conserving this unique phytogeographic domain.

These data, combined with the species occurrence point data recently mobilized by data digitization and repatriation projects such as Re flora (Morim & Nic Lughadha, 2015) represent important new resources enabling enhanced modelling of the potential distribution of plant species and assemblages in the CPD. These approaches can provide important insights of immediate relevance e.g. in pinpointing areas expected to have higher species richness which should be targeted for fieldwork, and in the medium- to long-term in evaluating how species/assemblages may respond to climate change.

All of the above approaches will be important in informing the selection of and maximizing the effectiveness of proposed extensions to the Protected Area network in the Caatinga from the 7.4 % of the biome reported in 2015 to the 17 % required to meet Brazil's national target 11 (Brazil 2015).

Looking beyond the borders of Caatinga, and even of Brazil, an important goal in achieving an enhanced understanding of the biodiversity of dry formations would be the comparison at continental or world scale of biogeographical patterns of SDTF taxa

and modelling the main macroecological factors underpinning the distribution of biodiversity in these dry biomes. Ideally, such studies should be based not only on data concerning woody plants, but also for the species rich non woody component and selected groups of animals.

Conclusions

The idea that the Caatinga Phytogeographical Domain has at least two floristic nuclei, one in crystalline and other in sedimentary sites, was corroborated here, with a larger and more comprehensive dataset than previously used to test this hypothesis. Moreover we present a more complete plant diversity synthesis for the Caatinga, analysing the phytogeography of other environments within the CPD such as the inselbergs, riverine forests, agreste ecotone, arboreal caatingas and the caatingas in the Chapada Diamantina. Arboreal caatingas and the caatingas in the Chapada Diamantina seem to be on the periphery of a long latitudinal gradient within the crystalline environment. A better understanding would be achieved with data on the crystalline caatingas of Bahia and with data on non woody plants from the arboreal caatinga and the caatinga in the Chapada Diamantina. We provide here a large synthesis of the biogeographic floristic relationships between the main plant communities within the CPD, highlighting the occurrence of more than one floristic nucleus within this phytogeographical domain.

We highlight the importance of non woody plants to the biodiversity of semiarid areas and encourage botanists studying arid and semiarid ecosystems not to focus only on woody plants when undertaking biodiversity studies, but to devote time to sampling the herbaceous plants too. Despite previous studies having been strongly skewed towards woody plants, non woody plants constituted almost half of the species documented in our synthesis and in some sites they represented over 60 % of the total species richness, with therophytes being the most common life-form in crystalline caatinga sites. We show that crystalline and sedimentary caatingas are distinct not only in the composition of their flora, but also in the structure of their vegetation, with different life-form spectra found in these contrasting environments. Nevertheless, when these spectra are considered in a global context the semiarid CPD as a whole was distinguishable from the main world biomes, reinforcing the idea that semiarid ecosystems deserve the recognition as a particular biome type, distinct from both forests, deserts and savannas.

Acknowledgments This article was the outcome of the doctoral thesis of the first author combined with additional data collated during his post-doctoral research. We thank the São Paulo Research Foundation (Fundação de Amparo à Pesquisa do Estado de São Paulo) for the doctoral funds (FAPESP 2009/14266-7) and the international interchange grant (FAPESP 2011/22498-5) awarded to the first author during his doctoral studies as well as the post-doctoral grant awarded to him (FAPESP 2013/15280-9), which enabled further improvements to the database and manuscript before publication. We are grateful to Antônio Sérgio F. Castro and Marcelo O. Teles de Menezes for helping us with the classification of Raunkiaerian life-forms of some species; to Antônio Sérgio F. Castro, Marcelo O. Teles de Menezes, Domingos Cardoso and Luciano Paganucci de Queiroz for allowing us to use some of their photos and to Mariana Bezerra Macedo for preparing the photographic plates for this paper.

Appendix 1

Table 6 List of references used in the biogeographical analysis

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
1	Arboreal Caatinga	MG-Arb1-Januária	MG	Only woody plants	Ratter, J.A.; Askew, G.P.; Montgomery, R.F.; Gifford, D.R.	1978	Revista Brasileira de Botânica 1: 47–58
2	Arboreal Caatinga	MG-Arb8-Juvenília	MG	Only woody plants	Santos, R.M.; Vieira, F.A.; Santos, P.F.; Moraes, V.M.; Medeiros, M.A.	2008	Revista Caatinga 21(4): 154–162
3	Arboreal Caatinga	MG-Arb3-Juvenília	MG	Only woody plants	Santos, R.M.; Vieira, F.A.; Fagundes, M.; Nunes, Y.R.F.; Gusmão, E.	2007	Revista Árvore 31(1): 135–144
4	Arboreal Caatinga	MG-Arb4-Juvenília	MG	Only woody plants	Santos, R.M.; Vieira, F.A.; Fagundes, M.; Nunes, Y.R.F.; Gusmão, E.	2007	Revista Árvore 31(1): 135–144
5	Arboreal Caatinga	MG-Arb5-Juvenília	MG	Only woody plants	Santos, R.M.; Vieira, F.A.; Fagundes, M.; Nunes, Y.R.F.; Gusmão, E.	2007	Revista Árvore 31(1): 135–144
6	Arboreal Caatinga	MG-Arb6-Juvenília	MG	Only woody plants	Santos, R.M.; Vieira, F.A.; Fagundes, M.; Nunes, Y.R.F.; Gusmão, E.	2007	Revista Árvore 31(1): 135–144
7	Arboreal Caatinga	MG-Arb7-Juvenília	MG	Only woody plants	Santos, R.M.; Vieira, F.A.; Fagundes, M.; Nunes, Y.R.F.; Gusmão, E.	2007	Revista Árvore 31(1): 135–144
8	Arboreal Caatinga	MG-Arb2-Juvenília	MG	Only woody plants	Santos, R.M.; Barbosa, A.C.M.C.; Almeida, H.S.; Vieira, F.A.; Santos, P.F.; Carvalho, D.A.; Oliveira-Filho, A.T.	2011	Cerne 17(2): 247–258
9	Arboreal Caatinga	MG-Arb9-Montalv	MG	Only woody plants		2007	Revista Árvore 31(1): 135–144

Table 6 (continued)

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
10	Caatinga in Agreste (Ecotone to the Atlantic Forest)	PB-Agr3-Areia	PB	Only woody plants	Santos, R.M.; Vieira, F.A.; Fagundes, M.; Nunes, Y.R.F.; Gusmão, E.	2003	Biotropica 35 (2): 154–165
11	Caatinga in Agreste (Ecotone to the Atlantic Forest)	PB-Agr2-LagoaSeca	PB	Woody and non woody plants	Pereira, I.M.; Andrade, L.A.; Sampaio, E.V.S.B.; Barbosa, M.R.V. (includes Pereira et al. 2001; 2002) Lourenço, C.E.L.; Barbosa, M.R.V.	2003	Revista Nordestina de Biologia 17 (1/2): 23–58
12	Caatinga in Agreste (Ecotone to the Atlantic Forest)	PB-Agr1-Pocinhos	PB	Only woody plants	Andrade, L.A.; Oliveira, F.X.; Neves, C.M.L.; Felix, L.P.	2007	Revista Brasileira de Ciências Agrárias 2(2): 135–142
13	Caatinga in Agreste (Ecotone to the Atlantic Forest)	PE-Agr2-BrejoMDeus	PE	Only woody plants	Andrade, W.M.; Lima, E.A.; Rodal, M.J.N.; Encarnação, C.R.F.; Pimentel, R.M.M.	2009	Revista de Geografia 26(2): 161–184
14	Caatinga in Agreste (Ecotone to the Atlantic Forest)	PE-Agr1-Caruaru	PE	Woody and non woody plants	Alcoforado-Filho, F.G.; Sampaio, E.V.S.B.; Rodal, M.J.N.	2003	Acta Botanica Brasílica 17(2): 287–303
15	Caatinga in Agreste (Ecotone to the Atlantic Forest)	PE-Agr4-Caruaru	PE	Only non woody plants	Reis, A.M.S.; Araújo, E.L.; Ferraz, E.M.N.; Moura, A.N. (includes Araújo et al. 2005)	2006	Revista Brasileira de Botânica 29(3): 497–508
16	Caatinga in Campo Maior (Ecotone to the Cerrado)	PI-CMaior1-CMaior	PI	Only woody plants	Barros, J.S.; Castro, A.A.J.F.	2006	Interações 8(13): 119–130
17	Caatinga in Campo Maior (Ecotone to the Cerrado)	PI-CMaior2-CMaior	PI	Only woody plants	Farias, R.R.S.; Castro, A.A.J.F.	2004	Acta Botanica Brasílica 18(4): 949–963
18			BA	Only woody plants	Lima, P.C.F.; Lima, J.L.S.	1998	

Table 6 (continued)

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
	Caatinga in the Chapada Diamantina	BA-C.Diam3-Contendas					Acta Botanica Brasiliica 12(3): 441–450
19	Caatinga in the Chapada Diamantina	BA-C.Diam2-Jacobina	BA	Only woody plants	Ramalho, C.I.; Andrade, A.P.; Félix, L.P.; Lacerda, A.V.; Maracajá, P.B.	2009	Revista Caatinga 22(3): 182–190
20	Caatinga in the Chapada Diamantina	BA-C.Diam1-SBonfim	BA	Only woody plants	Ramalho, C.I.; Andrade, A.P.; Félix, L.P.; Lacerda, A.V.; Maracajá, P.B.	2009	Revista Caatinga 22(3): 182–190
21	Crystalline Caatinga	CE-Cry1-Crateús	CE	Woody and non woody plants	Araújo, F.S.; Costa, R.C.; Lima, J.R.; Vasconcelos, S.F.; Girão, L.C.; Sobrinho, M.S.; Bruno, M.M.A.; Souza, S.S.G. et al.	2011	Rodriguésia 62(2): 341–366
22	Crystalline Caatinga	CE-Cry2-Quixadá	CE	Woody and non woody plants	Costa, R.C.; Araújo, F.S.; Lima-Verde, L.W.	2007	Journal of Arid Environments 68: 237–247
23	Crystalline Caatinga	PB-Cry3-S/Carri	PB	Only non woody plants	Andrade, M.V.M.; Andrade, A.P.; Silva, D.S.; Bruno, R.L.A.; Guedes, D.S.	2009	Revista Caatinga 22(1): 229–237
24	Crystalline Caatinga	PB-Cry5-S/Corteiros	PB	Only woody plants	Barbosa, M.R.V.; Lima, I.B.; Lima, J.R.; Cunha, J.P.; Agra, M.F.; Thomas, W.W.	2007	Oecologia Brasiliensis 11(3): 313–322
25	Crystalline Caatinga	PB-Cry9-S/Branca	PB	Only woody plants	Gomes, M.A.F.	1980	Vegetalia 14: 1–27
26	Crystalline Caatinga	PE-Cry11-Bet/Florest	PE	Only non woody plants	Pessoa, L.M.; Rodal, M.J.N.; Silva, A.C.B.L.; Costa, K.C.C.	2004	Revista Nordestina de Biologia 18(1): 27–53
27	Crystalline Caatinga	PE-Cry16-Custodia	PE	Only woody plants	Rodal, M.J.N.; Martins, F.R.; Sampaio, E.V.S.B.	2008	Revista Caatinga 21(3): 192–205
28	Crystalline Caatinga	PE-Cry17-Floresta	PE			2009	

Table 6 (continued)

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
29	Crystalline Caatinga	PE-Cry5-Bet/Floresta	PE	Woody and non woody plants	Santos, M.F.A.V.; Guerra, T.N.F.; Sotero, M.C.; Santos, J.I.N.	2009	Rodriguésia 60(2): 389–402
30	Crystalline Caatinga	PE-Cry7-SerraTalhada	PE	Only woody plants	Costa, K.C.; Lima, A.L.A.; Fernandes, C.H.M.; Silva, M.C.N.A.; Lins e Silva, A.C.B.; Rodal, M.J.N.	1998	Revista Brasileira de Ciências Agrárias 4(1): 48–54
31	Crystalline Caatinga	PE-Cry8-SerraTalhada	PE	Only woody plants	Ferraz, E.M.N.; Rodal, M.J.N.; Sampaio, E.V.S.B.; Pereira, R.C.A.	1998	Revista Brasileira de Botânica 21(1): 7–15
32	Crystalline Caatinga	PE-Cry10-SerraTalhada	PE	Only woody plants	Ferraz, E.M.N.; Rodal, M.J.N.; Sampaio, E.V.S.B.	2003	Phytocoenologia 33(1): 71–92
33	Inselberg	BA-Ins3-Feira	BA	Woody and non woody plants	França, F.; Melo, E.; Santos, A.K.A.; Melo, J.A.N.; Marques, M.; Silva-Filho, M.F.B.; Moraes, L.; Machado, C.	2005	Hoeftia 32(1): 93–101
34	Inselberg	BA-Ins1-Itaim	BA	Woody and non woody plants	França, F.; Melo, E.; Santos, C.C.	1997	Sitientibus 17: 163–176
35	Inselberg	BA-Ins2-Itaim	BA	Woody and non woody plants	França, F.; Melo, E.; Santos, C.C.	1997	Sitientibus 17: 163–184
36	Inselberg	CE-Ins1-Quixadá	CE	Woody and non woody plants	Araújo, F.S.; Oliveira, R.F.; Lima-Verde, L.W.	2008	Rodriguésia 59(4): 659–671
37	Inselberg	PB-Ins2-Esperança	PB	Woody and non woody plants	Porto, P.A.F.; Almeida, A.; Pessoa, W.J.; Tróvão, D.; Félix, L.P.	2008	Revista Caatinga 21(2): 214–222
38	Inselberg	PB-Ins3-Puximanã	PB	Woody and non woody plants	Tölke, E.E.A.; Silva, J.B.; Pereira, A.R.L.; Melo, J.I.M.	2011	Biotemas 24(4): 39–48
39	Inselberg	PE-Ins3-Altinho	PE		Gomes, P.; Alves, M.	2010	

Table 6 (continued)

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
40	Inselberg	PE-Ins1-Bezerros	PE	Woody and non woody plants	Gomes, P.; Alves, M.	2009	Revista Brasileira de Botânica 33(4): 661–676 Edinburgh Journal of Botany 66(2): 329–346
41	Inselberg	PE-Ins2-SJMonte	PE	Woody and non woody plants	Gomes, P.; Alves, M.	2010	Revista Brasileira de Botânica 33(4): 661–676
42	Inselberg	PE-Ins4-Venturosa	PE	Woody and non woody plants	Gomes, P.; Costa, K.C.C.; Rodal, M.J.N.; Alves, M.	2011	Check List 7(2): 173–181
43	Riverine forest	PB-Riv7-Monteiro	PB	Only woody plants	Pegado, C.M.A.; Andrade, L.A.; Félix, L.P.; Pereira, I.M.	2006	Acta Botanica Brasiliica 20(4): 887–898
44	Riverine forest	PB-Riv5-SJCarri	PB	Only woody plants	Lacerda, A.V.; Barbosa, F.M.; Soares, J.J.; Barbosa, M.R.V.	2010	Biota Neotropica 10(4): 275–284
45	Riverine forest	PB-Riv6-SJCarri	PB	Only woody plants	Lacerda, A.V.; Barbosa, F.M.; Soares, J.J.; Barbosa, M.R.V.	2010	Biota Neotropica 10(4): 275–284
46	Riverine forest	PB-Riv4-SJCordeiros	PB	Only woody plants	Lacerda, A.V.; Barbosa, F.M.; Soares, J.J.; Barbosa, M.R.V.	2010	Biota Neotropica 10(4): 275–284
47	Riverine forest	PB-Riv1-Taperoá	PB	Only woody plants	Andrade, L.A.; Fabricante, J.R.; Alves, A.S.	2008	Natureza & Conservação 6(2): 61–67
48	Riverine forest	PB-Riv3-SJCarri	PB	Only woody plants	Lacerda, A.V.; Barbosa, F.M.; Barbosa, M.R.V.	2007	Oecologia Brasiliensis 11(3): 331–340
49	Riverine forest	PE-Riv2-Floresta	PE	Woody and non woody plants	Souza, J.A.N.; Rodal, M.J.N.	2010	Revista Caatinga 23(4): 54–62
50	Riverine forest	PE-Riv3-Petrolina	PE	Only woody plants	Nascimento, C.E.S.; Rodal, M.J.N.; Cavalcanti, A.C.	2003	

Table 6 (continued)

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
51	Sedimentary Caatinga	BA-Sed2-Barra	BA	Woody and non woody plants	Rocha, P.L.B.; Queiroz, L.P.; Pirani, J.R.	2004	Revista Brasileira de Botânica 26(3): 271–287
52	Sedimentary Caatinga	BA-Sed1-Uaiúá	BA	Woody and non woody plants	Guedes, R.R.	1985	Revista Brasileira de Botânica 27(4): 739–755
53	Sedimentary Caatinga	CE-Sed8-Crateús	CE	Only woody plants	Vasconcelos, S.F.; Araújo, F.S.; Lopes, A.V.	2010	Rodriguésia 37(62): 5–8
54	Sedimentary Caatinga	CE-Sed1-Crateús	CE	Woody and non woody plants	Araújo, F.S.; Costa, R.C.; Lima, J.R.; Vasconcelos, S.F.; Girão, L.C.; Sobrinho, M.S.; Bruno, M.M.A.; Souza, S.S.G. et al.	2011	Biodiversity & Conservation 19: 2263–2289
55	Sedimentary Caatinga	CE-Sed2-Crateús	CE	Woody and non woody plants	Araújo, F.S.; Costa, R.C.; Lima, J.R.; Vasconcelos, S.F.; Girão, L.C.; Sobrinho, M.S.; Bruno, M.M.A.; Souza, S.S.G. et al. (includes Lima et al. 2009)	2011	Rodriguésia 62(2): 341–366
56	Sedimentary Caatinga	CE-Sed4-NovoHoriente	CE	Woody and non woody plants	Araújo, F.S.; Sampaio, E.V.S.B.; Figueiredo, M.A.; Rodal, M.J.N.; Fernandes, A.G.	1998	Revista Brasileira de Botânica 21(2): 105–116
57	Sedimentary Caatinga	CE-Sed5-NovoHoriente	CE	Only woody plants	Araújo, F.S.; Sampaio, E.V.S.B.; Rodal, M.J.N.; Figueiredo, M.A.	1998	Revista Brasileira de Biologia 58(1): 85–95
58	Sedimentary Caatinga	CE-Sed6-NovoHoriente	CE	Only woody plants	Araújo, F.S.; Sampaio, E.V.S.B.; Rodal, M.J.N.; Figueiredo, M.A.	1998	Revista Brasileira de Biologia 58(1): 85–95

Table 6 (continued)

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
59	Sedimentary Caatinga	CE-Sed7- NovoHoriente	CE	Only woody plants	Araújo, F.S.; Sampaio, E.V.S.B.; Rodal, M.J.N.; Figueiredo, M.A.	1998	Revista Brasileira de Biologia 58(1): 85–95
60	Sedimentary Caatinga	CE-Sed3-Ubajara	CE	Only woody plants	Araújo, F.S.; Martins, F.R.; Shepherd, G.J.	1999	Revista Brasileira de Biologia 59(4): 663–678
61	Sedimentary Caatinga	PE-Sed1-Buique	PE	Woody and non woody plants	Andrade, K.V.S.A.; Rodal, M.J.N.; Lucena, M.F.A.; Gomes, A.P.S.	2004	Hoefta 31(3): 337–348
62	Sedimentary Caatinga	PE-Sed2-Buique	PE	Woody and non woody plants	Figueiredo, L.S.; Rodal, M.J.N.; Melo, A.L.	2000	Naturalia 25: 205–224
63	Sedimentary Caatinga	PE-Sed3-Buique	PE	Woody and non woody plants	Gomes, A.P.S.; Rodal, M.J.N.; Melo, A.L.	2006	Acta Botanica Brasiliica 20(1): 37–48
64	Sedimentary Caatinga	PE-Sed4-Buique	PE	Only woody plants	Rodal, M.J.N.; Andrade, K.V.A.; Sales, M.F.; Gomes, A.P.S.	1998	Revista Brasileira de Biologia 58(3): 517–526
65	Sedimentary Caatinga	PE-Sed5-Ibimirim	PE	Woody and non woody plants	Rodal, M.J.N.; Nascimento, L.M.; Melo, A.L.	1999	Acta Botanica Brasiliica 13(1): 15–28
66	Sedimentary Caatinga	PI-Sed1	PI	Only woody plants	Emperaire, L.	1987	Bull. Ecol. 18(4): 431–438
67	Sedimentary Caatinga	PI-Sed3-PadreMarcos	PI	Woody and non woody plants	Oliveira, M.E.A.; Sampaio, E.V.S.B.; Castro, A.A.J.F.; Rodal M.J.N.	1997	Naturalia 22: 131–150
68	Sedimentary Caatinga	PI-Sed2-SJPiaui	PI	Woody and non woody plants	Mendes, M.R.A.; Castro, A.A.J.F.	2010	Check List 6(1): 39–44
69	Transition crystalline/ sedimentary	CE-Tran1-Aiuaba	CE	Woody and non woody plants	Lemos, J.R.; Meguro, M.	2010	Revista Brasileira de Biociências 8(1): 34–43
70	Transition crystalline/ sedimentary	PE-Tran1-Floresta	PE	Only woody plants	Araújo, E.L.; Sampaio, E.V.S.B.; Rodal, M.J.N.	1995	

Table 6 (continued)

N°	Environment type	Code of the site	State	Assemblage sampled	Authors	Year	Journal
71	Transition crystalline/ sedimentary	PE-Tran2-Mirandiba	PE	Woody and non woody plants	Pinheiro, K.; Rodal, M.J.N.; Alves, M.	2010	Revista Brasileira de Biologia 55(4): 595–607
72	Transition crystalline/ sedimentary	PE-TranHerb3-Petrolá	PE	Only non woody plants	Silva, K.A.; Araújo, E.L.; Ferraz, E.M.N.	2009	Acta Botanica Brasílica 23(1): 100–110
73	Transition crystalline/ sedimentary	PI-Tran2-SRNNonato	PI	Only woody plants	Lemos, J.R.; Rodal, M.J.N.	2002	Acta Botanica Brasílica 16(1): 23–42
74	Transition crystalline/ sedimentary	PI-Tran1-SRNNonato	PI	Woody and non woody plants	Lemos, J.R.	2004	Rodriguésia 55(85): 55–66

Appendix 2

Table 7 Table with the life-form spectra used in the comparison of the Caatinga and main world biomes (as compiled by Batalha & Martins, 2002)

Site	Life-form class (%)						Reference
	Ph	Ch	He	Cr	Th		
Crystalline Caatinga							
Cratéis, CE, Brazil	28.5	19.0	5.1	1.5	46.0	Araújo et al. (2011)	
Quixadá, CE, Brazil	26.3	15.8	12.8	2.3	42.9	Costa et al. (2007)	
Floresta/Betânia 1, PE, Brazil	28.7	21.8	12.9	1.0	35.6	Costa et al. (2009)	
Floresta/Betânia 2, PE, Brazil	26.1	19.6	15.2	2.2	37.0	Rodal et al. (2005)	
Floresta, PE, Brazil	23.4	16.9	16.9	2.6	40.3	Rodal et al. (2005)	
Sedimentary Caatinga							
Cratéis 1, CE, Brazil	57.4	19.1	3.7	2.9	16.9	Araújo et al. (2011)	
Cratéis 2, CE, Brazil	58.0	23.2	2.4	3.2	13.2	Araújo et al. (2011)	
S. José do Piauí, PI, Brazil	71.3	12.5	8.1	3.7	4.4	Mendes and Castro (2010)	
Inselberg in the Caatinga							
Quixadá, CE, Brazil	26.0	14.3	13.0	2.6	44.2	Araújo et al. (2008)	
Inselberg in the Agreste							
S. Joaquim do Monte, PE, Brazil	49.4	6.5	4.5	11.7	27.9	Gomes and Alves (2010)	
Alinho/Agrestina, PE, Brazil	35.2	5.6	3.2	11.2	44.8	Gomes and Alves (2010)	
Esperança, PB, Brazil	39.7	12.7	4.8	0.8	42.1	Porto et al. (2008)	
Feira de Santana, BA, Brazil	60.4	18.8	8.3	6.3	6.3	França et al. (2005)	
Brazilian Cerrado							
Brasília, Brazil	39.1	13.5	44.9	1.8	0.7	Ratter et al. (1980)	

Table 7 (continued)

Site	Life-form class (%)						Reference
	Ph	Ch	He	Cr	Th		
Ernas National Park, Brazil	31.6	12.8	49.9	2	3.7	Batalha and Martins (2002)	
Lagoa Santa, Brazil	28.8	6.1	55.1	5.4	4.6	Warming (1892)	
Mojiguaçu, Brazil	30.9	12.2	47	2.1	7.8	Mantovani (1983)	
Pirassununga, Brazil	40.1	17.1	36.1	1.1	5.6	Batalha et al. (1997)	
Santa Rita do Passa Quatro, Brazil	45.3	17.2	30	0.8	6.7	Batalha and Mantovani (2001)	
Boreal forest							
Terra Nova National Park, Canada	37	12	32	19	0	Charest et al. (2000)	
Cold steppe							
Akron, Colorado, USA	0	19	58	8	15	Paulsen (1915) in Cain (1950)	
Danube, Southeastern Europe	7	5	55	10	23	Bojko (1934) in Cain (1950)	
Pamir Mountain	1	12	63	10	14	Paulsen (1912) in Cain (1950)	
Yekastmoslaw, Near East	5	3	55	13	24	Paulsen (1912) in Cain (1950)	
Dry temperate forest							
Sinjawi and Duki regions, Pakistan	31.1	10.7	27.7	2.5	27.9	Tareen and Qadir (1993)	
Hot desert							
Bir Ghanam, Lybia	0	27.3	9.1	4.5	59.1	Qadir and Shetvy (1986)	
Canary Islands	19	19	10	4	47	Børgesen (1924) in Cain (1950)	
California, USA	26	7	18	7	42	Raunkiaer (1934)	
Eastern Egypt	6.5	29	22	4.2	38.3	El-Ghani (1998)	
El Golea, central Sahara	9	13	15	7	56	Raunkiaer (1934)	
Gardhaia, north Africa	3	16	20	3	58	Raunkiaer (1934)	
Israel	8	16	16	7	52	Danin and Orshan (1990)	

Table 7 (continued)

Prevailing vegetation type	Life-form class (%)						Reference
	Ph	Ch	He	Cr	Th		
Jazan, Saudi Arabia	10.1	31.5	5.6	4.5	48.3	El-Demerdash et al. (1994)	
Lybia	12	21	20	5	42	Raunkiaer (1934)	
Ooldea, Australia	46	14	4	1	35	Adamson and Osborn (1922) in Cain (1950)	
Oudja, Morocco	0	4	17	6	73	Braun-Blanquet and Maire (1924) in Cain (1950)	
Transcaspian lowlands	11	7	27	14	41	Paulsen (1912) in Cain (1950)	
Zeltin, Lybia	0	14.3	9.5	0	76.2	Qadir and Shetvy (1986)	
Hot steppe							
Tucson, USA	18	11	24	0	47	Paulsen (1915) in Cain (1950)	
Cyrenaica, north Africa	8	14	19	8	50	Raunkiaer (1934)	
Madeira Islands	15	7	24	3	51	Raunkiaer (1934)	
Timbuctu, Africa	24	36	9	6	25	Hagerup (1930) in Cain (1950)	
Turhoona, Lybia	5.3	25.7	13.2	15.8	42.1	Qadir and Shetvy (1986)	
Zwara, Lybia	6.3	46.9	9.4	3.1	34.4	Qadir and Shetvy (1986)	
Mediterranean vegetation							
Crete	9	13	27	12	38	Turrill (1929) in Cain (1950)	
Ikaria, Greece	7	7	23	14	49	Christodoulakis (1996)	
Israel	8	9	23	10	49	Darin and Orshan (1990)	
Mount Killini, Greece	10.2	11	41.9	13.1	23.9	Dimopoulos and Georgiadis (1992)	
Samos, Greece	9	13	32	13	33	Raunkiaer (1934)	
Southern France	7	13	29	8	43		

Table 7 (continued)

Site	Prevailing vegetation type						Reference
	Life-form class (%)						
	Ph	Ch	He	Cr	Th		
Prairie							Braun-Blanquet (1925) in Cain (1950)
Konza, USA	11.1	0.9	33.1	24.9	29.9		Stalter et al. (1991)
Rain forest							
Alto do Palmital, Brazil	80	6	11	3	0		Cain et al. (1956)
Caiobá, Brazil	87	7	3	3	0		Cain et al. (1956)
Mucambo, Brazil	95	1	3	1	0		Cain et al. (1956)
Horto Botânico, Brazil	70	4	16	5	5		Cain et al. (1956)
Queensland, USA	96	2	0	2	0		Cromer and Pryor (1942) in Cain (1950)
Savanna							
Barinas, Venezuela	11	3	18	40	28		Sarmiento and Monasterio (1983)
Calabozo, Venezuela	28	7	31	5	29		Aristeguieta (1966) in Sarmiento and Monasterio (1983)
Ghanzi, Botswana	19.9	16.4	28.2	7.6	27.9		Cole and Brown (1976)
Lake Edward, Zaire	5	38	22	5	29		Lebrun (1947) in Sarmiento and Monasterio (1983)
Lamto, Ivory Coast	9	1	62	9	19		César (1971) in Sarmiento and Monasterio (1983)
Northern Surinam	8	3	38	28	23		Van Donseelaar-Tenbokkel

Table 7 (continued)

Site	Prevailing vegetation type						Reference
	Life-form class (%)						
	Ph	Ch	He	Cr	Th		
Ookemeji, Nigeria	30	0	23	21	25	Huimink (1966) in Sarmiento and Monasterio (1983)	
Southern Kalahari, Africa	13.3	12.2	34.5	7.4	32.7	Hopkins (1962) in Sarmiento and Monasterio (1983)	
Southwestern Madagascar	21	18	26	3	32	Cole and Brown (1976) Morat (1973) in Sarmiento and Monasterio (1983)	
Subtropical forest							
Matheran, India	66	17	2	5	10	Bharucha and Ferreira (1941) in Cain (1950)	
Temperate Forest							
Alabama, USA	17.6	3.1	47.8	17.1	14.4	Ennis (1928) in Cain (1950)	
Alberta, USA	25.8	1.8	48.2	17.1	7.1	Moss (1932) in Cain (1950)	
Cape Breton, USA	14.6	1.8	51.3	25.6	6.7	Ennis (1928) in Cain (1950)	
North Carolina, USA	59.6	0	36	4.5	0	Buell and Wilbur (1948)	
North Carolina, USA	35.9	2.8	44.1	17.2	0	Buell and Wilbur (1948)	
China	31.5	2.3	33.9	19.7	12.7	Gao and Chen (1998)	
Cincinnati, USA	33.6	3.9	34.4	23.4	3.9	Withdraw (1932) in Cain (1950)	
Cincinnati, USA	49.9	4.2	23.5	15.9	6.5	Withdraw (1932) in Cain (1950)	
Connecticut, USA	14.8	2	49.4	20.3	13.5	Ennis (1928) in Cain (1950)	
Scotland	13.5	18	53	13	2	Watt (1931) in Cain (1950)	
Georgia, USA	23	4	55	10	8	Raunkiaer (1934)	
Hondo, Japan	28.9	2	47.4	11.7	10		

Table 7 (continued)

Site	Prevailing vegetation type						Reference
	Life-form class (%)						
	Ph	Ch	He	Cr	Th		
Illinois, USA	16.3	1.3	49.7	18.6	14.1	Horikawa and Sato (1938) in Cain (1950)	
Indiana, USA	14.4	1.9	49	18	16.7	Ewer (1932) in Cain (1950)	
Iowa, USA	15.3	1	48.6	20.9	14.2	McDonald (1937) in Cain (1950)	
Long Island, USA	34.8	10.9	32.6	20.6	1.1	Ennis (1928) in Cain (1950)	
Michigan, USA	22.8	3.9	47	16.1	10.2	Cain (1936) in Cain (1950)	
Minnesota, USA	38.5	4.4	41.8	15.4	0	Gates (1930) in Cain (1950)	
Minnesota, USA	35.2	3.2	45.6	16	0	Buell and Wilbur (1948)	
Mississippi, USA	19.5	3.1	49.4	15.2	12.8	Buell and Wilbur (1948)	
New York, USA	16.5	5.3	33.3	31.9	13	Ennis (1928) in Cain (1950)	
Paris, France	8	6.5	51.5	25	9	Taylor (1918) in Cain (1950)	
North Carolina, USA	30	2.1	45	11.1	11.9	Allorge (1922) in Cain (1950)	
Serbia	28.7	11.3	46.2	9.1	4.7	Stalter et al. (1991)	
Stuttgart, Germany	9	3	54	17	17	Turrill (1929) in Cain (1950)	
Tennessee, USA	19.6	1.7	52.1	15.1	11.5	Raumkier (1934)	
Virginia, USA	18.6	1.4	51.7	11.3	17	Cain (1945) in Cain (1950)	
Tundra						Allard (1944) in Cain (1950)	
Spitzbergen	1	22	60	15	2	Raumkier (1934)	

The Caatinga life-form spectra presented here may differ a little from the data provided by original authors because we reclassified some species to match Raumkier's original categories and excluded exotic species and records not identified to species level

To download this table in text format and see the full reference for each cited work see [Appendix 3](#)

Appendix 3

Appendix 3 is composed by the raw database and matrices upon which we built our analyses, as well as other supporting files, including appendices 1 and 2 in text format. You can download these digital files at: <http://dx.doi.org/10.6084/m9.figshare.1497939>.

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