

Chapter 2

Diversity and Evolution of Flowering Plants of the Caatinga Domain

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Abstract The Caatinga Domain (CD) in northeastern Brazil harbors the largest and most continuous expanse of the seasonally dry tropical forest and woodland biome (SDTFW) in the New World. Phytogeographical data collected over the past 10 years support previous hypotheses that recognized two major biotas in Caatinga SDTFW: the Crystalline Caatinga, mostly associated with medium to highly fertile soils in the wide Sertaneja Depression; and the Sedimentary Caatinga, mostly associated with poor sandy soils derived from patchy sedimentary surfaces. A third floristic set is represented by tall Caatinga forests. The CD is the richest SDTFW area in the New World, with 3150 species in 930 genera and 152 families of flowering plants. About 23% of the species and 31 genera are endemic to the CD. We performed phylogenetic meta-analyses to estimate times of divergence and ancestral areas for SDTFW lineages, which indicated that plant diversity in the Caatinga arose mostly by in situ speciation following Mid to Late Miocene vicariance events with two major SDTFW nuclei: (1) the northwestern Caribbean dry coast of Colombia and Venezuela; and (2) the southwestern South American dry forests of southern Bolivia and northwestern Argentina. Phylogenetic analyses also uncovered unexpected patterns of recent radiations, with evolutionarily new species and incomplete lineage sorting that sharply contrast with the most common phylogenetic patterns found in SDTFW clades. Recent, mostly Pleistocene, ecological speciation better explains the emergence of distinct biotas on sandy and karstic surfaces.

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2.1 Introduction

The wealth of geologically diverse landscapes across the 912,000 km² of the Brazilian Caatinga region provided a spectacular evolutionary theater for the radiation of many unique and species-rich plant lineages unparalleled in any other global drylands. The plants of the Caatinga can be as extraordinarily morphologically distinctive as the cephalium-bearing and globular cactus *Melocactus pachyacanthus*, the ‘bonsai’ legume shrub *Calliandra depauperata*, the huge Brazilian baobab tree *Cavallinesia umbellata*, the modest deciduous legume tree *Tabaroa caatingicola* that was recently identified in its monospecific genus, or the leafless yellow mass-flowering *Tabebuia aurea* whose trunks once sheltered the elegant and critically endangered, probably extinct in the wild, blue Spix’s macaw (*Cyanopsitta spixii*). In sharp contrast to the better-known Amazonia and Atlantic tropical rainforests, plants in the Caatinga evolved unique adaptations to thrive in a harsh environment imposed by irregular rainfall and extended droughts. The vegetation there is dominated by small-leaved, thorny trees with twisted trunks as well as many succulents and therophytic herbs that efficiently respond to the minimal levels of precipitation (300–1000 mm/year) received during even the wettest years. This response is manifested by leaf flushing peaks at the beginning of the short rainy season that are often coordinated with synchronous flowering. Perhaps the most conspicuous feature of the Caatinga vegetation is the deciduousness of most of its trees and shrubs during the dry season. Indeed, the origin of the word ‘Caatinga’ (literally ‘whitish forest’ in the indigenous Tupi language) is rooted in the stark aspect of its seasonally deciduous vegetation. The proportion of species that keep their leaves during the dry season ranges from about 30% to almost 0% in areas where only the iconic juazeiro tree (*Sarcomphalus joazeiro*; Rhamnaceae) stands out as an evergreen.

The number of multifaceted plant studies have been increasing over recent decades, focusing on patterns of species distribution (Prado and Gibbs 1993; Prado 2000; Queiroz 2006, 2009; Cardoso and Queiroz 2011), analyses of similarities among floristic inventories (Oliveira-Filho et al. 2006; Santos et al. 2012; Neves et al. 2015; Moro et al. 2015a, 2016; DRYFLOR 2016), biome modeling (Särkinen et al. 2011), paleo-distribution modeling, palynological records (Werneck et al. 2011), community phylogenetics (Oliveira-Filho et al. 2013), and fossil-calibrated molecular phylogenies (Queiroz and Lavin 2011; Simon et al. 2011; Pennington and Lavin 2015), all designed to tackle questions concerning the origin, diversity, biogeography, and diversification history of the Caatinga dry forests and woodlands. These studies have sought to address various questions: How was the Caatinga flora assembled? Is the floristic composition of the Caatinga the result of an impoverishment of the surrounding biodiverse Atlantic Forest vegetation? Is the Caatinga

biodiversity evenly distributed? Where should the Caatinga vegetation be placed in the context of other neotropical or global dryland biomes? When did its plant lineages radiate? How has the interplay of geography and ecology shaped the evolutionary history of the plant lineages? How has historical climatic instability affected the stability of the Caatinga vegetation?

Since Andrade-Lima's (1981) seminal review on the Caatinga Domain (CD) emphasis has shifted away from primarily floristic-based studies towards incorporating methodological advances in historical biogeography and phylogenetic comparative analyses. Recent studies have collectively provided new insights into understanding diversity patterns and the biogeography and diversification processes of the highly diverse and endemic Caatinga flora (Queiroz and Lavin 2011; Werneck et al. 2011; Oliveira-Filho et al. 2013). The distribution patterns of species diversity and endemism in legumes (the Leguminosae family) coupled with evidence of idiosyncratic flowering and fruiting phenologies and different evolutionary histories in distinct geological terrains, for example, have allowed the first comprehensive historical reconstruction of Caatinga landscapes and their associated biodiversity (Queiroz 2006). It is now apparent that two different biotas covering geomorphologically diverse areas have long been associated with the generic term 'caatinga', but they do not necessarily share a common biogeographical history with the neotropical seasonally dry tropical forest and woodland (SDTFW) biome (Pennington et al. 2006). The biota strongly associated with soils primarily derived from crystalline basement rocks (and covering most of the Caatinga region) showed higher floristic relationships with other South American SDTFW nuclei, whereas another biota with strong ecological ties to disjunct sandy sedimentary surfaces is now recognized as evolutionarily distinct from the typical crystalline-derived Caatinga vegetation.

Ten years after Queiroz's (2006) reconstruction of the origin and distribution of the Caatinga biodiversity, we revisit the biogeography and evolutionary history of the plants inhabiting this highly threatened, yet still poorly known, Brazilian dry vegetation (Leal et al. 2005; Santos et al. 2011; Ribeiro et al. 2016). We first discuss here conceptual issues related to the biogeographical classification of the CD with respect to other global dry biomes. We then briefly describe the associated distinct biomes and main floristic units within the CD and provide an updated checklist of the generic endemism in different plant families. The evolutionary history of the plants of the Caatinga is reconsidered in light of dated molecular phylogenies that provide a better understanding of biome shifts and diversification processes.

2.2 Caatinga Vegetation in the Context of Global Biomes

The word 'Caatinga' has been used to classify the semiarid region of northeastern Brazil and refers to a wide array of phytogeographical categories, including biome (IBGE 2004; MMA 2014), province (Cabrera and Willink 1980), domain (Ab'Saber 1974; Andrade-Lima 1981), ecoregion (Olson et al. 2001), as well as vegetation

types (e.g., *caatinga s.s.*, *caatinga arbórea*, *caatinga arbustiva*). We believe that the lack of standardization in placing the Caatinga dry vegetation in a broader context of biome classification results in miscommunication and in poorly informative delimitation of natural biogeographical units related to the term.

Biomes can be defined as large clusters of globally distributed vegetation units that are structurally and functionally similar and recognizable mostly by the life-forms of the dominant species (Woodward et al. 2004; Moncrieff et al. 2016). Most traditional concepts of biomes include climatic parameters, whereby the underlying notion of climate serves as a proxy for functional plant traits (Schimper 1903; Walter 1973). Implicit in such a definition is the idea that global biomes are similar plant formations occurring in disjunct areas and that share similarities in structure and function due to convergent evolution driven by similar environmental filters—mostly climatic and edaphic conditions—driving niche conservatism of clades at different levels to share a common ecology over evolutionary time. Thus, biomes tell us about the general ecology under which a particular plant formation was assembled across different continents. It is important to emphasize that different areas of the same biome will not necessarily always share a common evolutionary history or show strong similarity in their floristic elements. The Tropical Rain Forest biome, for example, has long been recognized as a global biome despite the fact that it is dominated by quite distinct and phylogenetically unrelated groups on each continent (e.g., mimosoid and papilionoid legumes in the Neotropics, detarioid legumes in Africa, and dipterocarps in Australasia).

That said, we refer to the CD here as an ecologically and evolutionarily heterogeneous region encompassing floristic elements of at least four different biomes: SDTFWs, Savannas, Tropical Rain Forests, and Rupestrian Grasslands (*‘Campos Rupestres’*) (Queiroz 2006, 2009; Moro et al. 2015a; Conceição et al. 2016). The SDTFW is the most predominant biome in the CD and the word ‘Caatinga’ is commonly used to refer to that dry biome in northeastern Brazil. The other biomes are meagerly represented in the CD and are only briefly characterized here.

The frost-prone Chaco vegetation, the Brazilian Caatinga, and the grass-rich, fire-prone Cerrado represent the three main seasonally dry biomes of South America. These phytogeographical regions are often considered a single biogeographical unit under the general term ‘dry diagonal’ (*‘diagonal seca’*) in studies of floristic relationships and in biogeographical reconstructions of both the flora and fauna. The dry vegetation of the Caatinga, Chaco, and Cerrado harbor species that must survive severe droughts, although they belong to distinct biomes and present distinct species compositions, ecologies, and histories (Prado 2000; Pennington et al. 2006). It is now clear that such dry vegetation should never have been confused at any level of biogeographical regionalization, and attempts to unify them in biogeographical analyses are disconnected from ecological and evolutionary understandings of their biotas. The term ‘dry diagonal’ is conceptually equivocal in that it does not bring together ecological or evolutionary dimensions and combines distinct biomes that are merely superficially similar in their vegetation physiognomies.

2.2.1 *Minor Biomes within the Caatinga Domain*

2.2.1.1 Tropical Rain Forests

Wet forests within the CD are usually located in highlands and mountain ranges that experience orographic rainfall, with resulting precipitation in small, humid ‘islands’. Semi-deciduous and evergreen forests thrive in such highlands, surrounded by typical Caatinga SDTFW vegetation. Wet forests within the semiarid region are located in the Chapada Diamantina range in Bahia, and in smaller highlands (‘*serras*’ or ‘*brejos de altitude*’) in the Brazilian states of Pernambuco, Paraíba, and Ceará. These wet forests are floristically similar to coastal forest vegetation when located closer to the Atlantic Forest domain; those located more inland are more similar in their species composition to the crystalline SDTFW vegetation (Rodal et al. 2008). Phytogeographical and floristic studies of such wet forests have largely been limited to forests located closer to the Atlantic Forest domain (Santos et al. 2007; Rodal et al. 2008). However, wet enclaves that are floristically close to the Amazonian domain can also be found, such as the Baturité (Santos et al. 2007) and the Ubajara highlands in the Ibiapaba range of Ceará State (Moro et al. 2015a). Interestingly, those rain forest enclaves do not show any spectacular examples of endemic plant lineages, being chiefly composed by plant species that historically arrived from the Amazonian and Atlantic rain forest domains.

2.2.1.2 Savannas

Fire-prone savanna vegetation is also found scattered throughout the CD, growing especially on sedimentary latosol plateaus in the Chapada Diamantina range, on the Araripe Plateau, in small enclaves in southern Ceará, and in the dry coastal region of northeastern Brazil. Recent fossil-calibrated phylogenetic analyses have revealed that most of the floristic diversity and endemism of the savanna vegetation originated in situ from recent (Late Miocene/Pliocene) recruitment of unrelated ancestral lineages from other biomes (Simon et al. 2009). Although occurring under the same climatic conditions as SDTFW vegetation, savanna areas within the CD are mostly determined by edaphic factors, such as low nutrient content, low pH, high aluminum concentrations, and fire regimes, yet they are distinguished by their phylogenetic community structures (Oliveira-Filho et al. 2013). The CD savannas are dominated by an oligarchy of widespread tree species from the Cerrado domain, such as *Annona coriacea*, *Duguetia furfuracea* (Annonaceae), *Caryocar brasiliense* (Caryocaraceae), *Curatella americana* (Dilleniaceae), *Bowdichia virgilioides*, *Dalbergia miscolobium*, *Enterolobium gummiferum*, *Hymenaea stigonocarpa*, *Leptolobium dasycarpum*, *Pterodon pubescens* (Leguminosae), *Aegiphila lhotzkiana* (Lamiaceae), *Magonia pubescens* (Sapindaceae), and *Qualea grandiflora* (Vochysiaceae).

2.2.1.3 Rupestrian Grasslands

The Rupestrian Grasslands within the CD are restricted to the Chapada Diamantina range. They also occur in other South American mountains such as the southern Espinhaço range in Minas Gerais State, the central Brazilian mountains of the Cerrado Domain, and in the Pantepuis in Guyana Shield. The vegetation there is dominated by a xerophytic herbaceous layer and, like other old, climatically buffered, infertile landscapes (Hopper 2009), Rupestrian Grassland lineages show high phylogenetic niche conservatism and adaptations to enhance nutrient acquisition and conservation in exceptionally impoverished soils. Many species bear underground organs that allow repeated resprouting after fire damage (Giulietti et al. 1997; Conceição et al. 2016). Although showing similar ecologies and physiognomies to savanna vegetation, Rupestrian Grassland lineages tend to be both older and geographically and phylogenetically structured on mountain tops (Souza et al. 2013; Trovó et al. 2013; Hughes et al. 2013). They are remarkably rich in species and endemism. By far, most of the endemic plant species known in the CD come from the Rupestrian Grassland biome, including those of the endemic genera *Adamantina* (Orchidaceae) and *Rupestrea* (Melastomataceae). The quite distinct flora of Rupestrian Grasslands comprises plant families that are only poorly represented in the remaining CD biomes, such as Eriocaulaceae, Velloziaceae, Xyridaceae, and Orchidaceae.

2.3 Caatinga Seasonally Dry Tropical Forest and Woodlands (SDTFW)

The Caatinga dryland vegetation is part of a global biome that has been variously treated as dry forests (e.g., Gentry 1982), tropical dry forests (TDF) (e.g., Miles et al. 2006), or seasonally dry tropical forests (SDTF) (Mooney et al. 1995; Pennington et al. 2000, 2009; Prado 2000; DRYFLOR 2016). Most of these definitions emphasize the existence of a closed canopy tree layer (Dexter et al. 2015), but using such a narrow definition for a dry biome implies underestimation of the extent of dry tropical woody vegetation, its recognition as a functional unit, and the assessment of its global biodiversity (e.g., Global Land Cover 2000 2016; Sánchez-Azofeifa and Portillo-Quintero 2011). Although vegetation structure is extremely variable in the Caatinga region, there are strong floristic links between the different vegetation types, ranging from open cactus scrub (mostly on rock outcrops in the driest areas) to semi-deciduous forests on richer soils (at the other extreme, on moister sites). These local variations seem to be a common pattern in SDTFWs (Mooney et al. 1995). To account more accurately for the broad physiognomic variation of the neotropical dry woody vegetation, and following UNESCO's (1973) classification for global vegetation, we propose the addition of the descriptive term 'woodland' in the biome name.

A wider definition for the neotropical SDTFW vegetation that could be ecologically meaningful globally has been put forward by Schrire et al. (2005) in the circumscription of the global Succulent biome—which corresponds to zonoecotones II/III and zonobiome III in the Heinrich Walter classification scheme (Walter 1979). The Succulent biome comprises non-fire-adapted, tree-dominated, succulent-rich, grass-poor, dry tropical forests, woodlands, thickets, and bushlands, and includes species prone to bimodal or erratic rainfall patterns. It occurs in frost-free regions where rainfall is less than 1800 mm/year, with a period of at least 5–6 months receiving less than 100 mm (Gentry 1995; Murphy and Lugo 1986; Pennington et al. 2009). The concept of the SDTFW biome was recently broadened to the point that it coincides with the Succulent biome (Pennington et al. 2009).

Taking this wide SDTFW concept, we produced a new global map of this biome (Fig. 2.1) by modifying the ecoregion delimitations of Olson et al. (2001) to include in the SDTFW biome areas of Tropical Dry Broadleaf Forest biome, and some areas of Tropical Desert and Xeric Shrubland biome that fit the criteria presented above. This resulted in a total area of New World SDTFW of about 2,700,000 km², distributed in Mesoamerica (800,898 km²), the Caribbean (88,472 km²), and South America (1,811,741 km²). The Mesoamerican SDTFW range from the Taumalipan mezquital and Sinaloan dry forests in northern Mexico and southward to South America across the Pacific coast of Mexico and Central America, with a disjunct patch in the Yucatán peninsula. In South America, the SDTFW comprises an arc of separate patches along the edges of rain forests and savannas that occupy most of the continent, from its northwestern coast and the Apure-Villavicencio valleys in Colombia and Venezuela, Andean dry valleys, Pacific Ecuadorian dry forests, Tumbes-Piura dry forests in Ecuador and Peru, Bolivian montane and Chiquitano dry forests, Humid Chaco and Misiones dry forests in northern Argentina and Paraguay, and the Caatinga and Atlantic dry forests of eastern Brazil.

The SDTFW biome is characterized by highly endemic floras, strong niche conservatism, and high beta-diversity among different SDTFW nuclei (Lavin 2006; Pennington et al. 2006, 2009, 2010; Govindarajulu et al. 2011; Linares-Palomino et al. 2011; DRYFLOR 2016). These patterns seem to occur not only among the major neotropical SDTFW nuclei but also within the CD, resulting in highly heterogeneous vegetation types strongly influenced by local environmental conditions. The CD includes an area of SDTFW of around 849,516 km², thereby being the largest and most continuous expanse of SDTFW in the New World, corresponding to approximately 31% of the New World and 45% of the South American SDTFWs. Two major SDTFW floristic subgroups are central to understanding the biodiversity and phytogeography patterns of the CD: the vegetation growing on crystalline rock terrains (hereafter Crystalline Caatinga) and that growing on the sandy terrains of sedimentary basins (hereafter Sedimentary Caatinga). Other minor sites of SDTFW can be found on richer (mostly karstic) soils and on exposed areas with rocky surfaces.

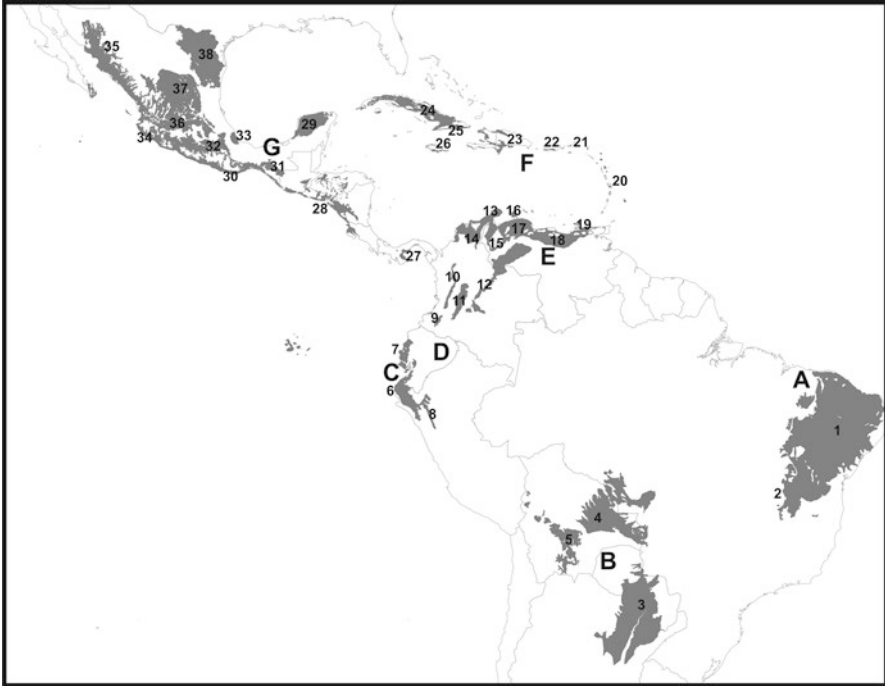


Fig. 2.1 Distribution of the Seasonally Dry Tropical Forest and Woodland (SDTFW) biome in the Neotropics (modified from Olson et al. 2001), with major groups indicated by capital letters and ecoregions of the Tropical and Subtropical Dry Broadleaf Forests and Deserts and Xeric Shrublands biomes (sensu Olson et al. 2001) indicated by numbers: (A) Caatinga: 1—Caatinga; 2—Atlantic Dry Forest; (B) southwestern South America: 3—Humid Chaco; 4—Chiquitano dry forests; 5—Bolivian montane dry forests; (C) Pacific South America: 6—Tumbes-Piura dry forests; 7—Ecuadorian dry forests; (D) Inter-Andean dry valleys: 8—Marañón dry forests; 9—Patía Valley dry forests; 10—Cauca Valley dry forests; 11—Magdalena Valley dry forests; 12—Apure-Villavicencio dry forests; (E) northwestern South America: 13—Guajira-Barranquilla xeric scrub; 14—Sinú Valley dry forests; 15—Maracaibo dry forests; 16—Paraguana xeric scrub; 17—Lara-Falcón dry forests; 18—La Costa xeric shrublands; 19—Araya and Paria xeric scrub; (F) Caribbean: 20—Lesser Antillean dry forests; 21—Caribbean shrublands; 22—Puerto Rican dry forests; 23—Hispaniolan dry forests; 24—Cuban dry forests; 25—Cuban cactus scrub; 26—Jamaican dry forests; and (G) Mesoamerica: 27—Panamanian dry forests; 28—Central American dry forests; 29—Yucatán dry forests; 30—Southern Pacific dry forests; 31—Chiapas Depression dry forests; 32—Balsas dry forests and Tehuacán Valley matorral; 33—Veracruz dry forests; 34—Jalisco dry forests; 35—Sinaloa dry forests; 36—Central Mexican matorral and Bajío dry forests; 37—Meseta Central matorral; 38—Tamaulipan mezquital

2.3.1 Crystalline Caatinga

Crystalline Caatinga is the most typical SDTFW vegetation type of the CD (Figs. 2.2, and 2.3a–b). It comprises deciduous and spiny woodlands or small forests mostly growing on exposed crystalline rock terrains of the Sertaneja Depression,

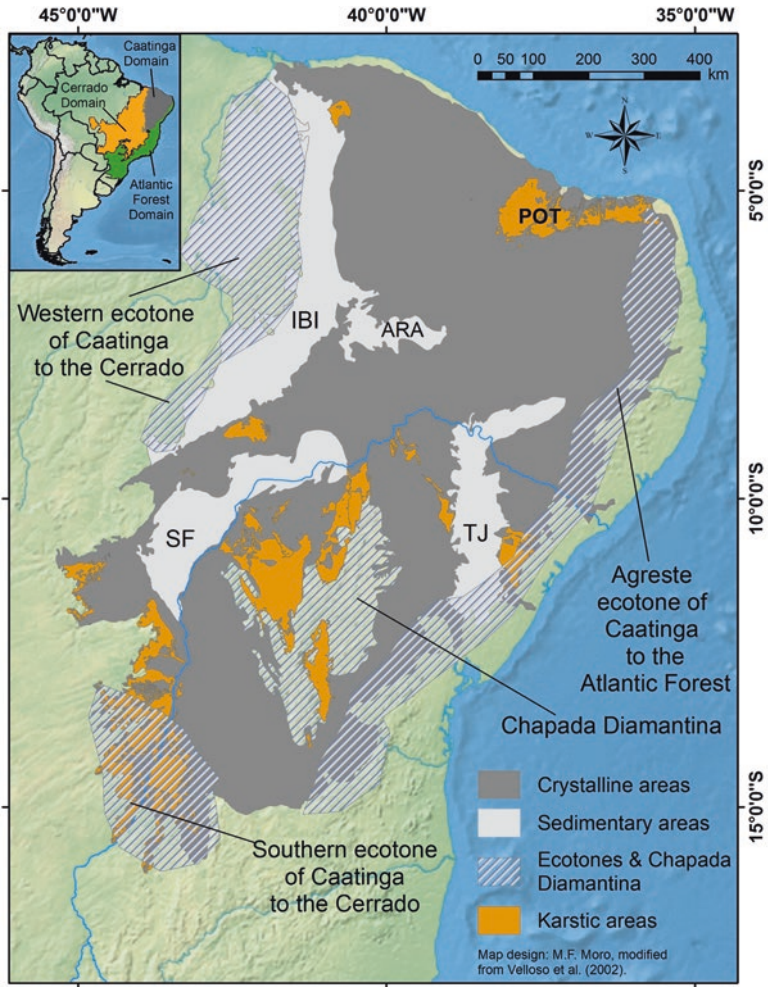


Fig. 2.2 Geographical overview of the Caatinga Domain, showing the main biogeographical units. The most typical Seasonally Dry Tropical Forest and Woodland (SDTFW) vegetation occurs in the crystalline terrains of the Sertaneja Depression, which has typically shallow and stony soils. Sedimentary terrains normally have deep and sandy soils that harbor the SDTFW Sedimentary Caatinga subtype. Expanses of Savanna (especially in sedimentary plateaus) and Tropical Rain Forest biomes (especially associated with highlands) also occur scattered within the Caatinga Domain (Map modified from Velloso et al. 2002). *ARA* Araripe sedimentary basin, *IBI* Ibiapaba highlands, *SF* São Francisco dunes, *TJ* Tucano-Jatobá sedimentary basin, *POT* Potiguar sedimentary basin



Fig. 2.3 Physiognomic diversity of the Seasonally Dry Tropical Forest and Woodland (SDTFW) vegetation in the Caatinga Domain. (a–b) Crystalline Caatinga woodlands during the rainy season in Ibotirama, Bahia state (a) and during the dry season, with the Baturité highlands behind, in Pentecoste, Ceará state (b); (c–d) semi-deciduous Caatinga forests during rainy season at Ruy Barbosa, Bahia state (c) and on karstic terrains of Januária, Minas Gerais state (d); (e–f) sedimentary caatinga in the Serra da Capivara National Park, growing on the lowlands and at the top of a sandstone plateau, Piauí state (e) and on the São Francisco sand dunes, Bahia state (f); (g–h) rupicolous habitats on granitic–gnaiss inselbergs at Feira de Santana, Bahia state (g) and on karstic terrains, Morro do Chapéu, Bahia state (h). Photos courtesy of (a, d) L.P. Queiroz; (b, e) M.F. Moro; (c, f, h) D. Cardoso; (g) F. França

which is largely composed of gently undulated lowlands underlain by granite and gneiss. The soils are shallow and very stony, and when the rainy season ends, edaphic water does not last very long. Woody plants are composed mostly of highly branched, deciduous small trees and shrubs, many of which are spiny, and herbs are mostly therophytes.

The flora of the Crystalline Caatinga is linked with those of other neotropical SDTFW nuclei (Queiroz 2006), as is deduced by the presence of ubiquitous elements that are distributed among different SDTFW nuclei, such as the legumes *Amburana cearensis* and *Mimosa tenuiflora*. These species seem to be confined to areas of intermediate- to high-fertility soils (Oliveira-Filho and Ratter 1995), found in large areas of the Sertaneja Depression. Dominant groups of the woody flora follow the same species-rich families seen overall in Caatinga SDTFW (see Sect. 2.3.5).

Non-woody plants, predominantly annual herbaceous therophytes, correspond to a large proportion of the species richness in Crystalline Caatinga (Queiroz et al. 2015a; Moro et al. 2016). They are mostly neglected in accounts of neotropical SDTFW, but the predominantly herbaceous families Poaceae, Asteraceae, Convolvulaceae, Malvaceae, and Rubiaceae are particularly important components of the ground layer of crystalline communities. Grasses are usually considered a minor component of SDTFW (Pennington et al. 2009), although they can be relatively species rich, especially in open formations, such as the Seridó region (Rio Grande do Norte and Paraíba), where grass species can represent twice the number of species of the woody flora (Ferreira et al. 2009).

Gallery forests can be found along riverbeds. While soils are usually shallow and stony in crystalline landscapes, sediments will accumulate along major riverbeds (usually with underground water reserves). Most rivers in the CD region are seasonal, but ground water accumulated in the soil is potentially accessible to trees with deep enough roots. While the vast majority of SDTFW woody plants are deciduous, many riverine forest plants are evergreen. They usually have thick, sclerophyllous or waxy leaves to reduce water losses but retain them throughout the year. The carnauba palm (*Copernicia prunifera*) is a conspicuous element along many rivers in the CD, and several of the tree species typical of CD riverine forests are widespread in riverbeds of semiarid areas across South America, such as *Licania rigida* (Chrysobalanaceae) and the legumes *Albizia inundata*, *Geoffroea spinosa*, and *Zygia latifolia* (Prado 2003; Queiroz 2006).

2.3.2 Sedimentary Caatinga

In addition to the crystalline terrains, the Brazilian semiarid CD encompasses extensive sandstone, siltstone, and limestone sedimentary basins, mostly with sandy, oligotrophic soils, supporting a vegetation type locally known as ‘carrasco’ (Araújo and Martins 1999), later denominated Arenicolous Caatinga (‘*caatinga de areia*’) or Sedimentary Caatinga (Moro et al. 2016). The Sedimentary Caatinga (Fig. 2.3e–f)

is recognized as a distinct floristic unit from the Crystalline Caatinga on the basis of historical biogeography, species assemblages, phylogenetic structures, and ecologies (Queiroz 2006; Cardoso and Queiroz 2007; Costa et al. 2015; Moro et al. 2015b, 2016). Phenological data available for caatinga woodland communities on sedimentary continental dunes have revealed that their vegetative and reproductive cycles are not strongly influenced by rainfall distribution, as budding and leaf drop, floral anthesis, and fruit production and dispersion are not synchronized among the different species, and at least 50% of the individuals maintain their leaves throughout the year (Rocha et al. 2004). This sharply contrasts with the marked leaf fall and strongly synchronous phenological patterns observed in the neotropical SDTFW, including Crystalline Caatinga (Guevara-de-Lampe et al. 1992; Bullock 1995; Machado et al. 1997). Soil differences (deep, poor sandy soils in sedimentary terrains versus shallow stony soils in crystalline terrains) may also play a key role in the ecological and floristic differences observed between Crystalline and Sedimentary Caatinga.

Plant assemblages and life-form spectra also show consistent differences between those ecosystems (Queiroz 2006; Cardoso and Queiroz 2007; Araújo et al. 2011; Costa et al. 2015; Moro et al. 2015b, 2016). In contrast to crystalline and inselberg communities, plant families showing high species richness in the ground layer (such as Asteraceae, Malvaceae, Poaceae, and Cyperaceae) are poorly represented in the Sedimentary Caatinga, while there is relatively high diversity and endemism of the Leguminosae and Rubiaceae (Rocha et al. 2004; Queiroz 2006; Pinheiro et al. 2010). Additionally, Cactaceae figures among the top five richest families in sedimentary communities (Rocha et al. 2004; Gomes et al. 2006; Mendes and Castro 2010). Myrtaceae and Erythroxylaceae are usually considered relatively rare or species-poor families in neotropical SDTFW (Gentry 1995) but show pronounced diversity in the Sedimentary Caatinga (Lemos 2004; Gomes et al. 2006; Costa et al. 2015), probably because they thrive in low-fertility soils, as exemplified by their high richness in coastal sand Restinga forests of the Atlantic rain forest domain.

The flora of the Sedimentary Caatinga is distinct from other CD floras, but also ecologically and physiognomically heterogeneous throughout its island-like distribution on patches of residual landscapes and continental sand dunes (Fig. 2.2). Some species occur disjunctly in those different sedimentary settings, such as *Harpochilus neesianus* (Acanthaceae), *Cratylia mollis*, *Dahlstedtia araripensis*, *Luetzelburgia bahiensis*, and *Trischidium molle* (Leguminosae), but most species show restricted ranges, and each sedimentary community has its own set of endemic species. The São Francisco River sand dunes are noteworthy, for example, for their high number of endemic species, several of which were described only in the last 15 years, such as *Croton arenosus* (Euphorbiaceae), *Aeschynomene sabulicola*, *Copaifera coriacea*, *Dioclea marginata*, *Mimosa xiquexiquensis*, *Pterocarpus monophyllus* (Leguminosae), *Glischrothamnus ulei* (Molluginaceae), *Diacrodon compressus*, and *Staëlia catechosperma* (Rubiaceae).

2.3.3 Tall Deciduous and Semi-Deciduous Caatinga Forests

In the southernmost part of the CD (Minas Gerais and southern Bahia) and bordering the eastern slopes of the Chapada Diamantina mountain range, we can find SDTFW vegetation with larger trees and forest physiognomies (Fig. 2.3c–d), usually called Arboreal Caatinga (*'caatinga arbórea'* or *'mata seca'*). Richer soils and greater water supplies probably allow these forests to develop. Typical tree species of these forests include *Aralia warmingiana* (Araliaceae), *Brasiliopuntia brasiliensis* (Cactaceae), *Crataeva tapia* (Capparaceae), *Cnidoscolus oligandrus*, *Jatropha mollissima* (Euphorbiaceae), *Blanchetiodendron blanchetii*, *Goniorrhachis marginata*, *Peltophorum dubium*, *Samanea inopinata* (Leguminosae), *Cavanillesia umbellata* (Malvaceae), *Astrocasia jacobinensis* (Phyllanthaceae), and *Alseis floribunda* (Rubiaceae). Santos et al. (2012) had argued that the flora of these tall dry forests represents a distinct subgroup within the Caatinga flora. Nevertheless, the recent biogeographical analysis of Neves et al. (2015), which comprehensively sampled 282 seasonally dry sites across South American SDTFW, showed that while Caatinga forests constitute a floristically distinct subgroup within the CD, from a broader perspective they represent part of a continental species turnover gradient starting from the northernmost part of the CD to the flora of dry forest sites inside the central Brazilian Cerrado Domain.

When Caatinga forests grow on soils derived from karstic deposits of the Bambuí group, they can produce remarkable landscapes where succulents and large trees grow between razor-sharp limestone outcrops (Fig. 2.3d). Such karstic communities within the Brazilian semiarid environment are not restricted to the southern limits of the CD, but can also be found throughout the Chapada Diamantina (see Fig. 2.2), in the Chapada do Araripe (between Ceará and Pernambuco states), in the Potiguar basin (between Rio Grande do Norte and Ceará states), as well as in other smaller areas (Sallun Filho and Karmann 2012; Lima and Nolasco 2015; Maia and Bezerra 2015; Morales and Assine 2015). Interesting examples of plant endemism in such karstic forests are *Luetzelburgia andrade-limae* (Leguminosae) and the recently described *Allamanda calcicola* (Apocynaceae), *Ficus bonijesulapensis* (Moraceae), and the bombacoid trees *Ceiba rubriflora* and *Pseudobombax calcicola* (Malvaceae). Additional biogeographical analyses of the floras of karstic terrains are still needed. Most scientific efforts have been concentrated in the arboreal caatinga in karstic Minas Gerais, while karstic sites in the Chapada Diamantina and the Potiguar basin have been at most only sparsely sampled (Santos et al. 2012).

2.3.4 *Special Environments within the Caatinga SDTFW Biome*

2.3.4.1 Rocky Outcrops

Rocky environments in which dry vegetation flourishes on bare rocks or in very shallow soils (litholic neosols) are as geologically distinct as sandstone outcrops in sedimentary basins or crystalline granitic inselbergs, and provide abundant surfaces for rupicolous plants in the CD (Fig. 2.3g–h). Rocky sites with flat features are locally called ‘*lajedos*’, regardless of their crystalline or sedimentary origins.

The floristic composition of inselbergs is affected by the surrounding vegetation, although they host physiognomically unique floras with adaptations to survive in harsh environments with strong water deficits and high incident solar radiation. Characteristically adapted bromeliads and cacti (e.g., *Encholirium spectabile*, *Pilosocereus gounellei*, *Melocactus* spp.) are better represented on inselbergs than in Crystalline Caatinga woodlands; the bromeliad *Encholirium spectabile* is ubiquitous on inselbergs, where it usually forms large and dense populations. Inselberg communities also show high monocot diversity, such as Poaceae and Cyperaceae, two families likewise diverse on rocky outcrops globally (Porembski 2007).

2.3.4.2 Aquatic Plant Communities

The CD has few permanent but many temporary aquatic ecosystems. Except for the extensive São Francisco and Parnaíba rivers, most rivers, lakes, and ponds are temporary. Floristic studies of aquatic plant communities in the CD have shown considerable numbers of species. In fact, aquatic plants represent a higher proportion of the total flora in the CD than in the Amazonia or Atlantic Forest domains (BFG – The Brazil Flora Group 2015). Caatinga aquatic communities comprise about 227 plant species in 136 genera and 54 families. As expected, the essentially aquatic Pontederiaceae (three genera/15 species), *Nymphaea* (eight species), Hydrocharitaceae (four/eight), and Cabombaceae (one/four) are among the most conspicuous lineages, yet Cyperaceae (nine/54) and Poaceae (nine/20) are the most diverse.

The alternation of the dry and wet seasons has selected for plant communities that can survive several months without water. An erratic water supply appears to be an important filter promoting isolation and speciation of aquatic plants and the evolution of specialized adaptive mechanisms in the CD. In the cosmopolitan aquatic family Nymphaeaceae, the two endemic Caatinga species (*Nymphaea caatingae* and *N. vanilidae*) reproduce through proliferant pseudanthia that are formed close to the floral pedunculus and released as vegetative buds, thus allowing rapid vegetative reproduction under erratic environmental conditions (Lima 2015). A striking example of aquatic endemism is the monospecific genus *Anamaria* from temporary ponds in the CD, which could represent an isolated and early-diverging lineage in the tribe Gratioleae (Plantaginaceae; Scatigna 2014).

2.3.5 *Plant Diversity and Endemism in the Caatinga SDTFW*

We present here a summary of the flora of the Caatinga SDTFW based on the catalogue of plants of the CD (Moro et al. 2014) and the Brazilian Flora Checklist (*Flora do Brasil 2020* 2016), produced by adding two filters. The first corresponds to ‘phytogeographic domain’, set as ‘Caatinga’. In order to include only those species occurring in the SDTFW as well as aquatic communities within it, we conducted four independent searches with different options for the second filter, corresponding to ‘vegetation’: ‘aquatic’, ‘caatinga strict sensu’, ‘deciduous forest’, and ‘semi-deciduous forest’. As a result, we surveyed a total of 4662 native species in the CD, including all four major biomes. For the SDTFW (including aquatic communities) we encountered 3150 species in 930 genera and 152 families of flowering plants. These figures confirm the impressively high species richness of the CD in comparison to the remaining nuclei of the neotropical SDTFW (Pennington et al. 2006). These numbers are also very likely conservative, as large parts of the CD are still unexplored or only poorly botanized (Tabarelli and Vicente 2002; Moro et al. 2014).

The most diverse families are Leguminosae (112 genera/474 species), Euphorbiaceae (25/187), Poaceae (58/151), Asteraceae (71/127), Rubiaceae (45/106), Malvaceae (27/109), Cyperaceae (13/101), Convolvulaceae (ten/88), Apocynaceae (23/85), Bromeliaceae (14/78), and Cactaceae (22/73). Together, these families correspond to more than 50% of the total number of species in the Caatinga SDTFW.

Neotropical SDTFW exhibit high levels of species endemism but also include many relatively old, endemic genera (Pennington et al. 2006, 2009). A similar pattern of high endemism is observed in the Caatinga SDTFW. We surveyed here 31 endemic genera in the CD as whole, most of which are restricted to SDTFW vegetation in the Caatinga (Table 2.1). The CD has the highest number of endemic genera amongst neotropical SDTFW. Gentry (1995), for example, cited 12 endemic genera from Mexican SDTFW, which had the highest number of endemic genera in his analysis (the CD was not included). The genera *Harpochilus*, *Keraunea*, *Mcvaughia*, and *Mysanthus* are treated here as endemic to the CD, although they also occur in neighboring, ecologically similar areas in eastern Brazil. *Mcvaughia* has one species endemic to the CD (*M. bahiana*), with another species (*M. sergipana*) recently described from coastal open sandy scrub vegetation in Sergipe (Amorim and Almeida 2015); a similar pattern is also observed in *Harpochilus* with two species in the CD and a third in the coastal sandy restinga of southern Bahia. *Keraunea* was known only in southern borders of the CD (*K. brasiliensis*; Cheek and Simão-Bianchini 2013), but a second species was recently described in rocky outcrops in Espírito Santo (Lombardi 2014). *Mysanthus uleanus* is found in the Chapada Diamantina and on karstic outcrops in the neighboring state of Goiás. The monotypic genus *Oiospermum* (Asteraceae) was not considered here as being endemic to the CD because recent collections were made in disturbed moist coastal forest sites.

Table 2.1 Genera endemic to the Caatinga Domain

Family	Genus	Distribution
Acanthaceae	<i>Harpochillus</i> ^a	Mostly Sedimentary Caatinga
Amaryllidaceae	<i>Cearanthes</i>	Ibiapaba range
Anacardiaceae	<i>Apterokarpos</i>	Mostly Sedimentary Caatinga
Asteraceae	<i>Caatinganthus</i>	Two locally endemic species at Rio Grande do Norte and southern Bahia
	<i>Dissothrix</i>	Ibipaba range (Ceará)
	<i>Piqueriella</i>	Local in Northern Sertaneja Depression in Ceará
	<i>Telmatophila</i>	Araripe Plateau
Bromeliaceae	<i>Neoglaziovia</i>	Widespread in Caatinga
Cactaceae	<i>Espositoopsis</i>	Southern Sertaneja Depression in Bahia
	<i>Facheiroa</i> ^b	Widespread in Caatinga
	<i>Leocereus</i> ^b	Mostly in Southern Sertaneja Depression and Chapada Diamantina in Bahia
	<i>Stephanocereus</i>	Mostly at Chapada Diamantina
Celastraceae	<i>Fraunhoferia</i>	Mostly Sedimentary Caatinga
Cleomaceae	<i>Haptocarpum</i>	Local in Southern Sertaneja Depression, probably near Bom Jesus da Lapa (Bahia)
Convolvulaceae	<i>Keraunea</i> ^c	Southern Sertaneja Depression (Bahia)
Euphorbiaceae	<i>Gradyana</i>	Raso da Catarina
Leguminosae	<i>Mysanthus</i> ^b	Mostly at Chapada Diamantina
	<i>Tabaroa</i>	Locally endemic in Southern Sertaneja Depression at southern border of the Chapada Diamantina (Bahia)
Malpighiaceae	<i>Mcvaughia</i> ^a	Raso da Catarina
Martyniaceae	<i>Holoregmia</i>	Southern Sertaneja Depression
Melastomataceae	<i>Rupestrea</i>	Chapada Diamantina
Molluginaceae	<i>Glischrothamnus</i>	São Francisco dunes
Orchidaceae	<i>Adamantina</i>	Chapada Diamantina
Plantaginaceae	<i>Anamaria</i>	Widespread in temporary ponds
	<i>Dizygostemon</i>	Sertaneja Depression
Poaceae	<i>Neesiochloa</i>	Sertaneja Depression
Pontederiaceae	<i>Hydrothrix</i>	Widespread in temporary ponds
Rhamnaceae	<i>Alvimiantha</i>	Mostly Sedimentary Caatinga
Rubiaceae	<i>Diacrodon</i>	Mostly Sedimentary Caatinga
Scrophulariaceae	<i>Ameroglossum</i>	Northern Sertaneja Depression
Violaceae	<i>Hybanthopsis</i>	Southern Sertaneja Depression

^a 1–2 species in the Caatinga Domain and another in sandy coastal scrubs

^b Also found in dry forests on karstic outcrops in neighbor western Bahia and Goiás state

^c 1 species in the Caatinga Domain and another recently described in rocky outcrops of Espírito Santo state

Most CD endemic genera are narrowly distributed and locally rare, as suggested by the few available herbarium records, which show them to be mostly restricted to one Caatinga ecoregion (Figs. 2.4 and 2.5; Table 2.1). Only three of these genera are widespread in the CD, with *Anamaria* and *Hydrothrix* occurring in temporary ponds; the terrestrial bromeliad *Neoglaziovia* is most commonly found in the understory of Caatinga forests and woodlands. Eleven endemic genera have ecological preferences for the Crystalline Caatinga: three are widespread (*Caatinganthus*, *Dizygostemon*, and *Neesiochloa*); two inhabit the Northern Sertaneja Depression (*Ameroglossum* and *Piqueriella*); and the remaining six genera are found in the Southern Sertaneja Depression (*Epostopsis*, *Haptoctarpum*, *Holoregmia*, *Hybanthopsis*, *Keraunea*, and *Tabaroa*). Ten genera are more typical of the Sedimentary Caatinga: four occur in more than one disjunct sandy community (*Alvimiantha*, *Apterokarpos*, *Diacrodon*, and *Fraunhoferia*); and two genera are restricted to the Ibiabapa mountain range (*Cearanthes* and *Dissothrix*), one to the Araripe plateau (*Telmatophila*), two to the Raso da Catarina (*Gradyana* and *Mcvaughia*), and one to the São Francisco dunes (*Glischrothamnus*).

Our estimate of overall CD species endemism is approximately 23% (702 species), which is close to the previous taxonomic estimate of 30% suggested by Giulietti et al. (2002). Although it is difficult to compare absolute numbers among different SDTFW patches (as few floristic studies take into account the whole flora of an entire nucleus), the Caatinga appears to have comparable rates of endemism if we consider only proportional numbers; for example, 33% of the Peruvian SDTFW flora is endemic (Linares-Palomino 2006). The Leguminosae show the highest number of endemic species (112), which represents 24% of the diversity of the entire family in the CD and 16% of all endemics for Caatinga SDTFW. In addition to composing the emblematical dry landscape of the Caatinga, the Cactaceae are the most remarkable example of high endemism in the CD, with around 50% being endemic.

Endemism at the genus and species levels could reflect different evolutionary processes. Preliminary phylogenetic data presented here (see Sect. 2.4) indicate that several endemic species arose through in situ speciation, mostly in the last 10 million years, with a burst of speciation during the Pleistocene. Data from endemic genera indicate, however, that they could represent old phylogenetically isolated lineages, perhaps relicts of more diverse groups in the past. The divergence of the monotypic Caatinga endemic genus *Tabaroa* (Leguminosae) from its sister Amazonian rain forest endemic genus *Amphiodon*, for example, was estimated at circa 29 million years ago (Mya). This estimate is quite close to the 28 Mya for the divergence of *Mcvaughia* (Malpighiaceae; Willis et al. 2014). Our estimate for the divergence of the Caatinga endemic *Holoregmia* from a mostly southern South America clade of Martyniaceae was, however, more recent, dating from circa 9.4 Mya.

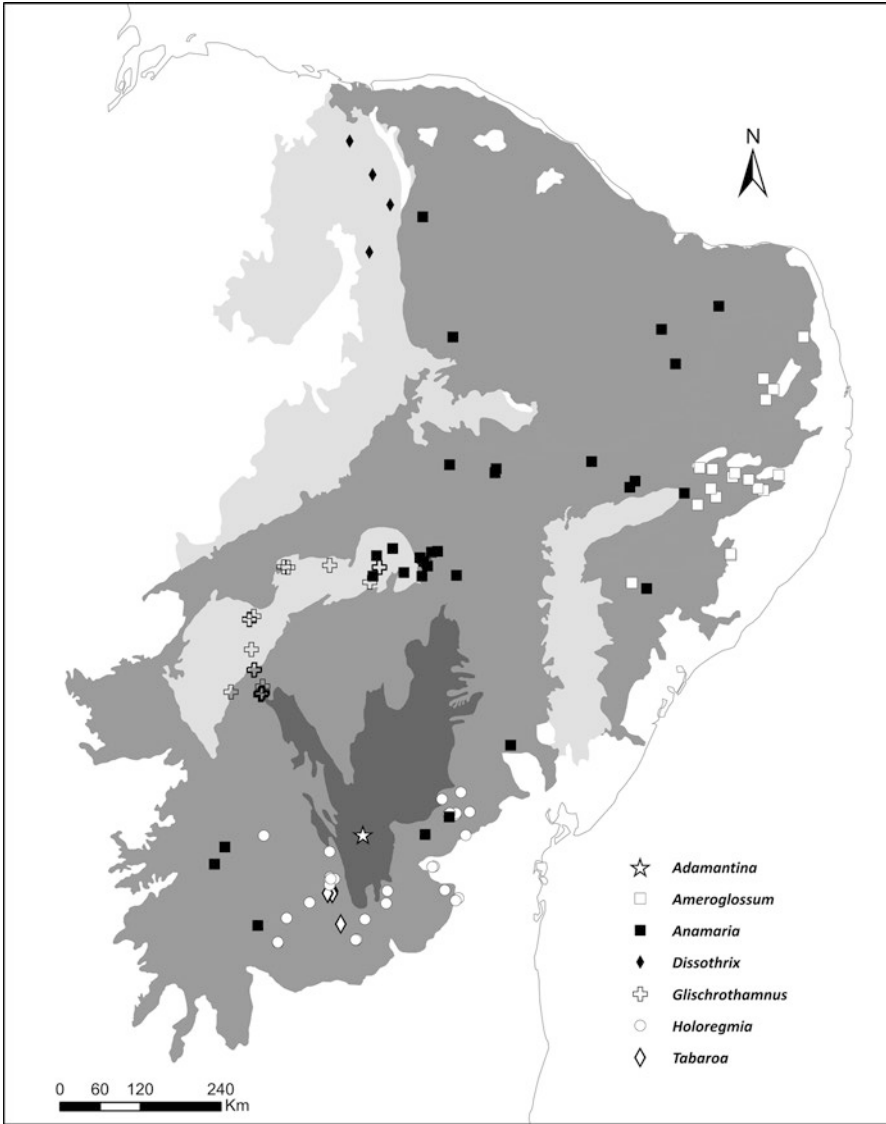


Fig. 2.4 Distribution patterns of some endemic genera of the Caatinga Domain in the crystalline (gray), sedimentary (light gray), and Chapada Diamantina mountain range (dark gray) surfaces (distribution data according to the records available in the INCT Herbário Virtual da Flora e dos Fungos database, <http://inct.splink.org.br/>)

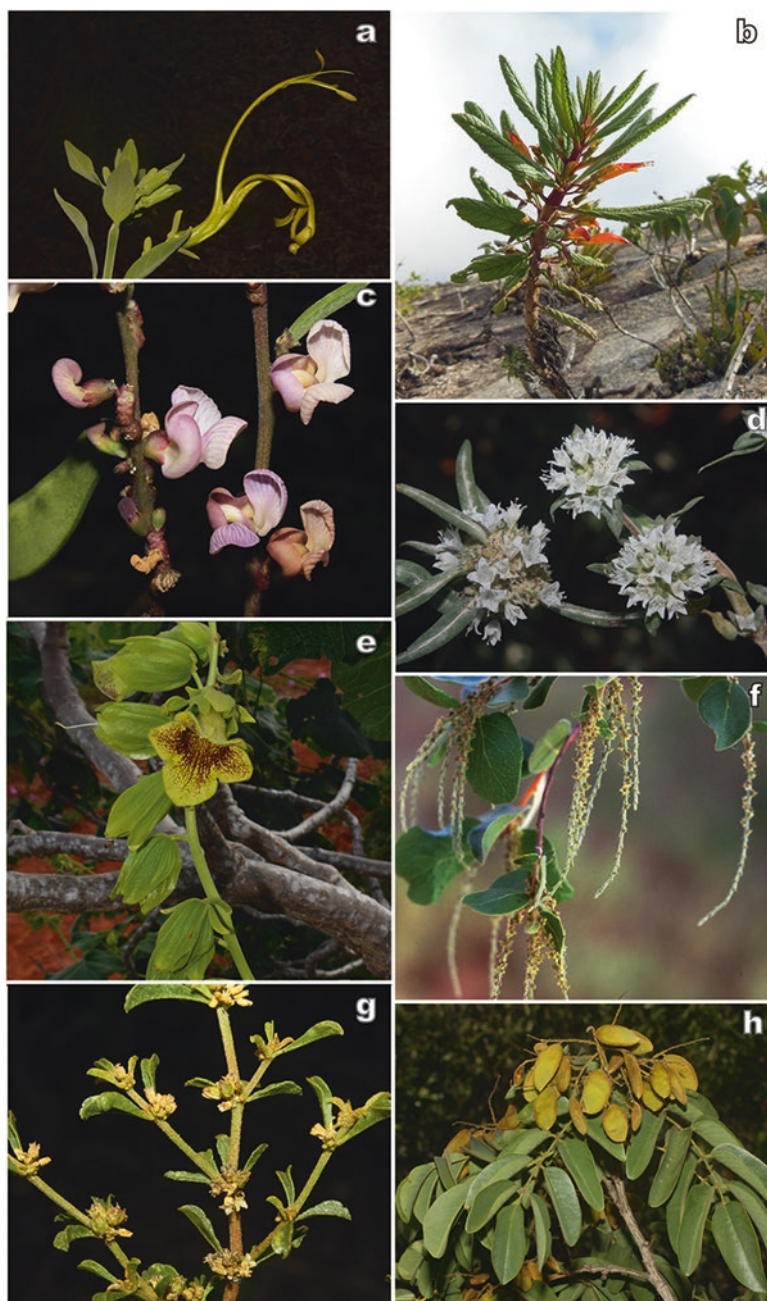


Fig. 2.5 Representatives of some endemic genera of the Caatinga Domain: (a) *Harpochilus neesianus* (Acanthaceae); (b) *Ameroglossum pernambucense* (Scrophulariaceae); (c) *Misanthus uleanus* (Leguminosae); (d) *Diacrodon compressus* (Rubiaceae); (e) *Holoregmia viscida* (Martyniaceae); (f) *Fraunhoferia multiflora* (Celastraceae); (g) *Glischrothamnus ulei* (Molluginaceae); (h) *Tabaroa caatingicola* (Leguminosae). Photos courtesy of (a, e, f) L.P. Queiroz; (b) A.M. Wanderley; (c, d, g, h) D. Cardoso

2.4 Origin and Evolution of SDTFW Plant Lineages in the Caatinga

A major topic in biogeography is determining the balance of migration (*ex situ* origin) and diversification (*in situ* origin) in assembling the current flora in a local community (Emerson and Gillespie 2008). *In situ* speciation tends to be prevalent in old and relatively isolated habitats, while migration should be the dominant process in new habitats, especially those relatively close to similar habitats with a pool of pre-adapted species (Losos and Ricklefs 2010). The Brazilian semiarid Caatinga harbors a large expanse of SDTFW that is isolated from other major SDTFW areas by at least 1300 km by huge expanses of tropical rain forests (the Amazonia to the northwest and the Brazilian Atlantic Forest to the east) and the fire-prone savanna vegetation of the Brazilian–Bolivian Cerrado to the south and southwest, except for small island-like SDTFW patches in both Amazonia and Cerrado.

Previous hypotheses on the origin of the Caatinga flora considered that Caatinga species arose mostly from Atlantic Forest elements that were newly adapted to the harsh semiarid conditions (Rizzini 1979; Andrade-Lima 1981). This hypothesis clearly implied a prevalent biome shift process based on the long-predominant view of the Caatinga as having an impoverished flora lacking considerable numbers of endemic lineages or species. This idea loses its strength, however, in light of mounting evidence that most plant lineages, particularly those of SDTFW, exhibit strong phylogenetic niche conservatism (*i.e.*, the trend of descendent species to inherit the niche of its ancestor during evolutionary history; Donoghue 2008; Crisp et al. 2009), a process that shaped the evolution of the highly diversified flora within the Caatinga. We investigated here the putative roles of migration versus diversification in assembling the present species-rich Caatinga flora, taking advantage of the accumulated dated phylogenies of Caatinga plant lineages. Additionally, we performed divergence time estimation (using BEAST 1.8.2 software; Drummond et al. 2012) and statistical dispersal-vicariance ancestral area reconstruction (as implemented in RASP software; Yu et al. 2015) meta-analyses based on data available at TreeBASE (treebase.org) on groups including Caatinga endemic species (Table 2.2). Results of the analyses are briefly presented here, but are described in length and available as Electronic Supplementary Material to this chapter in the Figshare repository at <https://doi.org/10.6084/m9.figshare.5263120>.

Despite some uncertainties concerning the time of origin of the Caatinga dry vegetation, a wealth of accumulated geological, paleontological, and molecular phylogenetic evidence has given new insights towards unfolding the tempo and diversification processes of the remarkable Caatinga biodiversity. Sparse available paleoclimate information indicates that a mostly semiarid climate has predominated in northeastern Brazil since the end of Tertiary (Ab'Saber 1974; Tritcart 1985). However, fossil-calibrated molecular phylogenies indicate much older ages, and reveal that the divergence of Caatinga endemic lineages could be tracked to the Mid-Miocene (Queiroz and Lavin 2011). This seems to be in line with geomorphological facies, as the Caatinga is mostly covered with shallow soils, sometimes

Table 2.2 Data on the origin of selected groups present in the Caatinga Domain

Group	MRCA of the group			MRCA of a Caatinga clade/species			Sources
	MCA (Mya)	Reconstructed place of origin	MSA (Mya)	MCA (Mya)	Reconstructed process	Possible route	
Acanthaceae							
Thyracanthus clade	5.2	Mesoamerican SDFW					Côrtes et al. (2015)
<i>Scaevola humuliflora</i> clade			4.2	3.3	Vicariance + in situ speciation	Northern	3 (1 endemic)
Anacardiaceae							
<i>Spondias</i>	20.3	Equivocal					Machado (2014)
<i>S. tuberosa</i> clade			13.3	8	Dispersal + in situ speciation	Northern	3 (2 endemic)
Burseraceae							
<i>Commiphora</i>	36.6	African SDFW					Gostel et al. (2016)
<i>C. Leptophloeos</i>			8.5	3.8	Dispersal + allopatric speciation	Trans-Atlantic from Africa	1
Cactaceae							
<i>Pereskia</i>	26.6	Mesoamerican SDFW					Meta-analysis from Edwards et al. 2005
<i>P. bahiensis</i> clade			3.4	1.3	Vicariance + in situ speciation	Southern	2
<i>P. aureiflora</i>			8.1		Dispersal + allopatric speciation	Northern	1

(continued)

Table 2.2 (continued)

Group	MRCA of the group		MRCA of a Caatinga clade/species					Sources
	MCA (Mya)	Reconstructed place of origin	MSA (Mya)	MCA (Mya)	Reconstructed process	Possible route	Number of descendent species	
Tacinga–Brasilopuntia clade	3.2	SW South American SDTFW						Meta-analysis from Majure et al. (2012)
<i>Tacinga</i>			3.2	1.9	Vicariance? + in situ speciation	Southern	8 (7 endemic)	
Leguminosae								
<i>Chloroleucon</i>	5	Mesoamerican SDFTW	5	3.7	Vicariance + in situ speciation	Northern	4 (2 endemic)	Almeida (2014)
<i>Calliandra</i>	13.1	Equivocal						Souza et al. (2013)
<i>Microcallis</i> clade		Mesoamerican SDFTW	6.7	5.1	Vicariance + in situ speciation	Northern	4 (3 endemic)	
<i>Spinosa</i> clade			8.8	7	Equivocal + in situ speciation	Northern	15 (10 in Caatinga, 5 endemic)	
<i>C. parvifolia</i> clade		Equivocal	4.1	2.4	Equivocal	?	2	

<i>Cratylia</i>	3.8	Eastern Brazil	3.8	1.8	Biome shift	Eastern Brazilian RFs	1	Meta-analysis from Queiroz et al. (2015b)
<i>C. mollis</i>								
<i>Dioeclea</i> (Pachylobium clade)	5.6	Amazonian RF						Meta-analysis from Cardoso et al. (2013)
<i>D. grandiflora</i> clade			3.1	1.1	Biome shift	Eastern Brazilian RF	4 (2 endemic)	
<i>Galactia-Camptosema-Collaea</i> clade	5.4	Equivocal						Meta-analysis from Simon et al. (2011)
<i>G. remansoana</i>			2		Dispersal + allopatric speciation	Northern (Caribbean SDFW)	1	
<i>Laetzelburgia</i>	6.3	Eastern Brazil	4.7	3.9	Biome shift +in situ speciation	Eastern Brazilian RF	7 (5 endemic)	Meta-analysis from Cardoso et al. (2013)
Caatinga clade								
<i>Mimosa</i>	23.7	Equivocal						Meta-analysis from Simon et al. (2011)
<i>M. irrigua</i> clade			10.1	4.6	Biome shift	Amazonia	3 (2 endemic)	
<i>M. ophthalmocentra</i> clade			6.8	4.3	Dispersal + in situ speciation	Northern (Mesoamerican SDFW)	5 (1 endemic)	Meta-analysis from Simon et al. (2011)
<i>M. filipes</i> clade			9.6	4.7	Biome shift	Cerrado	4 (3 endemic)	
<i>M. misera</i> clade			12.8	9.3	Vicariance	Northern (Mesoamerican SDFW)	10 (8 endemic)	Meta-analysis from Simon et al. (2011)
<i>M. adenophylla</i> clade			3.6	2.0	Biome shift	Cerrado	5 (2 endemic)	
<i>M. honesta</i> clade			5.8	4.1	Biome shift	Cerrado	3 (2 endemic)	(continued)

		Carvalho-Sobrinho (2014)				
<i>Ceiba</i>	13.4	Mesoamerican SDTFW	10.1	6.8	Northern	7 (1 endemic)
<i>C. jasminodora</i> clade					Equivocal + in situ speciation	
<i>Pseudobombax</i>	20.2	Mesoamerican SDTFW				
<i>P. parvifolium</i> clade			5.2	2.1	Northern	3 (endemic)
<i>Pachira</i> (probably not monophyletic)	14.8	South American RFs			Vicariance + in situ speciation	
<i>P. retusa</i> clade			5.4	2.5	Biome shift + in situ speciation	3 (1 endemic)
<i>Spirotheca</i>	17.1	Probably South American RFs (more samples needed)				
<i>S. elegans</i>			12		Biome shift	1 (endemic)
Martyniaceae	24	Equivocal				
South American clade	17	SW South American SDTFW				
<i>Holoregmia</i>			9.4	(mono specific)	Vicariance	1 (endemic)

We show information of the estimated time (in millions of years ago) on the origin of the most recent common ancestor of the group and the estimated time and processes that gave origin to Caatinga lineages
MCA mean crown age, *MRCAs* most recent common ancestor, *MSA* mean stem age, *MYA* million years ago, *RF* rain forest, *SDTFW* seasonally dry tropical forest and woodland

exposing the bedrock, and by inselbergs—landscapes typical of dry environments that largely arise from pediplanation (Ab'Saber 1974).

Several floristic stocks and migration routes have been proposed to explain the origin of the dry vegetation in northeastern Brazil. New phylogenetic data highlight the role of in situ speciation in generating the current species diversity (Queiroz and Lavin 2011; Hughes et al. 2013), whereas other workers have emphasized the dry Caatinga flora as a collection of immigrant elements, mostly from the adjacent Atlantic Forest (Rizzini 1979; Andrade-Lima 1981). Because plant lineages of the patchily distributed neotropical SDTFW biome tend to be strongly shaped by phylogenetic niche conservatism and dispersal limitations (Pennington et al. 2009) and its harsh climatic conditions pose severe limits to establishment of immigrant plants that are not pre-adapted to the long and erratic dry season, it seems reasonable to envisage that most successful immigrant lineages into a new SDTFW community should come from other disjunct patches of the same biome. Prado (2003) summarized a number of hypotheses regarding putative migration routes of dry vegetation lineages into the Caatinga. Densely sampled and dated phylogenies could provide a way to test floristic hypotheses raised by Prado (2003) by providing minimum age estimates for the caatinga vegetation and indicating the most probable origin and routes.

An African–Caatinga connection has been suggested to explain the origin of mostly African genera such as *Ziziphus* (Rhamnaceae), *Cochlospermum* (Bixaceae), *Commiphora* (Burseraceae), and *Parkinsonia* (Leguminosae) from a time of greater proximity between South America and Africa (Prado 2003), thus placing this route in a timeframe just following the breakup of the Gondwana. Data derived from dated phylogenies, however, favor more recent long-distance trans-Atlantic dispersal rather than older dispersals across a short water gap. In fact, strict disjunctions between American and African elements are relatively rare among dry vegetation plants. Of the 110 genera with range disjunctions between South America and Africa reviewed by Renner (2004), only *Parkinsonia*, *Commiphora*, and *Celtis* (Cannabaceae) could be considered SDTFW specialists. Furthermore, the inferred trans-Atlantic migration between Africa and South America has involved mostly rain forest plants, perhaps because the major sea currents running from Africa to South America reach more to the north with respect to the Caatinga region (Houle 1999).

The genus *Commiphora* (Burseraceae) shows perhaps the most striking example of a recent trans-Atlantic dispersal and establishment from Africa that contributed to the assembly of the Caatinga flora. The genus comprises approximately 190 species mostly from *Acacia-Commiphora* woodlands of tropical east Africa and western Madagascar (Olson and Dinerstein 2002); only *C. leptophloeos* occurs in South America, across the Caatinga and Bolivian SDTFW. This species diverged within a clade of African species between 8.5 and 3.5 Mya (Gostel et al. 2016) and probably reached the Caatinga by trans-Atlantic dispersal. Other alleged Gondwanan disjunctions involving Caatinga plant lineages, such as *Ziziphus* and *Parkinsonia*, have gained new views after recent reappraisals of their taxonomies and phylogenies. The American species of *Ziziphus* were recently re-classified to the genus

Sarcomphalus (Hauenschild et al. 2016) and even though the age of *Sarcomphalus* has not been estimated, the reconstructed stem age for *Ziziphus* s.l. (including *Sarcomphalus*) falls in the Mid-Miocene (Richardson et al. 2004), thus also favoring a transoceanic dispersal route. The caesalpinoid legume genus *Parkinsonia* is represented in the Caatinga only by *P. aculeata*, a widespread species in Mesoamerica, the Caribbean, and South America. It is largely associated with disturbed sites in the Caatinga, suggesting a recent colonization of such areas. Although not extensively reviewed here, *Commiphora leptophloeos* is the only confirmed SDTFW element in the Caatinga with an African origin. However, most molecular phylogenetic evidence suggests only weak floristic connections between dry floras of Africa and Caatinga, and such trans-Atlantic dispersals have been dated relatively recently in the Pliocene (Gostel et al. 2016) to account for a boreotropical route or an ancient Gondwanan vicariance.

Biome shifts into the Caatinga seem to have played a less significant role than previously proposed (Rizzini 1979; Andrade-Lima 1981). Some well-supported examples, however, illustrate rainforest-predominant lineages that have undergone niche evolution into the Caatinga drylands. In the tribe Diocleae (Leguminosae), the *D. grandiflora* clade, with four species (two Caatinga endemics), successfully became established in the Caatinga in the Plio-Pleistocene (3.1–1.1 Mya). A similar timespan was recovered for the origin of the Caatinga-inhabiting *Cratylia mollis* (3.8–1.8 Mya). Both *C. mollis* and the *D. grandiflora* clade are nested in lineages with exclusive distributions in the eastern Brazilian rain forests (Fig. 2.6).

The Bombacoideae (Malvaceae) also provide insightful examples of biome shifts originating Caatinga lineages, as revealed in the recent description of new dry forest species from within the predominantly rain forest genera *Spirotheca* and *Pachira*. The *P. retusa* stem clade may have originated in the Plio-Pleistocene (5.4–2.5 Mya; Carvalho-Sobrinho 2014) and diversified into three species, including the Caatinga-endemic *P. retusa* and the recently described *P. moreirae* (Carvalho-Sobrinho et al. 2014). The origin of the Caatinga-endemic *S. elegans* was estimated at circa 12 Mya (Carvalho-Sobrinho 2014), but could reflect rather sparse sampling in the genus.

The Spinosa clade in the legume genus *Calliandra* has some cases of Caatinga SDTFW species (usually with restricted ranges) that are sister to savanna species (usually with a wide range in the Cerrado and Rupestrian Grasslands areas), such as *C. spinosa* and *C. sessilis* (from SDTFW and savanna species, respectively), *C. macrocalyx*–*C. dysantha*, *C. umbellifera*–*C. parvifolia*, and *C. blanchetii*–*C. longipes* (Souza et al. 2013). This suggests a relatively uncommon pattern of biome shifts from SDTFW towards savanna (Fig. 2.6).

Despite the relative importance of biome shifts in the assembly of the Caatinga flora, we show here that most plant lineages found in the Caatinga drylands come from other major neotropical SDTFW communities, with subsequent in situ diversification in the Caatinga. The dated phylogenies of SDTFW lineages converge towards greater antiquity and possible origins in Mesoamerican (mostly Mexican) dry forests and woodlands. In fact, the region corresponding to modern northern and

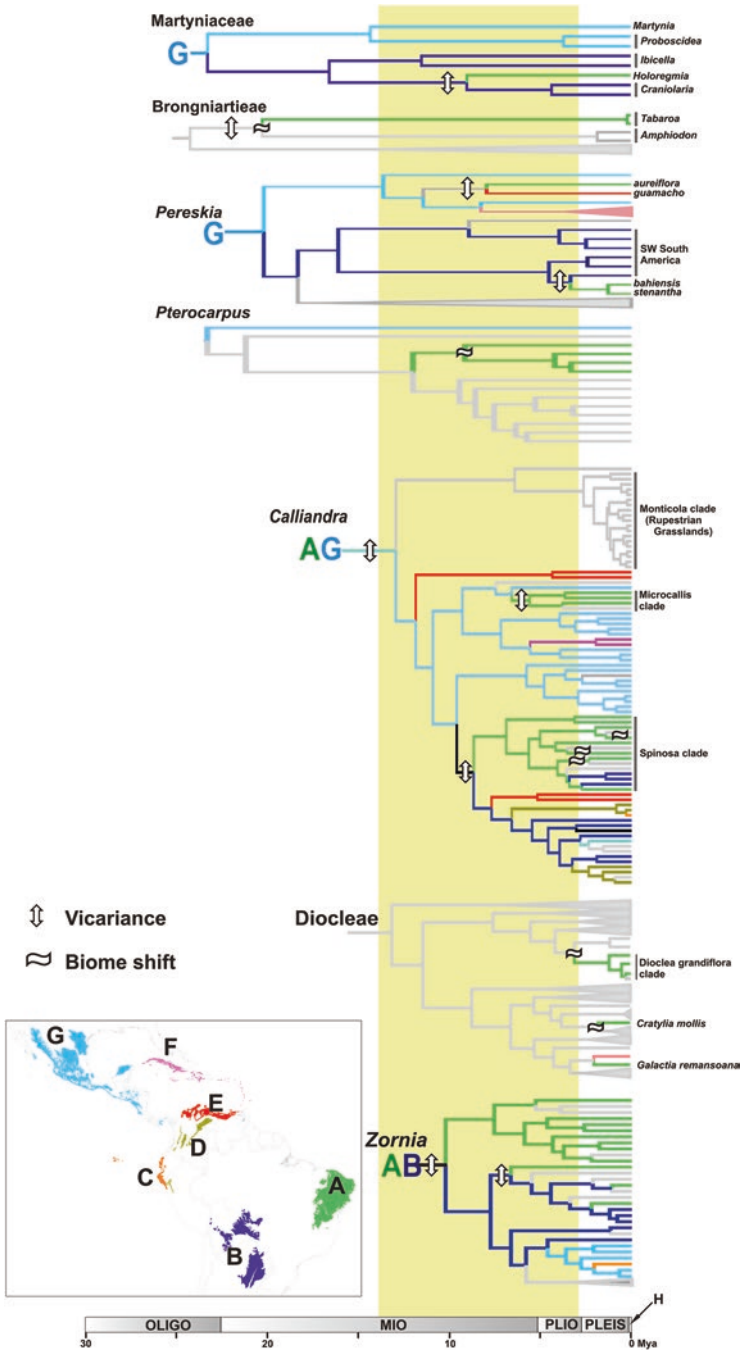


Fig. 2.6 Selected dated phylogenies obtained from meta-analyses of molecular data. Reconstructed neotropical seasonally dry tropical forest and woodland (SDTFW) ancestral areas are represented

central Mexico has been arid since its emergence from the North America epicontinental sea in the Early Tertiary because of its latitudinal position in the descending arm of the Hadley convection cell and rain shadows at lower elevations (Graham 2010). A Mesoamerican origin has been reconstructed in several independent SDTFW plant lineages occurring in the Caatinga such as the *Thyrsacanthus* clade (Acanthaceae; Côrtes et al. 2015), *Pereskia* (Cactaceae), *Chloroleucon* (Almeida 2014), *Coursetia* (Leguminosae; Queiroz and Lavin 2011), *Ceiba* and *Pseudobombax* (Malvaceae, Bombacoideae; Carvalho-Sobrinho 2014; Carvalho-Sobrinho et al. 2016). The origin of these lineages has been dated to between 26 and 5 Mya, and most of them migrated to the Caatinga (stem age of Caatinga-inhabiting lineages) between 17 and 3.4 Mya (Mid-Miocene to Pliocene) and became established in the Caatinga (crown age) between 9 and 1 Mya (Late Miocene to Pleistocene). The Malpighiaceae genus *Amorimia* (Willis et al. 2014) and the legume genus *Zornia* are among the few unequivocal examples of Caatinga lineages that originated in dry areas in South America.

Two major routes have been proposed between the disjunct patches of SDTFW connecting the Caatinga region. The herein designated northern route was proposed by Sarmiento (1975), who observed great floristic similarity between the Caatinga and the Guajira province on the northern coast of Colombia and Venezuela. These two regions are separated by approximately 3000 km and are currently isolated by the mountains of the Guyana shield and the vastness of the Amazonian rain forest. However, it has been demonstrated that as the global climate became cooler and dryer after the Mid-Miocene climatic optimum, it was accompanied by growing aridity (Zachos et al. 2008) and increasing diversification rates of plant lineages with particular adaptive syndromes to strongly seasonal climates, such as the succulents (Arakaki et al. 2011; Christin et al. 2011) and C4 grasses (Edwards et al. 2010). In addition to promoting some potential dry vegetation corridors, lower sea levels in drier times should have exposed significant portions of the wide and shallow northern South American continental shelf, which could have connected otherwise widely isolated areas such as the Caatinga and Guajira regions along a northern coastal route. Interestingly, the present day SDTFW distribution reaches coastal areas in both the Guajira and Caatinga regions.

The second major biogeographic route, herein designated the southern route, would have connected the Caatinga to the dry forests of southern Bolivia and northern Argentina (Müller 1973; Haynes and Holmes-Nielsen 1989). In this case, the recent (Mid-Miocene) appearance of the fire-prone savanna vegetation in central Brazil (Simon et al. 2009) imposed a barrier to the fire-sensitive dry forest lineages



Fig. 2.6 (continued) by color branches following the major areas depicted at the inset map (see Fig. 2.1 for detail on the areas). Branches in gray represent other biomes. Most Caatinga radiations could be dated to Mid-Miocene to Pliocene whether they arose from vicariance of other SDTFW areas (as in mostly SDTFW-inhabiting Martyniaceae) or by biome shift from another biome (as in the mostly rain forest genus *Pterocarpus*). Only major clades and taxa discussed in the text are shown. Complete chronograms, with full taxon names, are available at <https://doi.org/10.6084/m9.figshare.5263120>

and promoted the vicariance of their floras (Côrtes et al. 2015). Putative past connections among currently isolated SDTFW patches thus predated the Pleistocene climatic fluctuations, as suggested by the Pleistocene Arc hypothesis (Prado and Gibbs 1993).

Pleistocene climatic events apparently had only small (if any) impact on the origin and diversification of SDTFW lineages. A close look at the diversification history of individual SDTFW species or lineages in the robinoid legumes and the genus *Indigofera* (Lavin 2006; Pennington et al. 2004; Schrire et al. 2009), for example, shows that their times of divergence mostly predated the Pleistocene. This same pattern of old stem species ages is also common in the Caatinga flora. The endemic Caatinga Microcallis clade radiation of the genus *Calliandra* (Table 2.2), for example, shows divergence between individual species dated at circa 3.8 Mya. In the *Schaueria humiliflora* clade (Acanthaceae), speciation events within the Caatinga occurred between 2.5 and 3.3 Mya (Côrtes et al. 2015). Perhaps the most emblematic example of pre-Pleistocene diversification in the Caatinga is the divergence of the endemic species *Coursetia rostrata* and *C. caatingicola*, dated at circa 9.3 Mya (Queiroz and Lavin 2011).

It is worth emphasizing the idiosyncrasy of some Caatinga habitats that, in contrast, were occupied by recent species radiations. This is the case of Sedimentary Caatinga on sandy soils. Our data from dated molecular phylogenies indicate that they were assembled mostly by independent events of ecological speciation over the last 1.5 million years. Such in situ diversification due to ecological specialization is best exemplified by the very recent origin of the legumes *Calliandra macrocalyx* and *Dioclea marginata*, the cacti *Pereskia bahiensis* and *P. stenantha*, and the Bombacoideae *Pseudobombax simplicifolium*. Similar new ages have been recovered from species endemic to limestone outcrops, such as *Ceiba rubriflora* and *Pseudobombax calcicola* (Carvalho-Sobrinho 2014). These independent synchronous speciation events in particular habitats within the CD suggest that a major environmental driver may have contributed to producing new habitats suitable for lineages pre-adapted to dry vegetation (in situ speciation). Scarce fossil records in the Caatinga suggest that in the Pleistocene/Holocene transition, the climate was much wetter and rain forests covered areas presently harboring SDTFW vegetation on sandy soils, as it is the case of the São Francisco sand dunes (Oliveira et al. 1999, 2014). In dry areas with limestone outcrops, the discovery of now extinct mammal megafauna suggests the existence of a mosaic of wet forests and savannas under humid and sub-humid climates until the last glacial maximum (Alves et al. 2007; Kinoshita et al. 2005, 2008; Oliveira et al. 2010). These empirical data allow us to reject the hypothesis that those sandy surfaces harbor the oldest Caatinga biota (Queiroz 2006). On the other hand, they do help to explain the distinctiveness of the biotas on crystalline, sandy, and rocky surfaces as products of recent ecological speciation in habitats that only recently became available.

2.4.1 *Did Evolutionary Processes Shape the Phylogenetic Patterns of the Caatinga Plant Lineages Equally?*

Dated phylogenies of SDTFW plant lineages with strong ecological predilection for the SDTFW biome often reveal the interplay of phylogenetic niche conservatism and dispersal limitation in the historic assembly of SDTFW plant diversity, where clades are geographically structured and have persisted for evolutionary periods that greatly transcend the Pleistocene, and species with long stem branches are often dated as remotely as the early Miocene (Pennington et al. 2004, 2010; Lavin 2006; De-Nova et al. 2012; Govindarajulu et al. 2011; Queiroz and Lavin 2011; Simon et al. 2011; Särkinen et al. 2012). Old evolutionary divergences could also explain why Caatinga species are monophyletic in phylogenies that are densely sampled with multiple accessions at species level, contrasting sharply with the phylogenetic patterns observed in rainforest woody lineages such as the mimosoid legume *Inga* (Pennington and Lavin 2015). A representative SDTFW example can be seen in the legume genus *Coursetia*, in which the Caatinga endemics *C. rostrata* and *C. caatingicola* are each reciprocally monophyletic, with stem ages as old as 9.3 Mya, and present well-supported geographical structure (Fig. 2.7; Queiroz and Lavin 2011).

Although such phylogenetic patterns of old species diversification, species coalescence, and geographical phylogenetic structure have emerged in a myriad of SDTFW plant clades (e.g., Lavin 2006; De-Nova et al. 2012; Govindarajulu et al. 2011; Pennington et al. 2010; Queiroz and Lavin 2011; Särkinen et al. 2011, 2012; Simon et al. 2011), did the evolutionary processes related to dispersal limitation, niche conservatism, and ecological stability (Pennington and Lavin 2015) shape the phylogenies of Caatinga plant lineages equally?

We present here a counterexample of the recent diversification history of the papilionoid legume genus *Luetzelburgia*, which has 14 species that are mostly ecologically associated with the South American SDTFW (Cardoso et al. 2014). Seven species of *Luetzelburgia* occur in the Caatinga. *Luetzelburgia auriculata* and *L. praecox* are widely encountered throughout savannas and dry woodlands in central and northeastern Brazil. The remaining species are each narrowly distributed in disjunct dry forest patches in the Atlantic Forest domain of southeastern Brazil, in southern and northern Amazonia, and the Bolivian Chiquitano and inter-Andean dry valleys. The *Luetzelburgia* phylogeny is also geographically structured (as might be expected for lineages largely associated with the SDTFW biome). Geographic phylogenetic structure emerges in the *Luetzelburgia* phylogeny, but with weak clade support, as revealed in both multi-locus and single-gene phylogenetic analyses (Cardoso et al. 2013). Furthermore, we have detected widespread species non-monophyly by incomplete lineage sorting in the analysis of a densely sampled ITS dataset involving more than 200 accessions across all known geographical distribution and morphological variation of the genus (Fig. 2.7). The relatively recent diversification of *Luetzelburgia* in the SDTFW biome only within the last 4.6 million years may explain why its phylogeny is less geographically structured than other SDTFW lineages. Using densely sampled dated phylogenies to shine light on the

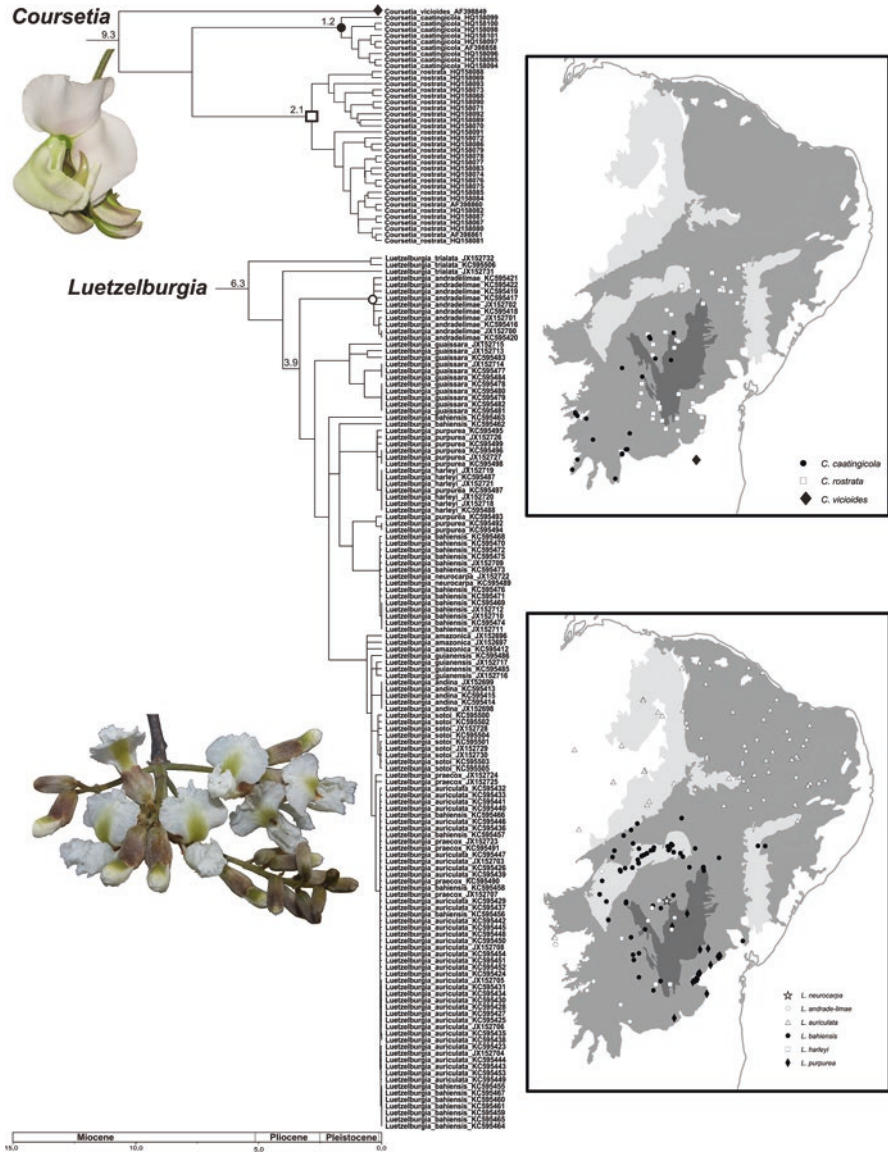


Fig. 2.7 Contrasting diversification patterns in Caatinga seasonally dry tropical forest and woodland (SDTFW) lineages. The legume genus *Coursetia* exemplifies the phylogenetic pattern commonly found in SDTFW lineages with strong geographical structure and coalescence of multiple accessions in relatively anciently diverging monophyletic species. The legume genus *Luetzelburgia* has much more recent diversification and the multiple accessions do not coalesce in monophyletic species. The genera are represented with photos of *Coursetia rostrata* and *Luetzelburgia bahiensis* (courtesy of D. Cardoso)

historical biogeography of the Caatinga will help us to better understand why evolutionary and ecological processes have acted unevenly to generate distinct patterns of plant diversity, distribution, and relationships in dry woodlands.

2.5 Conclusions

The data summarized here indicate that the Caatinga region is the most diverse SDTFW expanse in the New World and harbors a highly endemic flora with the astonishing number of 31 endemic genera. This review provides support for previous findings that identified the Crystalline and Sedimentary Caatinga as the principal plant biotas, but also indicated deciduous and semi-deciduous forests, vegetation on rocky outcrops, and aquatic communities as additional floristic units.

The phylogenetic meta-analyses of different plant lineages performed here shed light on the historical relationships of the Caatinga flora at both the continental and regional scale. On a broad scale, the prevalent vicariance processes suggest that the Caatinga flora should have been connected to two other major areas of the SDTFW biome by the Mid to Late Miocene. One of those areas is the dry vegetation of the Colombian and Venezuelan coast of northern South America, which could have been linked to the Caatinga drylands by the exposed continental shelf in times of greater aridity. The second area includes the dry forests and woodlands of southwestern South America (southern Bolivia and northern Argentina), with the appearance of the fire-prone savanna flora of the Cerrado Domain probably promoting vicariance of the fire-sensitive SDTFW floras of the Caatinga and southwestern South America.

On a regional scale, phylogenies showed that the current Caatinga diversity was assembled mostly by in situ speciation from the Late Miocene to Pliocene. Additionally, the reappraisal of phylogenetic patterns allowed the rejection of previous views hypothesizing that the flora of the Sedimentary Caatinga was assembled through vicariance of the sedimentary surfaces. Instead, they provide support for a new view that the endemic species of the sandy and karstic areas arose by recent (mostly Pleistocene) ecological speciation from lineages inhabiting the Crystalline Caatinga.

The finding of distinct diversification patterns in Caatinga lineages, as exemplified by the legume genera *Coursetia* and *Luetzelburgia*, highlights the need for more data to produce a more thorough picture of the processes that resulted in its floristic assembly. Moreover, despite sound progress towards a better understanding of the diversity of the Caatinga, there are areas still poorly botanized and lacking information as basic as species checklists. Given the high local environmental and floristic diversity of the Caatinga, and its distinct phylogenetic patterns, we urgently need to increase both the floristic and phylogenetic information. Combining floristic and phylogenetic data will allow us to better understand the distribution of phylogenetic diversity across the CD and more effectively contribute to the conservation of its rich and unique biodiversity.

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