José Maria Cardoso da Silva
Inara R. Leal
Marcelo Tabarelli *Editors*

Caatinga

The Largest Tropical Dry Forest Region in South America

Springer

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Foreword

For decades, the fate of the two species of macaws endemic to the Caatinga has drawn my attention to this region, which is a unique semiarid region of Brazil that is surrounded by two of the world's richest tropical rain forests, Amazonia and the Atlantic forest, and the world's most diverse savanna region, the Cerrado. The first of these is the Spix's macaw, a wonderful blue macaw that once lived in the gallery forests dominated by Caraibeira trees (*Tabebuia aurea*) in the valleys of the São Francisco River and its tributaries, but was exploited for the rare bird trade. It has been extinction in the wild since 2000, but fortunately more than 120 still exist in captivity, most of them in the Al Wabra facility in Qatar, a long way from Brazil. The second species is Lear's macaw, a larger and equally spectacular bird that is a true flagship species for the Caatinga. It has been the subject of intense research and conservation efforts by my friends from Biodiversitas, one of the oldest and best biodiversity-focused non-profit organizations in Brazil which dates back to the late 1980s.

The poor state of conservation of these two species two decades ago made me worry about the fate of the biodiversity of the Caatinga overall. To learn more of this region, I traveled there in 2000, accompanied by my two sons, John and Michael, and by the late Ilmar Bastos Santos, one of the founders of Biodiversitas. Indeed, my son John's interest in the Spix's macaw was a major reason for this visit, since he was already a hard-core ornithologist at that time, and is now finishing his doctorate at Oxford. We were extremely fortunate in that we were able to see the last wild Spix's macaw twice in one day, an individual that had been the only wild representative of his species for a decade and that lived in the company of a much small Illiger's macaw. We were also able to see Lear's macaws flying back to their roosting sites late in the afternoon in the Toca Velha Canyon. This trip made clear to us the enormous challenges that the low-income local population of this region faces during the long droughts that hit the Caatinga periodically. My conclusion from our time there was that any sound conservation strategy for the Caatinga should reconcile biodiversity conservation with poverty alleviation, a path that I had already been exploring in Madagascar for decades in order to protect that country's biodiversity.

Since then, I have followed and supported the efforts of my Brazilian colleagues to conserve the biodiversity of the region and helped to highlight the importance of the Caatinga for global conservation, including the addition of the Caatinga as one of the world's wilderness regions in our 2004 book entitled *Wilderness*. What is more, I continue to have a strong interest in those two macaws, hoping to see the captive population of the Spix's macaw reintroduced into the wild at some point in the near future.

Given my deep interest in and concern about the Caatinga's biodiversity and its people, I very much welcome and strongly recommend this volume organized by my friends José Silva, Inara Leal, and Marcelo Tabarelli. They have coordinated a superb collective effort by 61 scientists, most of them working in Brazil, to introduce the Caatinga to an international audience. The chapters cover all themes relevant to the region, including biodiversity, ecosystem services, threats, solutions, and prospects for a more sustainable future. I have even learned that the Caatinga is richer in species than I originally thought. I was amazed to find out, for instance, that 52.9% of the region's fish species are found nowhere else. At the same time, I was sad to learn that at least 63.6% of the Caatinga has now been modified by human activities and that the region's protected area system is still far from adequate to protect the incredible biodiversity that has been revealed by biologists in the last 20 years.

I consider this book an excellent example of how scientists worldwide can mobilize their efforts to propose sound solutions for one of the biggest challenges of the modern times: how to protect the world's natural ecosystems while improving human well-being. I am sure this book will inspire more research and conservation action in the region and perhaps encourage other groups of scientists to produce similar syntheses about their regions. In the end, I am a strong believer that the globally enormously important issue of biodiversity conservation ultimately can only be successful if it fully engages and works with local communities.

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Russell Mittermeier, PhD

Preface

This is a book about the Caatinga, the New World's largest and most diverse seasonally dry tropical forest (SDTF). Scientists outside Brazil know very little about the region, as no synthesis on it exists in English. In news magazines and literary fiction in English, the Caatinga is usually depicted as a hostile semiarid environment in which a few species of thorny trees serve as a background for an impoverished rural population, whose small-scale agriculture and livestock are ruined by the long and recurrent droughts that hit the region. However, the Caatinga that emerges in this book is very different. Occupying an area of 912,529 km^2 in the hinterland of northeastern Brazil, the Caatinga is better described as a rich and complex socio-ecological system that still harbors a unique natural and cultural heritage of global importance.

On a global scale, the Caatinga is part of the SDTFs, a global biome that was not recognized by the scientific community as distinct until a few years ago. In general, most SDTFs still remain poorly studied and protected compared with the adjacent tropical rain forests and savannas. However, they are home to almost 1 billion people worldwide and are among the ecological systems most vulnerable to climate change. The mismanagement of SDTFs can lead to biodiversity loss and a reduction in the flows of the ecosystem services that sustain millions of low-income people. Failure to address this challenge can exacerbate social conflicts and massive migrations. Therefore, SDTFs are socio-ecological hotspots that deserve very close attention from three major international groups: the scientific, conservation, and development communities.

The Caatinga is composed of at least 135 geo-environmental units and nine distinctive ecoregions. This significant environmental variation sustains at least the following species numbers: 3150 plants, 276 ants, 386 fishes, 98 amphibians, 79 reptiles, 548 birds, and 183 mammals. Several of these species are found nowhere else. The proportion of endemic species ranges from 6% in mammals to an astonishing 52.9% in fishes. These numbers—very impressive for a semiarid region—are not definitive though. In all biological groups, new species continue to be discovered, and many places still remain to be sampled by scientists. Biogeographical studies have indicated a complex evolutionary history for the Caatinga's biota in which periods of intense biotic exchanges with the adjacent ecological regions are followed by periods of biotic isolation and species production. As a consequence of these dynamics, endemic species have been accumulated over an extended period. Such species, based on DNA analyses, date from the Early Holocene to the Mid-Miocene. Life in the local ecosystems that compose the Caatinga is controlled by rainfall seasonality. The species that live in the region exhibit a myriad of adaptations to cope with this seasonality, several of which have not been described yet.

The Caatinga is home to 28.6 million people. Since the 1980s, the region has become mostly urban. Currently, around 64% of the population lives in cities, which presents several infrastructure challenges. Despite a significant improvement in the last decades, the Caatinga still has Brazil's lowest human development indicators. The interactions between people and nature in the Caatinga are complex. The rural poor population continues to be dependent on the native vegetation for their livelihoods, leading to slow but continuous changes in the ecosystems. In addition, new infrastructure projects and commercial agriculture designed to sustain the economic activities of the urban centers has resulted in fast and large-scale land-use changes. The result is that at least 63.6% of the Caatinga has been modified by human activities. The most obvious societal response to mitigate the adverse effects of land-use changes is the demarcation of protected areas, but they cover only 7.4% of the region. Unsustainable use of the land in semiarid regions can lead to desertification. In fact, 94% of the Caatinga has a moderate to high desertification risk. This risk could increase still more, taking into account the fact that the region is one of the most vulnerable to climate change.

Although the Caatinga is Brazil's only large ecological region that is not shared with any other country, its importance in conserving the national but also global natural heritage had remained largely overlooked by policy-makers until the end of the last century. During the last decade, we have mobilized colleagues and edited some of the most impactful books in Brazil on the Caatinga, which has helped raise awareness about the biological importance of the region. However, all of these books were published in Portuguese, which limited their use by an international audience. Recognizing this gap, we accepted the kind invitation from Springer to edit a book that compiles and synthesizes the most up-to-date information about the Caatinga, with an emphasis on the human–nature relationship. During this project, we were fortunate enough to mobilize an extraordinary group of 61 authors, the vast majority of whom work for academic institutions located in northeastern Brazil and, as a consequence, have a thorough understanding of the region and its challenges. This volume was designed to provide the international audience with the basic information required for understanding the Caatinga. We hope that this book will stimulate more collaborative research about the region and offer some lessons or insights for those concerned about the fate of SDTFs globally.

The book is organized into five sections. Part I is composed of one chapter (Chap. 1) that provides a brief introduction to the geographical boundaries, ecological systems, human systems, and the interaction between ecological and human systems. It also outlines some of the major regional challenges to moving the region toward a more sustainable and resilient future. Part II focuses on the ecological systems. It is composed of chapters about plants (Chap. 2), ants (Chap. 3), fishes (Chap. 4), amphibians (Chap. 5), reptiles (Chap. 6), birds (Chap. 7), mammals (Chap. 8), and plant–animal interactions (Chap. 9). Part III provides information about the still early research about ecosystem services in the Caatinga, covering freshwater availability (Chap. 10), multiple forest resources (Chap. 11), and cultural services (Chap. 12). Part IV describes the major threats to the socio-ecological systems in the Caatinga and includes chapters about fast and large-scale land-use changes (Chap. 13); slow and small-scale land-use changes, also known as chronic human disturbances (Chap. 14); and climate change (Chap. 15). Part V outlines some potential solutions for a more sustainable development for the Caatinga. It encompasses chapters about sustainable agriculture (Chap. 16), conservation systems (Chap. 17), and sustainable development (Chap. 18). Part VI is about the future of the Caatinga. It has one chapter (Chap. 19) that brings together the information and insights produced in all the previous chapters in the broad context of the socio-ecological systems to propose ten major actions that will enable the transformation of the Caatinga into a place where people and nature can thrive together.

Finally, we would like to thank Roberta Gazzarolle (formerly a Springer Editor in Brazil) for inviting us to organize this book and Maria Alice Alves (Universidade Estadual do Rio de Janeiro) for her constructive review of the initial book proposal. We are grateful to Luciana Christande (Editor, Life Sciences), Susan Westendorff (Project Coordinator), and Sindhuraj Thulasingam (Production Editor) for all their support and patience during the execution of this project. Inara R. Leal (process 305611/2014-3) and Marcelo Tabarelli (process 310228/2016-6) received a productivity grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). They also received financial support from CNPq, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), and Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE). José Silva received support from the University of Miami and the Swift Action Fund.

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Contents

Part I Introduction

Part II Biodiversity

Part III Ecosystem Services

Part IV Threats

Part V Solutions

Part VI Conclusions

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Part I
Introduction

Chapter 1
The Caatinga: Understanding the Challenges

José Maria Cardoso da Silva, Luis Cláudio Fernandes Barbosa, Inara R. Leal, and Marcelo Tabarelli

Abstract The Caatinga is a well-recognized ecological region that lies in the semiarid hinterland of northeastern Brazil and that covers 912,529 km^2. The term ‘Caatinga’ refers mostly to a seasonally dry tropical forest (SDTF) that presents a mosaic of different physiognomies. The Caatinga is a very heterogeneous region that can be divided into nine ecoregions. It was home to 28.6 million people in 2010. The region has an economy based mostly on public services, and its human development indicators are the lowest in Brazil. The interactions between humans and nature in the region have been marked by a frontier mindset in which natural resources are perceived as infinite. The combination of acute disturbances, chronic disturbances, the proliferation of exotic species, and climate change can lead to the disruption of critical ecological services. A significant regional shift toward sustainable development in this region is urgent. It will require persistence, creativity, consistent financial and political support, and a robust and evident connection between the improvement of human livelihoods and the conservation of natural landscapes.

Keywords Dry lands • Ecosystem services • Seasonally dry tropical forest • Socio-ecological system • Sustainable development

1.1 Introduction

The Caatinga is a well-recognized ecological region that lies in the semiarid hinterland of northeastern Brazil (Ab’Saber 1977; Prado 2003; IBGE 2004). The dominant vegetation type in the region is a seasonally dry tropical forest (SDTF) (sensu Pennington et al. 2009; see also Chap. 2) that exhibits at least 13 different physiognomies spanning a broad range of woody plant densities and is referred to

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collectively as the caatingas (Andrade-Lima 1981; Prado 2003). As in any other semiarid region, the Caatinga has an extended dry period in which rainfall is scarce. As a result, most of the vegetation is deciduous (Prado 2003). The deciduousness of the caatingas explains the name, which comes from Tupi, the language spoken by the Ameridians who still live in small numbers in the region, and means 'white forest', possibly because of the magnificent view offered by a 'sea' of leafless trees during the dry season (Prado 2003). In addition to being an ecological region, the Caatinga is also considered a well-defined social region. The Caatinga's human population is a product of the miscegenation of the native indigenous peoples with the Portuguese who colonized the area during the 1600s (Théry and Mello 2005). This population has developed strong and resilient cultural traditions based on cattle ranching and subsistence agriculture. However, political constraints have slowed human development in the Caatinga, making it Brazil's most underdeveloped region (Buainain and Garcia 2013).

Socio-ecological systems comprise ecological systems, human systems, and the interactions between them (Liu et al. 2007). They can be found in any spatial level, from local to global, and a good understanding of their spatial and temporal dynamics is fundamental for proposing sound sustainable development policies that seek to conciliate significant improvements in human welfare while conserving natural ecosystems. In fact, policies based on a reductionist approach have caused recurrent failures in semiarid regions, thus undermining human prosperity (Silva 2007). Here we propose that the Caatinga is a large-scale socio-ecological system that is predicted to exhibit the same properties that have been used to describe other socio-ecological systems worldwide: non-linear dynamics with thresholds, reciprocal feedback loops, time lags, resilience, heterogeneity, and surprises (Liu et al. 2007). We suggest that understanding the principles of the processes that govern such a large-scale system is the first step toward a better framework that enables scientists and policy-makers to find sound solutions for the region. In this chapter, we provide a brief description of the Caatinga's socio-ecological system. We start by describing the boundaries of the region, and we then describe its ecological system, its human system, and the interactions between them. We close with a discussion of the relationship between science and policy in a region that requires immediate political actions to move toward a more sustainable and resilient development path.

1.2 Geographical Boundaries

Large socio-ecological systems, such as the Caatinga, do not have stable borders. In fact, they are under a permanent state of flow due to recurrent global changes. However, to understand the ecological and social processes that are operating within the region, it is necessary to delimit its boundaries. The position of the boundaries of an ecological region depends on both the dataset and the methods used to delimit it. In 2004, the IBGE (Instituto Brasileiro de Geografia e Estatística) identified six major ecological regions (or biomes) in Brazil, aiming to provide a guide for both

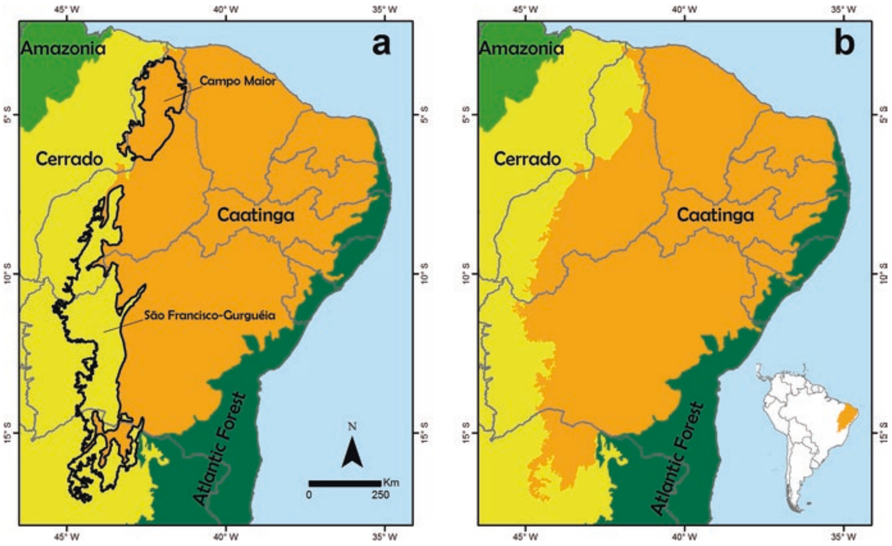

Fig. 1.1 Comparison of the Caatinga's limits proposed by the IBGE (Instituto Brasileiro de Geografia e Estatística) (2004) (**a**) with those proposed in this chapter (**b**). Note that we excluded Campo Maior from the Caatinga and included the seasonally tropical dry forests of the São Francisco-Gurgéia

environmental policies and research. These ecological regions were delimited based on the country's vegetation map at the scale of 1:5,000,000 (IBGE 2004). The following criteria were used: (a) the region should encompass a vast and continuous areas dominated by one vegetation type; (b) the enclaves of other vegetation types found within the region should be included within it; (c) the transition zones between ecological regions should be merged with one of the adjacent regions based on the vegetation type that dominates the transition zone; and (d) because of the mapping scale, all coastal environments had to be segmented and merged with the adjacent large ecological region.

In the IBGE's classification, the Caatinga was recognized as the ecological region that encompasses most of the hinterland of northeastern Brazil and that is delimited based on the distribution of the caatingas. Although dominated by the caatingas, the Caatinga as a region also encompasses all the enclaves of humid tropical forests, wetlands, transitional vegetation types, grasslands, and rupestrian grasslands found within it (for a full description, see Chap. 2). The IBGE's map included the region of Campo Maior within the Caatinga (Fig. 1.1). However, this region is dominated by grasslands, and the few patches of caatinga found there have limited floristic affinity to the remaining caatingas (Moro et al. 2014, 2016). In contrast, the IBGE's map excluded from the Caatinga a significant portion of the SDTFs found along the middle valley of the São Francisco River (Fig. 1.1). They were merged with the Cerrado, a region dominated by a savanna-like vegetation. This decision is not sound because the SDTFs of the São Francisco River have always been considered physiognomic units of the caatingas (Andrade-Lima 1981; Prado 2003; Chapter 2). Based on these two findings, we proposed a new limit for the Caatinga (Fig. 1.1). We maintained most of the boundaries suggested by the IBGE, but excluded from it the Campo Maior (which was transferred to the Cerrado) and included all the SDTFs along the Middle São Francisco River. According to the new boundaries, the Caatinga has an area of 912,529 km^2, which corresponds to 10.7% of the Brazilian territory or a region roughly equivalent to the areas of Italy, Germany, and the United Kingdom together.

1.3 Ecological System

The Caatinga has around 70% of its area in crystalline basements (Proterozoic) and 30% in sedimentary basins (Paleozoic and Mesozoic) forming flattened surfaces between 300 and 500 m above sea level (Cole 1986; Sampaio 1995, Chap. 2). Isolated mountain ranges and high-altitude plateaus (up to 1000 m) are scattered across the region, modifying the local climate and acting as present-day refuges for species assemblages well distinct from the ones found in the lowest terrains (Andrade-Lima 1982). The region has different soil types, ranging from shallow, rocky, and relatively fertile to profound, sandy, and unfertile ones (Sampaio 2010). Across most of the region, the climate is semiarid because the precipitation/potential evapotranspiration rate is <0.65 (Sampaio 2010). Average mean temperature is constant over the year, ranging from 25 to 30 °C. However, annual rainfall varies widely in time and space. Most of the region (68.8%) receives between 600 and 1000 mm of rain a year, with only 0.6% receiving less than 400 mm and 1.6% receiving more than 1200 mm (Chap. 10). In a few mountain areas, due to orographic effects, rainfall can go up to 1800 mm a year (Chap. 10).

Most of the rainfall is concentrated in three consecutive months, although wide annual variations and recurrent droughts are frequent (Nimer 1972). The number of dry months increases from the edges to the core of the region, with some areas experiencing periods of 7–10 months without water availability for plants (Prado 2003). An important feature of the Caatinga is the high inter-annual variability in rainfall, with droughts that can last for years (Nimer 1972). These long droughts impose severe conditions on the people living in the region and are the basis for the development of unique adaptations by the region’s biota. Some mountain ranges benefit from orographic rains and reduced average temperatures, which provide mesic conditions for the maintenance of species from the adjacent biomes.

The dominant vegetation, the caatingas, ranges from open scrublands to tall, dry forests (see Chap. 2). These tall, dry forests were once the most dominant physiognomy along the rivers and mountain slopes, but, currently, most of the region is occupied by open physiognomies and woodlands, possibly due to human disturbances (Coimbra-Filho and Câmara 1996). Along the major rivers, wetlands and seasonally flooded grasslands were once common (Siqueira Filho 2012). Humid forests once covered the slopes of the mountains and high plateaus, creating ecological gradients found nowhere else. On the top of some plateaus, there are patches of cerrado and rupestrian grasslands, a unique vegetation type with a high level of endemism. In total, the flora of the Caatinga is very rich, with a relatively high proportion of endemic species compared with other SDTFs (Chap. 2). On a regional scale, vegetation dynamics, as measured by remote sensing and using vegetation indices, such as the Normalized Difference Vegetation Index (NDVI), shows a wide variation across time and space and is strongly correlated with rainfall (Schucknecht et al. 2013). In fact, the plants of the caatingas usually grow and produce flowers and fruits during the wet season (Sampaio 2010).

The Caatinga has a dense river network composed of both perennial and intermittent rivers, both of which have been strongly disturbed by human activities (Fig. 1.2). Perennial rivers are few, and their headwaters are generally outside the Caatinga. The São Francisco is the largest and most important perennial river in the region, and its valley is where most of the energy and irrigation projects are located. The São Francisco River had large and productive wetlands along its valley in the past, but most of these ecosystems have been lost (Siqueira Filho 2012). Intermittent rivers are the ones that cease to flow every year or at least twice every 5 years (Steffan 1977). They experience flash floods and prolonged droughts, both of which act as agents of hydrologic disturbance and have a strong influence on aquatic plants and animals. In addition, when well-conserved, intermittent rivers help to maintain riparian forests along their valleys. These forests, in turn, act as refuges for plants and animals during the dry season. However, most of the riparian forests have been lost due to the expansion of cattle ranching and agriculture across the region.

The Caatinga is not a homogeneous region. Rodrigues and Silva et al. (2000) recognized at least 135 geo-environmental areas within the Caatinga. These units, in turn, can be grouped into nine ecoregions (Velloso et al. 2002). Here we propose a new map of the Caatinga ecoregions that seeks to align Velloso and colleague's map with the new map of the Caatinga (Fig. 1.3). The new ecoregion map differs from the previous one as follows: (a) the Campo Maior ecoregion has been removed from the Caatinga; and (b) a new ecoregion (São Francisco-Gurgéia) has been proposed to highlight the uniqueness of the SDTFs of this region (Fig. 1.3).

1.4 Human System

The Caatinga was the home of 28.6 million people in 2010, corresponding to 14.5% of the Brazilian population. This population lived in 1213 municipalities whose limits overlapped 50% or more with the Caatinga's boundaries (Fig. 1.4). These municipalities are nested into ten Brazilian states (Piaui, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Paraíba, Alagoas, Sergipe, Bahia, and Minas Gerais) (Fig. 1.4). The region includes two state capitals (Fortaleza and Natal) that are located in the segments of the coastline that were merged with the Caatinga by the IBGE (2004). The combined population of these two large urban centers was 11.4% of the Caatinga's population. Since the 1980s, the proportion of the population

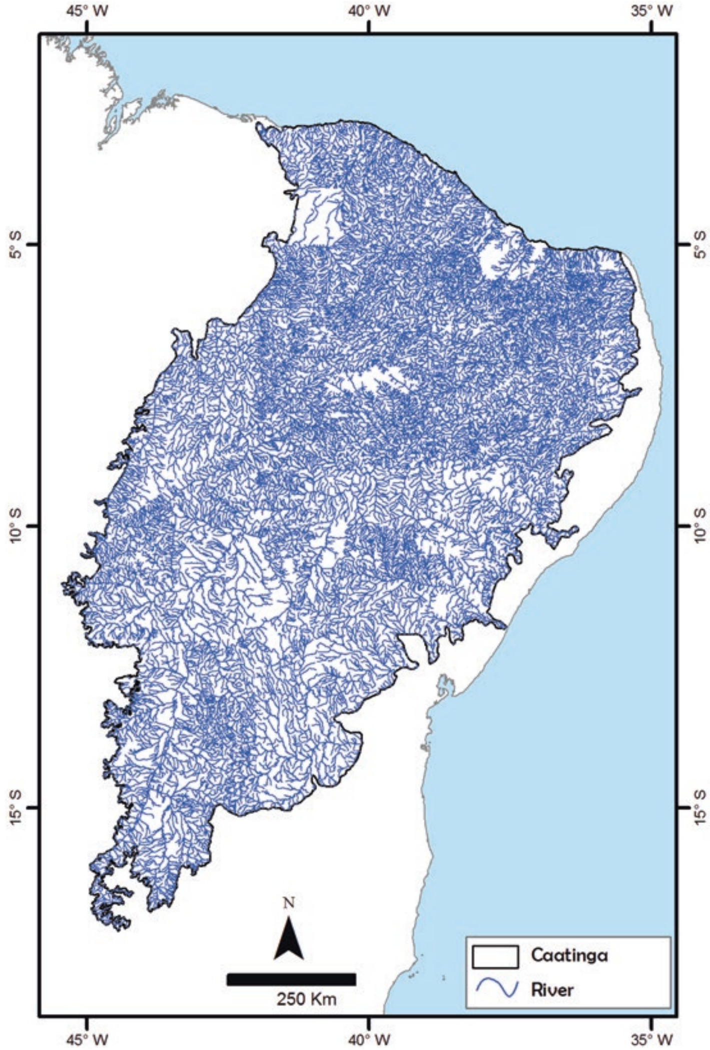

Fig. 1.2 Rivers of the Caatinga (Source: www.ana.gov.br)

living in cities within the Caatinga has been higher than that in rural settings (Théry and Mello 2005). In 2010, 66.7% of the population lived in cities.

The regional population density in 2010 was 33.1/km^2; however, if only the rural population is counted, this number declines to 10.4/km^2, which is a high rural density for a semiarid region (Ab'Saber 1999). The population density is not homogenous across the region. High densities are found along the eastern borders of the region as well as along the coastline (Fig. 1.5). In contrast, municipalities with low population densities are found mostly along the western borders in the transition to the Cerrado (Fig. 1.5). Few municipalities (6.3%) have population densities below

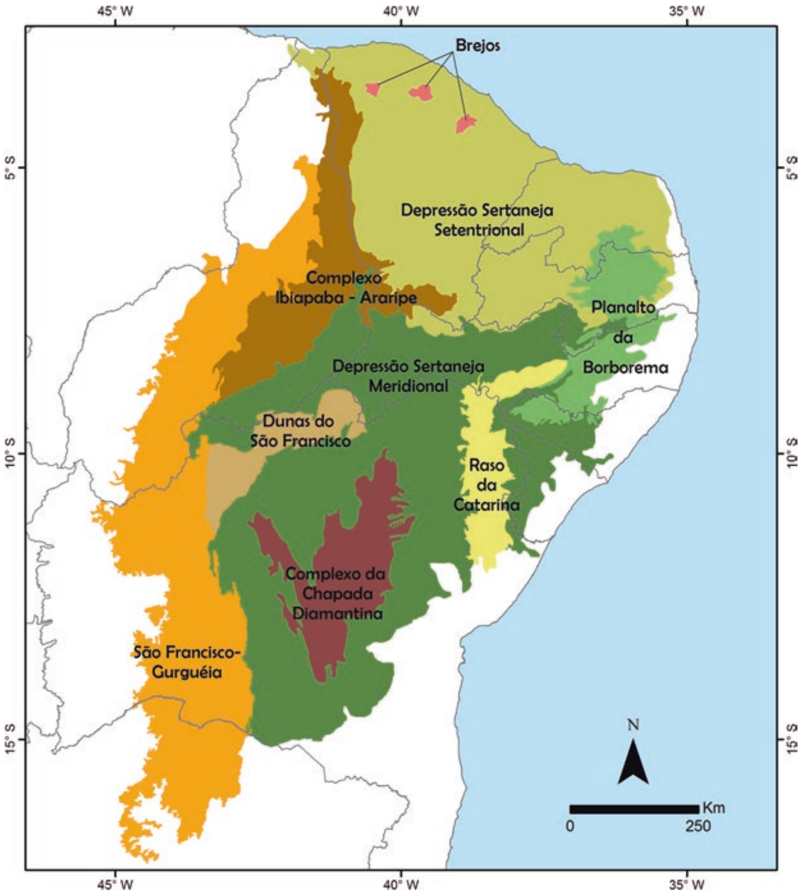

Fig. 1.3 Ecoregions of the Caatinga (Modified from Velloso et al. 2002)

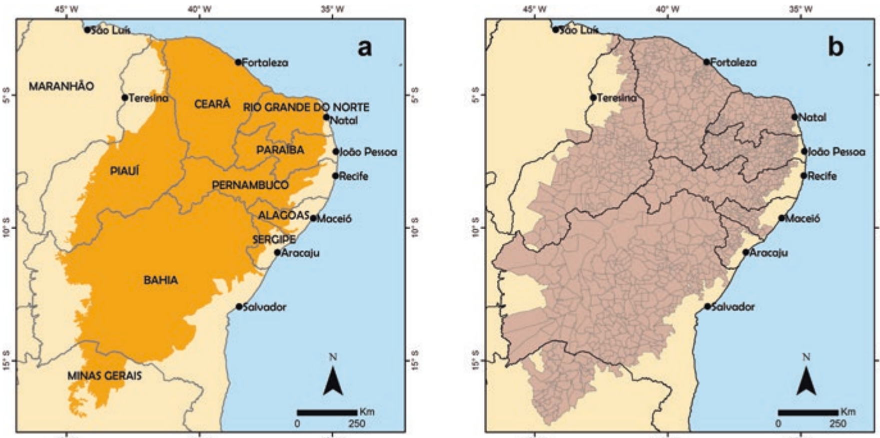

Fig. 1.4 Political map of the Caatinga: (**a**) division in states; (**b**) division in municipalities

5/km^2. However, these 77 municipalities are large and cover 23.2% of the region (Fig. 1.5). The percentage of the population living in rural settings presents a wide geographical variation, and a large number of municipalities (46.5%) have populations that are still mostly rural (Fig. 1.5). These rural municipalities cover 49.2% of the region and comprise 27.6% of the population.

In 2010, the Caatinga's gross domestic product (GDP) was around US$73 billion, corresponding to roughly 10% of Brazil's GDP. A total of 25% of the regional economic activity is centered around 11 municipalities in the states of Ceará (Fortaleza, Caucaia, Maracanaú, and Sobral), Rio Grande do Norte (Mossoró and Natal), Paraíba (Campina Grande), Pernambuco (Caruaru and Petrolina), Bahia (Feira de Santana), and Minas Gerais (Montes Claros) (Fig. 1.6). These municipalities together cover 1.61% of the region's area but are home to 21.5% of its population. The region's formal economy is based mostly on services (Fig. 1.7). On average, services contribute to 69.7% of the municipalities' GDP. An economy based on services would be considered good news if they were mostly provided by the private sector rather than by the governments. However, in the Caatinga, public services (e.g., pensions and government expenditures) are responsible, on average, for 44.4% of the local GDP. Although most of the Caatinga's rural population depends on agriculture (Buainain and Garcia 2013), it contributes only 11% of the local economic activity on average. This fact could be a consequence of the low

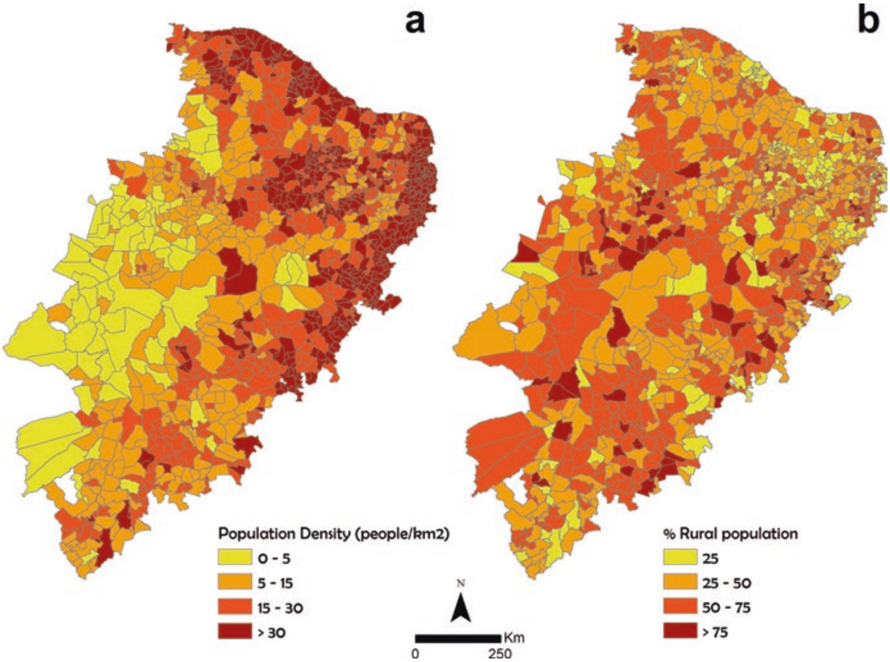

Fig. 1.5 Geographical variation in (**a**) population density (people/km^2) and (**b**) percentage of the rural population in the municipalities of the Caatinga (Source: http://seriesestatisticas.ibge.gov.br/)

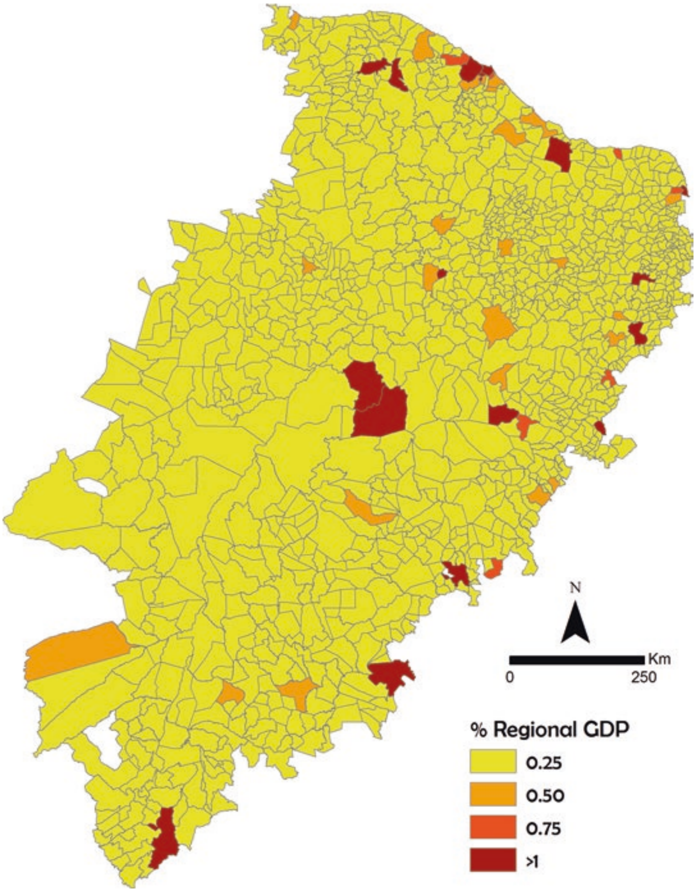

Fig. 1.6 Contribution of the different municipalities to the Caatinga's gross domestic product (GDP) (Source: http://seriesestatisticas.ibge.gov.br/)

productivity of the agriculture systems across the region but also because most of the agricultural output from the region is either for subsistence or traded on informal markets. The contribution of agriculture to the economy is high in a few municipalities along the border with the Cerrado and in the irrigated agriculture poles in Pernambuco and Bahia (Fig. 1.7). Industrial activities contribute on average slightly more (12.5%) to the local economies than agriculture. The importance of this sector to the economy is high in a few scattered major urban centers along the coastline and in central Bahia (Fig. 1.7).

The Caatinga has Brazil's lowest indicators of human development, as measured by the Human Development Index (HDI) at the municipality level. The HDI is a synthetic index that measures three basic dimensions of human well-being (health, education, and income) and ranges from 0 to 1. The municipalities can be classified into five categories according to their HDIs: very low (below 0.49), low (0.50–0.59),

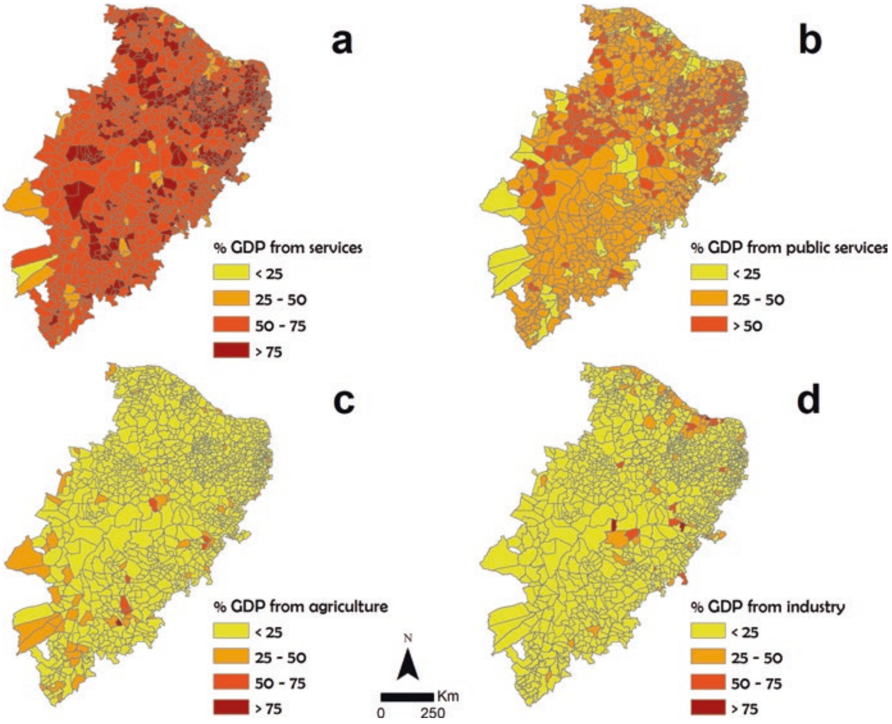

Fig. 1.7 Contribution of different economic sectors to the gross domestic product (GDP) of the Caatinga's municipalities (Source: http://seriesestatisticas.ibge.gov.br/)

medium (0.6–0.69), high (above 0.7–0.799), and very high (above 8). The proportion of the municipalities in each of these categories has changed over time (Fig. 1.8). In 1991, almost all municipalities had very low HDI. From 1991 to 2000, the situation did not change very much, but at least some municipalities (113) moved up to low and medium HDI. From 2000 to 2010, the region experienced a development burst that helped to move most of the municipalities to low and medium HDI. In addition, a few municipalities (20) moved up to high HDI (Fig. 1.8). In 2010, the HDI of the Caatinga's municipalities ranged from 0.48 to 0.77, with an average of 0.59. The regional average value is lower than the mean of all the municipalities in Brazil (0.66).

1.5 Interactions Between Natural and Human Systems

The interaction between humans and nature in the Caatinga began in the Late Pleistocene–Holocene, when the first populations arrived in the region, possibly following a coastal migratory route (Martin 2005; Bueno and Dias 2015). The indigenous people lived mostly along the major rivers and other humid spots, using

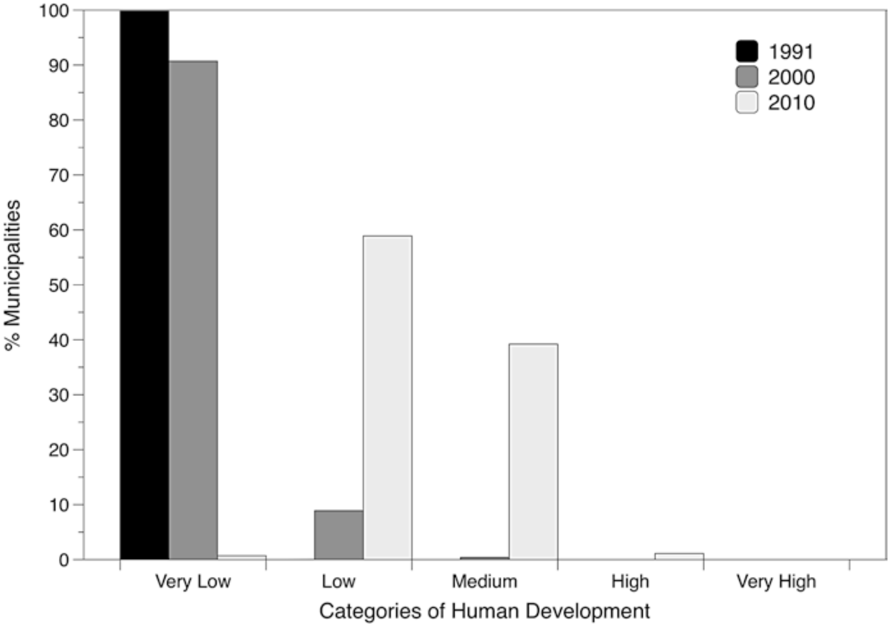

Fig. 1.8 Temporal changes in the classification of the Caatinga municipalities according to categories of the Human Development Index. Categories are as follows: very low (below 0.49), low (0.50–0.59), medium (0.6–0.69), high (above 0.7–0.799), and very high (above 8) (Source: http://atlasbrasil.org.br)

the caatingas during the wet season. When the Portuguese decided to colonize the Caatinga from their settlements along the coast, they opted to establish vast cattle ranches along the major rivers, such as São Francisco and Paraguaçu (Hemming 1978). This decision put the colonizers against the indigenous populations that had lived for thousands of years in such places. A long and cruel war took place, and thousands of indigenous people were slaughtered as a consequence (Puntoni 2002). With the venues opened to more intense colonization, cattle ranching expanded across the region, first, from the São Francisco to Parnaíba, and then to all other regions (Hemming 1978). Soon, the colonizers learned that it was possible to use the native vegetation to feed their cattle, which allowed them to move away from the major rivers (Hemming 1987). They had also begun to extract timber as construction material for their ranches and as firewood to provide the energy that they needed. Agriculture was mostly for subsistence and based on the traditional slash-and-burn method. In a few decades, the colonizers increased their dependency on the caatingas and developed a solid regional culture, with their leather clothes, food, music, poetry, traditions, and adaptations to the long droughts that eventually affected the region (Andrade 1998; Chaps. 11 and 12). Over time, losses caused by the recurrent droughts and competition with meat coming from elsewhere led to the decline of the regional cattle-ranching industry, which limited the growth of the regional economy when compared with other regions in Brazil (Prado-Júnior 1987).

For some time, cotton plantations in some areas generated good expectations (Silva 1977), but mismanagement of the land and weevils caused them to fail.

The negative impact of the long droughts on the population led to the adoption of emergency actions by the governments (Andrade 1998). However, these measures benefited only the wealthy and powerful and produced no long-term positive impact on the poor (Silva 2007). Inequalities that had always been high increased over time, deepening the regional social gap. Even today, millions have only a few hectares to produce and prosper, while a few control most of the land and other resources, including access to fresh water (Buainain and Garcia 2013b). Long droughts led to water scarcity. People unable to store water lost their farms and became hungry. Without food, they either moved to the main cities or stayed in the region and became vulnerable to all kinds of exploitation by the local elite, including exchanging hard work for poverty wages.

Because emergency programs were not successful, the governments decided to adopt a more permanent and scientifically based program to combat the droughts. The new program defined water shortage as the main obstacle to local development and determined that by building new reservoirs and creating water distribution mechanisms, such as new roads, the local population would thrive. The ‘hydraulic solution’ to the Caatinga’s problems mobilized large sums of public funds over decades and transformed the Caatinga into a semiarid region with the world’s greatest capacity to stock freshwater and with one with the densest road networks (Ab’Saber 1999). However, most of the reservoirs were built on private rather than public land; the water distribution mechanisms were not efficient and, as a consequence, chronic regional water shortages remained a challenge (Ab’Saber 1999; Silva 2007). Roads opened the few pristine areas for colonization, leading to more deforestation. In addition to the physical infrastructure, the programs to combat drought envisioned new rural economic activities, such as the replacement of cattle with sheep and goats (there are currently 19 million sheep and goats in the Caatinga) as well as the introduction of exotic plant species that could be consumed by both people and livestock during the droughts (Almeida et al. 2015). The perspective that large-scale infrastructure is favorable for the Caatinga and its habitants has not changed over time. For instance, in 2005, the Federal Government began a new project to transfer water from the São Francisco River to four rivers and several reservoirs in the north of the region. The idea was to ensure a permanent water supply to 12 million people at the cost of US$2 billion. Initially promised to be delivered in 2010, this massive infrastructure project has not been completed to date. Its final costs are now estimated at US$3 billion. In the meantime, outright protection of critical areas to ensure the conservation of the Caatinga has not advanced at the same pace as in other Brazilian regions. Only 7.4% of the region is within protected areas (Fig. 1.9), and most of these protected areas are not funded properly (Oliveira and Bernard 2017).

The interactions between people and nature in the Caatinga have been marked by a frontier mindset in which natural resources are perceived as infinite and exploited ruthlessly due to weak governance. Three types of human disturbances to the

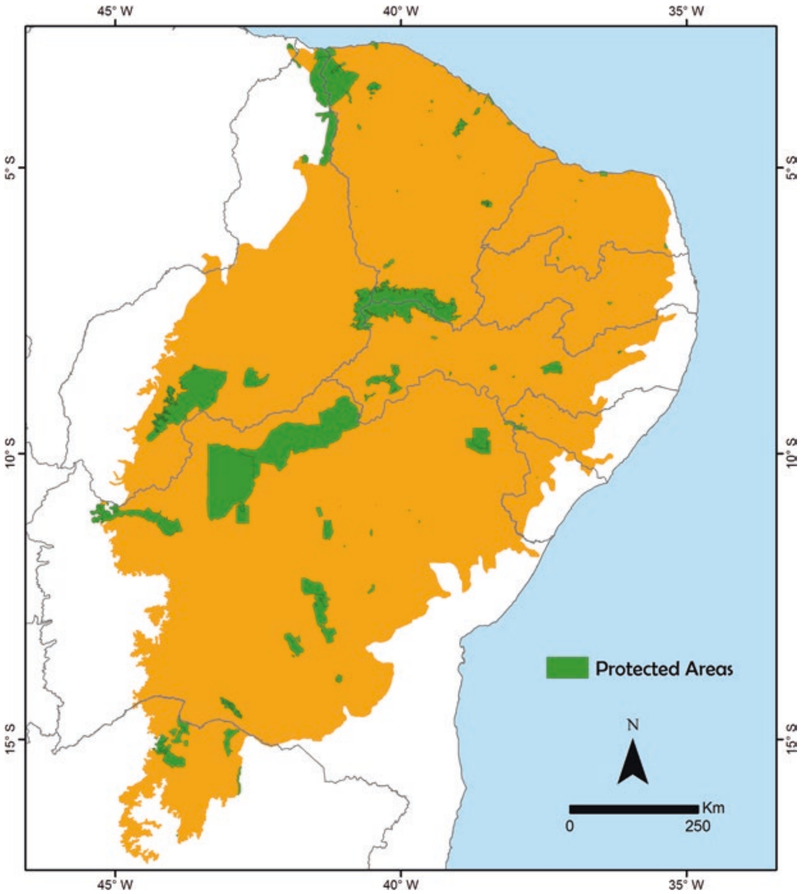

Fig. 1.9 Boundaries of the protected areas of the Caatinga (Source: http://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs/)

Caatinga's ecosystems have been detected. The first one is acute disturbances caused by the fast conversions of large areas of native vegetation into human-made ecosystems, with roads, reservoirs, or commercial agriculture. The second type is chronic disturbances caused by the slow but continuous overexploitation of the native vegetation, such as through establishing slash-and-burn agriculture, collecting firewood, and browsing by livestock (Singh 1998). Finally, the third type consists of the negative impacts caused by plant and animal exotic species that have been introduced into the region as a strategy to ensure food security for the rural population but that have reduced the populations of some native species (Nascimento et al. 2014). All three processes undermine the Caatinga's ecological systems that are so essential to sustaining the local populations but also to support globally relevant services.

1.6 The Challenges Ahead

The future of the Caatinga as a socio-ecological system will depend on how fast the regional society will move toward a new development paradigm that aims for the sustainable delivery of ecosystem services and benefits for human populations while simultaneously maintaining healthy, productive ecosystems. This paradigm requires the right mix of sound scientific knowledge and effective political action. In the last decade, knowledge about the Caatinga has increased exponentially (Fig. 1.10). We know more than ever about the biota of the Caatinga. It is now possible to model the ranges of the species, understand their evolution using DNA sequences, and use sophisticated computational methods to set priority areas for conservation. In addition, a new synthesis about regional archaeology, history, sociology, and economics has been produced, bringing new ideas and concepts about the Caatinga's past and current societies. In contrast, studies on the outcomes of the interaction between ecological and social systems are still in their infancy. Only recently, researchers have begun to estimate the magnitude of the impacts of the chronic disturbance on the Caatinga's biota (Ribeiro et al. 2015, 2016) and to understand how biodiversity loss can constrain the provision of the main ecosystem services (Leal et al. 2014, 2015; Sobrinho et al. 2016). There is still a long way to go to model how the Caatinga's biodiversity and ecosystem services are going to

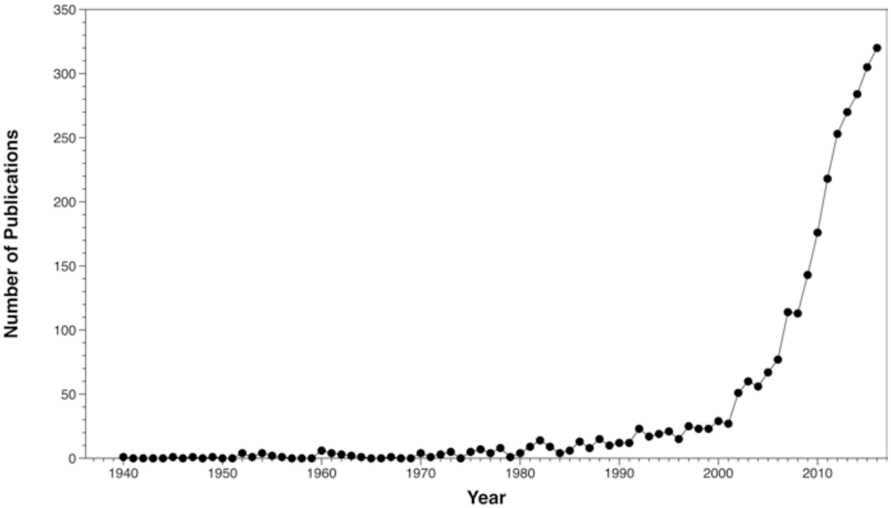

Fig. 1.10 Number of publications on the Caatinga in all citation databases in the Web of Knowledge, using 'caatinga' and 'caatingas' as topic search terms

simultaneously react to acute disturbances, chronic disturbances, exotic species, and climate change. Unfortunately, case studies describing the dynamics of local socio-ecological systems across the Caatinga are still scarce, possibly because the regional research teams have not yet cultivated and promoted transdisciplinary approaches in their graduate programs. We argue that more integrated studies combining the state-of-art from multiple disciplines are required to advance our knowledge on the Caatinga socio-ecological system and to support sound sustainable development policies. However, knowledge gaps cannot be used as an excuse to delay important political actions. We argue that in contrast with the scientific excitement that exists about the region, the political interest toward a major shift on how natural resources are managed in the Caatinga has vanished across all government levels in the last decade. Three facts seem to support our statement. First, despite all the awareness created by the importance of the Caatinga's biodiversity (Leal et al. 2003, 2005, Silva et al. 2004), protected areas remain inadequate to safeguard the region's biodiversity. Second, even though several studies have documented that 94% of the region has moderate to high risk of desertification due to intense and abusive land use practices (Sá and Angelotti 2009; Vieira et al. 2015), human disturbances across the region continue to increase and remain unchecked, as there is no system to monitor and evaluate the remaining native ecosystems. Finally, despite all the research demonstrating that the regional society is using the Caatinga's natural resources well beyond its carrying capacity (Gariglio et al. 2010), the most recent plans proposed to improve the regional economy continue to follow the same mindset that has dominated the region for centuries and that has failed miserably to deliver long-term prosperity for all. In spite of all these recent drawbacks in the political arena, we continue to be optimistic about a sustainable future for the Caatinga. As we stated 12 years ago (Leal et al. 2005), a significant regional shift toward sustainable development in this region will require persistence, creativity, consistent financial and political support, and a robust and evident connection between the improvement of human livelihoods and the conservation of natural landscapes. We hope all these enabling conditions will become available soon. Perhaps this book is another important step in this direction.

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Part II
Biodiversity

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 km^2 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 therophitic 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 *Adamantinia* (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 km^2, distributed in Mesoamerica (800,898 km^2), the Caribbean (88,472 km^2), and South America (1,811,741 km^2). 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 km^2, 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 STDFWs. 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.

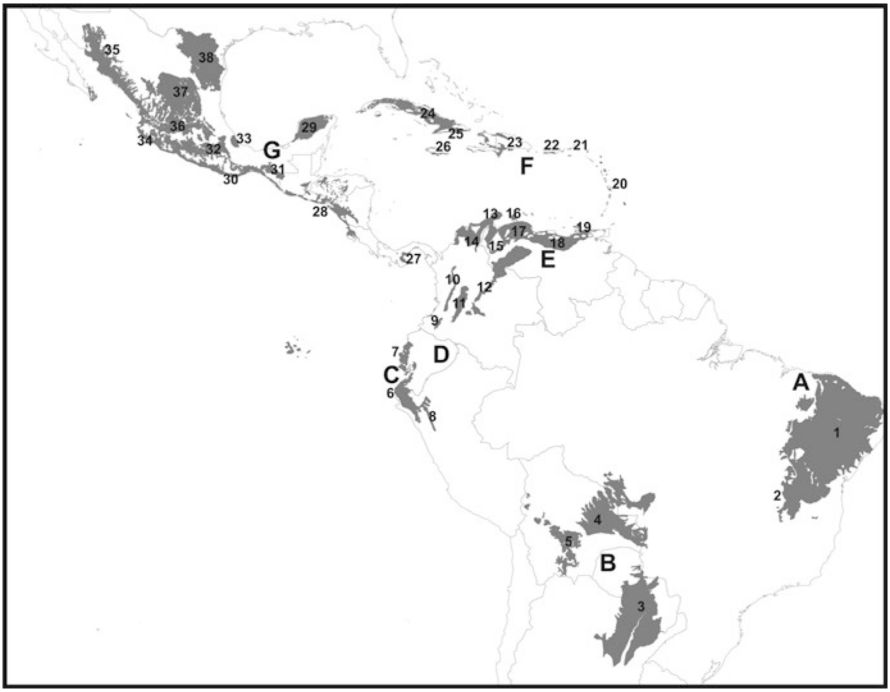

Fig. 2.1 Distribution of the Seasonally Dry Tropical Forest and Woodland (SDTFW) biome in the Neotropics (modified from Olson et al. 2001), with major groups indicated by capital letters and ecoregions of the Tropical and Subtropical Dry Broadleaf Forests and Deserts and Xeric Shrublands biomes (sensu 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*—Sinaloan 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,

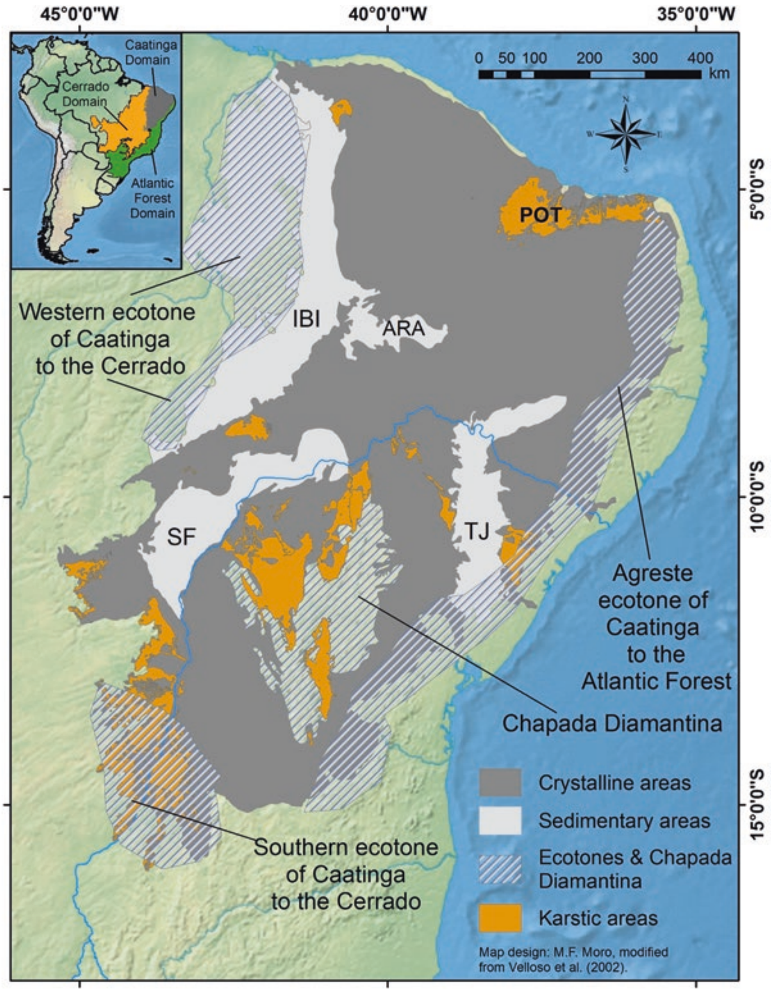

Fig. 2.2 Geographical overview of the Caatinga Domain, showing the main biogeographical units. The most typical Seasonally Dry Tropical Forest and Woodland (SDTFW) vegetation occurs in the crystalline terrains of the Sertaneja Depression, which has typically shallow and stony soils. Sedimentary terrains 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 sedimentar basin, *IBI* Ibiapaba highlands (part of the Parnaíba sedimentar basin), *SF* São Francisco dunes, *TJ* Tucano-Jatobá sedimentary basin, *POT* Potiguar sedimentar 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. vanildae*) 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	*Harpochillus*[a]	Mostly Sedimentary Caatinga
Amaryllidaceae	*Cearanthes*	Ibiapaba range
Anacardiaceae	*Apterokarpos*	Mostly Sedimentary Caatinga
Asteraceae	*Caatinganthus*	Two locally endemic species at Rio Grande do Norte and southern Bahia
	Dissothrix	Ibipaba range (Ceará)
	Piqueriella	Local in Northern Sertaneja Depression in Ceará
	Telmatophila	Araripe Plateau
Bromeliaceae	*Neoglaziovia*	Widespread in Caatinga
Cactaceae	*Espostoopsis*	Southern Sertaneja Depression in Bahia
	Facheiroa[b]	Widespread in Caatinga
	Leocereus[b]	Mostly in Southern Sertaneja Depression and Chapada Diamantina in Bahia
	Stephanocereus	Mostly at Chapada Diamantina
Celastraceae	*Fraunhofera*	Mostly Sedimentary Caatinga
Cleomaceae	*Haptocarpum*	Local in Southern Sertaneja Depression, probably near Bom Jesus da Lapa (Bahia)
Convolvulaceae	*Keraunea*[c]	Southern Sertaneja Depression (Bahia)
Euphorbiaceae	*Gradyana*	Raso da Catarina
Leguminosae	*Mysanthus*[b]	Mostly at Chapada Diamantina
	Tabaroa	Locally endemic in Southern Sertaneja Depression at southern border of the Chapada Diamantina (Bahia)
Malpighiaceae	*Mcvaughia*[a]	Raso da Catarina
Martyniaceae	*Holoregmia*	Southern Sertaneja Depression
Melastomataceae	*Rupestrea*	Chapada Diamantina
Molluginaceae	*Glischrothamnus*	São Francisco dunes
Orchidaceae	*Adamantinia*	Chapada Diamantina
Plantaginaceae	*Anamaria*	Widespread in temporary ponds
	Dizygostemon	Sertaneja Depression
Poaceae	*Neesiochloa*	Sertaneja Depression
Pontederiaceae	*Hydrothrix*	Widespread in temporary ponds
Rhamnaceae	*Alvimiantha*	Mostly Sedimentary Caatinga
Rubiaceae	*Diacrodon*	Mostly Sedimentary Caatinga
Scrophulariaceae	*Ameroglossum*	Northern Sertaneja Depression
Violaceae	*Hybanthopsis*	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 (*Epostoopsis*, *Haptocarpum*, *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 *Fraunhofera*); 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* (Malpighicaeae; 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.

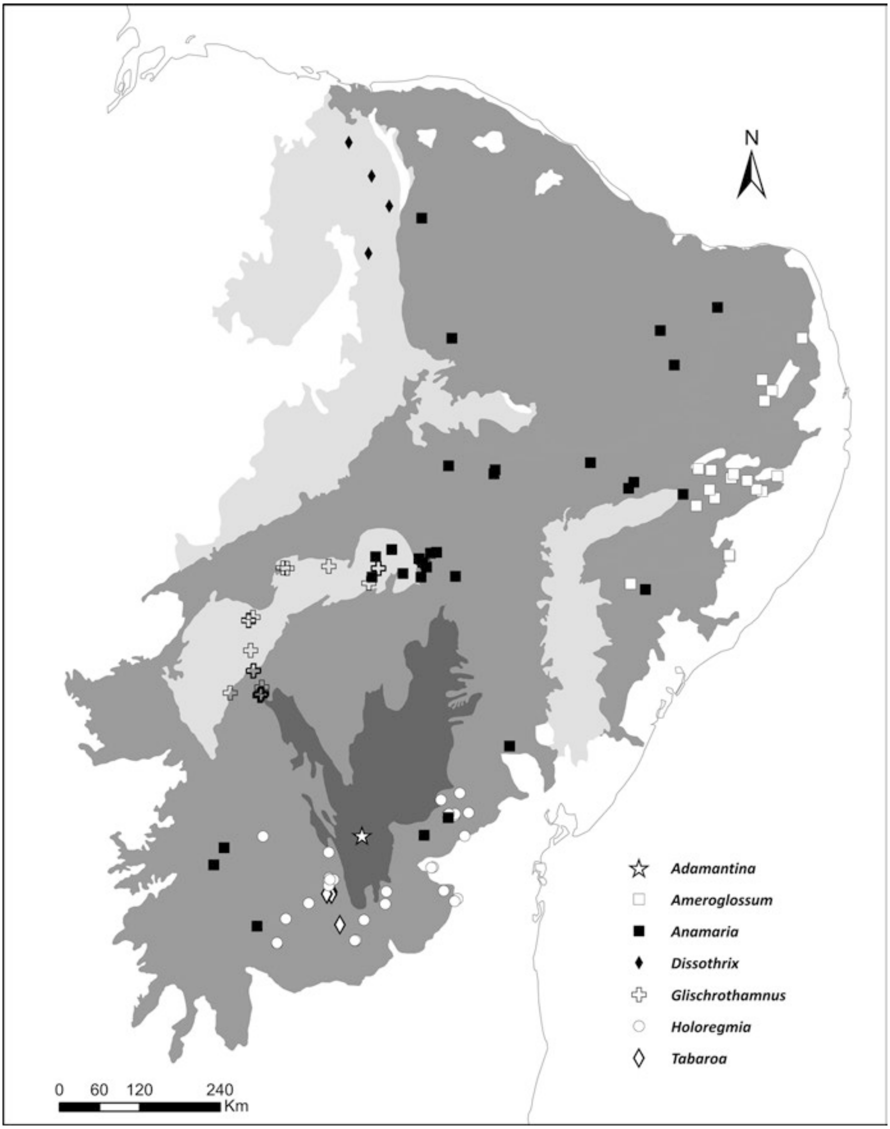

Fig. 2.4 Distribution patterns of some endemic genera of the Caatinga Domain in the crystalline (gray), sedimentary (light gray), and Chapada Diamantina mountain range (dark gray) surfaces (distribution data according to the records available in the INCT Herbário Virtual da Flora e dos Fungos database,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

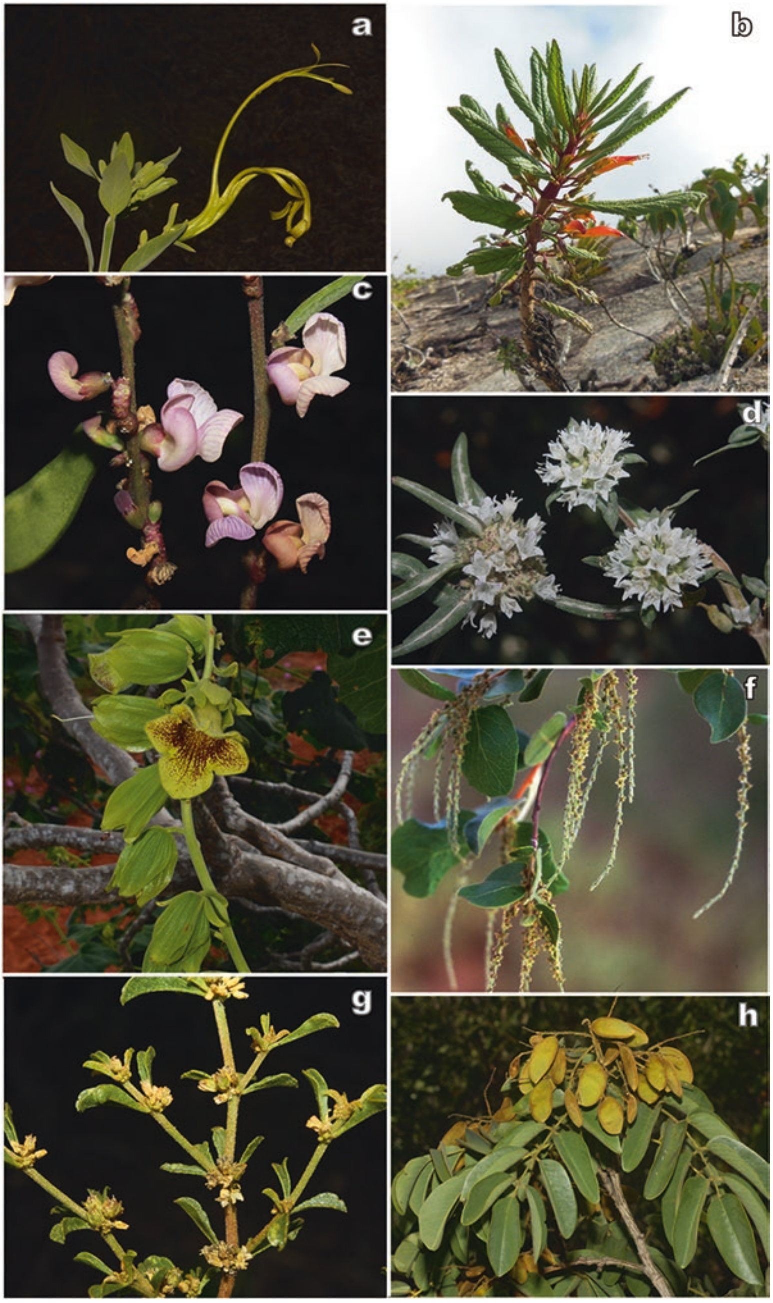

Fig. 2.5 Representatives of some endemic genera of the Caatinga Domain: (**a**) *Harpochilus neesianus* (Acanthaceae); (**b**) *Ameroglossum pernambucense* (Scrophulariaceae); (**c**) *Mysanthus uleanus* (Leguminosae); (**d**) *Diacrodon compressus* (Rubiaceae); (**e**) *Holoregmia viscida* (Martyniaceae); (**f**) *Fraunhofera 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	Number of descendent species	
Acanthaceae								
Thyrsacanthus clade	5.2	Mesoamerican SDTFW						Côrtes et al. (2015)
Schaueria humuliflora clade			4.2	3.3	Vicariance + in situ speciation	Northern	3 (1 endemic)	
Anacardiaceae								
Spondias	20.3	Equivocal						Machado (2014)
S. tuberosa clade			13.3	8	Dispersal + in situ speciation	Northern	3 (2 endemic)	
Burseraceae								
Commiphora	36.6	African SDTFW						Gostel et al. (2016)
C. Leptophloeos			8.5	3.8	Dispersal + allopatric speciation	Trans-Atlantic from Africa	1	
Cactaceae								
Pereskia	26.6	Mesoamerican SDFTW						Meta-analysis from Edwards et al. 2005
P. bahiensis clade			3.4	1.3	Vicariance + in situ speciation	Southern	2	
P. aureiflora			8.1		Dispersal + allopatric speciation	Northern	1	

(continued)

Table 2.2 (continued)

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

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

(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	
Coursetia								Meta-analysis from Queiroz and Lavin (2011)
C. rostrata clade			16.7	9.3	Vicariance + in situ speciation	Equivocal	3 (all endemic)	
Pterocarpus	24.3							Meta-analysis from Saslis-Lagoudakis et al. (2011)
P. zehntneri clade			12.1	9.2	Biome shift	Northern (Amazonian RFs)	3–4 (all endemic)	
Malpighiaceae								
Amorimia	9.9	South American SDTFW						Willis et al. (2014)
A. septemtrionalis clade			7.5	6.4	Equivocal + in situ speciation	?	4 (2 endemic)	
Mcvaughia			28	?	Biome shift	Amazonian RF	2 (1 endemic)	
Malvaceae–Bombacoideae								

Ceiba	13.4	Mesoamerican SDTFW					Carvalho-Sobrinho (2014)
C. jasminodora clade			10.1	6.8	Equivocal + in situ speciation	Northern	7 (1 endemic)
Pseudobombax	20.2	Mesoamerican SDTFW					
P. parvifolium clade			5.2	2.1	Vicariance + in situ speciation	Northern	3 (endemic)
Pachira (probably not monophyletic)	14.8	South American RFs					
P. retusa clade			5.4	2.5	Biome shift + in situ speciation	South American RFs	3 (1 endemic)
Spirotheca	17.1	Probably South American RFs (more samples needed)					
S. elegans			12		Biome shift	South American RFs	1 (endemic)
Martyniaceae	24	Equivocal					
South American clade	17	SW South American SDTFW					
Holoregmia			9.4	(mono specifc)	Vicariance	Southern	1 (endemic)	Meta-analysis from Gormley et al. (2015)

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, *MRCA* 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 caesalpinioid 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

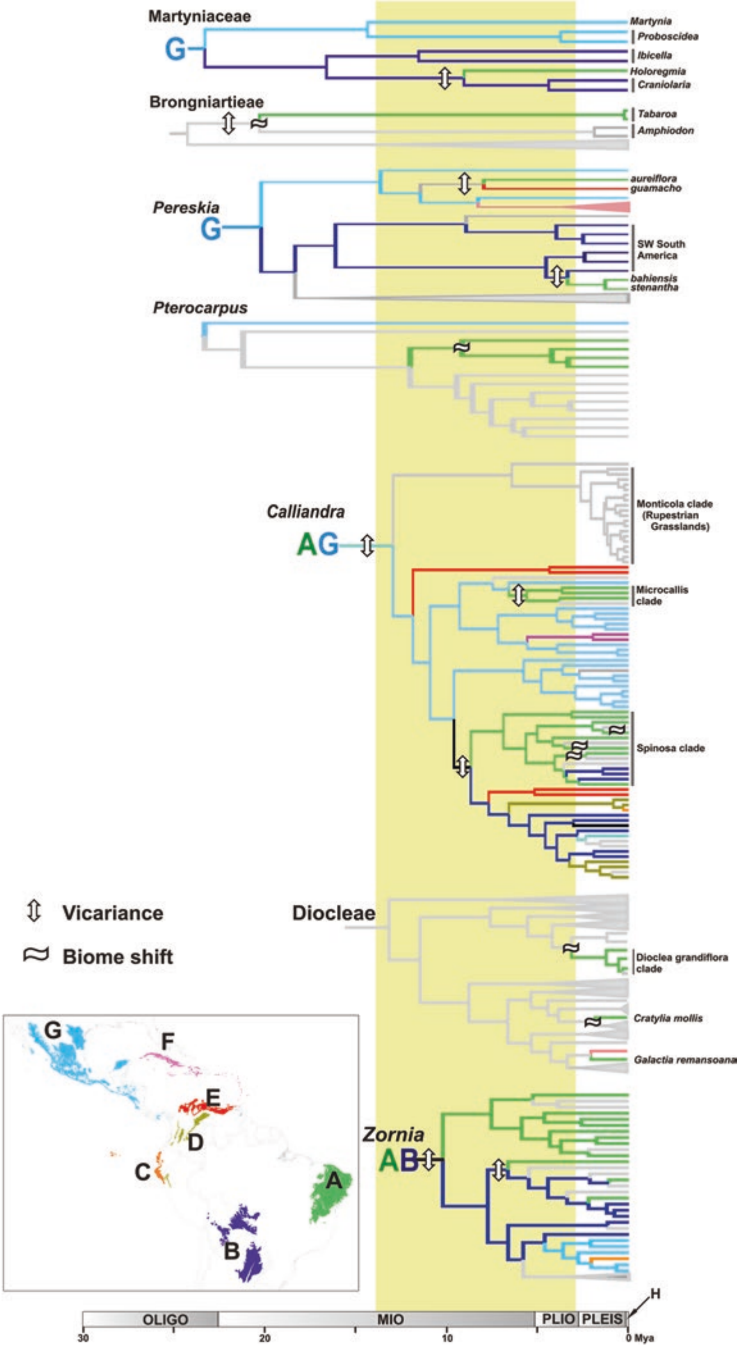

Fig. 2.6 Selected dated phylogenies obtained from meta-analyses of molecular data. Reconstructed neotropical seasonally dry tropical forest and woodland (SDTFW) ancestral areas are represented

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

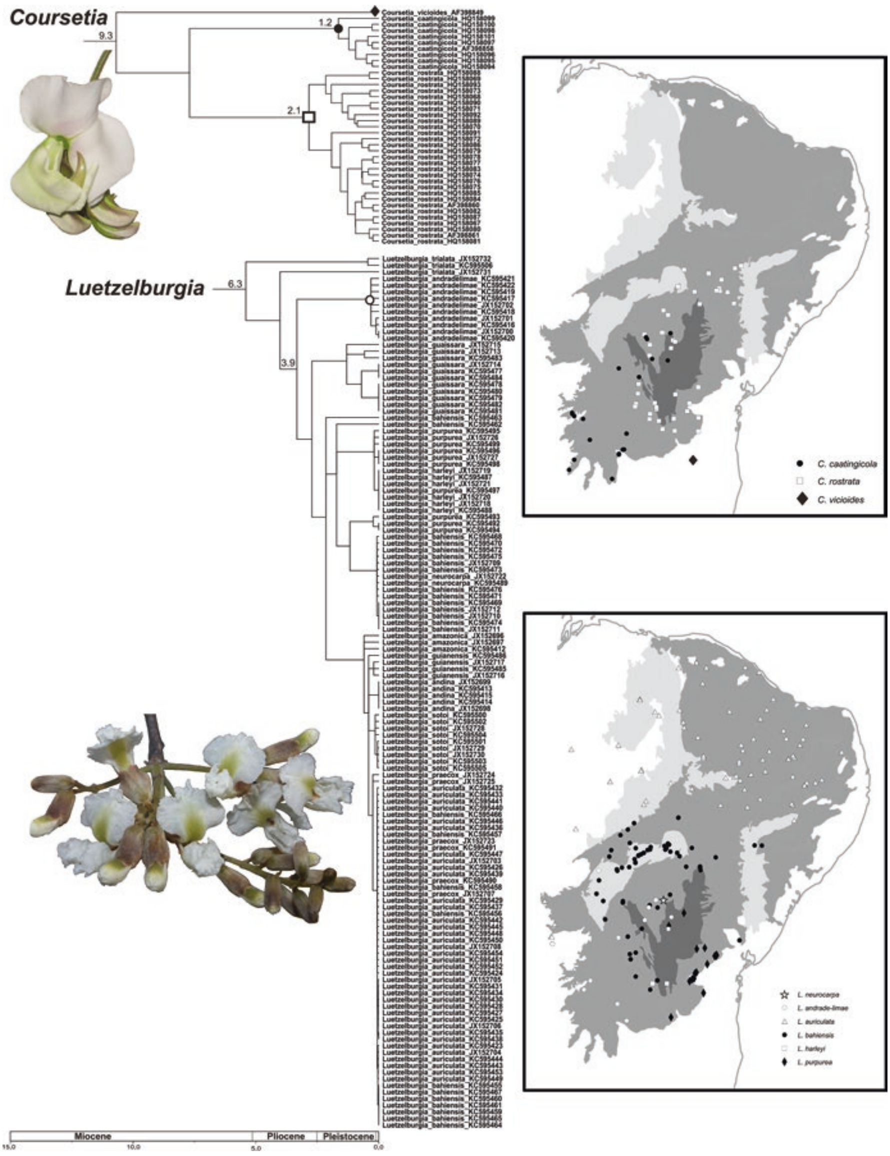

Fig. 2.7 Contrasting diversification patterns in Caatinga seasonally dry tropical forest and woodland (SDTFW) lineages. The legume genus *Coursetia* exemplifies the phylogenetic pattern commonly found in SDTFW lineages with strong geographical structure and coalescence of multiple accessions in relatively 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 had 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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Chapter 3

Ants of the Caatinga: Diversity, Biogeography, and Functional Responses to Anthropogenic Disturbance and Climate Change

Inara R. Leal, José Domingos Ribeiro-Neto, Xavier Arnan, Fernanda M.P. Oliveira, Gabriela B. Arcoverde, Rodrigo M. Feitosa, and Alan N. Andersen

Abstract Despite the outstanding diversity and ecological relevance of ants in most terrestrial ecosystems, current knowledge of the ants of the Caatinga is still incipient. This chapter offers an overview covering the diversity, taxonomy, biogeography, and functional composition of the Caatinga ant fauna, and a synthesis on ant response to chronic anthropogenic disturbance and increased aridity. We compiled a database consisting of 572 presence–absence ant records and 276 ant species from 37 localities in the Caatinga. As expected, most of the Caatinga has not been intensively sampled for ants, with the intensive sampling that has been conducted revealing high rates of species turnover across localities. Most ant species recorded

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in the Caatinga are widely distributed in other biomes, especially in Cerrado, and few species can be considered endemic to the Caatinga. Thus, the Caatinga ant fauna appears to represent an impoverished subset of the Cerrado's fauna. Such a reduced endemism and the occurrence of a highly depauperate ant fauna at a regional level contrast to the diversity patterns exhibited by the Caatinga flora and other faunal groups. Significant changes in ant taxonomic and functional composition in response to human disturbance are observed, with a predictable winner–loser replacement. Disturbance winners consist of generalist species exhibiting wide environmental tolerances and those inhabiting open habitats (Opportunists and Dominant Dolichoderinae). Highly specialized species are disturbance losers (Specialist predators). Aridity also affects both species occurrence and functional-group composition of local assemblages. Since several ant species and functional groups are sensitive to increasing disturbance and aridity, ant-mediated ecological services are already threatened in the Caatinga biota.

Keywords Chronic anthropogenic disturbance • Aridity • Winner–loser replacement • Ant functional groups

3.1 Introduction

Ants (Hymenoptera: Formicidae) are one of the most ubiquitous, widespread, and abundant groups of animals on Earth. The total ant population is estimated at more than 100 quadrillion (115,000,000,000,000,000) individuals (Hölldobler and Wilson 1994). A total of 13,300 species have been described (Bolton 2016), although total diversity could well exceed 25,000 species (Bolton 2003; Wilson 2003). Although this represents less than 1% of all described insect species (May 1988), ants are believed to represent at least 15% of total terrestrial animal biomass, including vertebrates (Fittkau and Klinge 1973). This remarkable numerical dominance is reflected in their ecological importance, as ants mediate many key ecological processes, including modifying soil, serving as predators and scavengers, recycling nutrients, dispersing seeds, protecting plants against herbivores, and engaging in mutualistic associations with other organisms (see reviews in Hölldobler and Wilson 1990, 1994; Lach et al. 2010; Del Toro et al. 2012). Their nests and underground activities have such broad effects on other organisms that ants are often referred to as 'ecosystem engineers' (Folgarait 1998; Meyer et al. 2011, 2013).

Ants have attracted considerable attention in disturbance studies because they are commonly used as bio-indicators in land management (Hoffmann and Andersen 2003; Andersen and Majer 2004). Ants are sensitive to a range of disturbances, including those associated with farming (Silva et al. 2009; Leal et al. 2012), logging (Vasconcelos et al. 2000; Arnan et al. 2009), mining (Majer et al. 1984), fire (Andersen et al. 2006; Arnan et al. 2006), and grazing by livestock (Hoffmann 2010). These studies document a predictable replacement of disturbance 'losers' (disturbance-sensitive taxa) by disturbance 'winners' (disturbance-adapted taxa; see Tabarelli et al. 2012), with disturbance typically favoring open-adapted taxa at the expense of highly specialized, forest-associated functional groups (Andersen 2000; Hoffmann and Andersen 2003; Beaumont et al. 2012; Leal et al. 2012).

Global climate change is another threat to ant communities. Shifting distributions in response to climate change have been predicted for several ant species (Colwell et al. 2008; Diamond et al. 2012; Warren II and Chick 2013; Resasco et al. 2014; Del Toro et al. 2015; Kwon et al. 2016). For example, Colwell et al. (2008) predict that as many as 80% of the ant species of a lowland rainforest could decline or disappear from the lowlands because of upslope range shifts and lowland extinctions due to higher temperatures. While species' range shifts at higher latitudes may be compensated for by species from lower latitudes as the climate warms, no species are available to replace the lowland tropical species that already live close to their thermal limits (Deutsch et al. 2008). Range-restricted, high-elevation species have nowhere to disperse (Nowrouzi et al. 2016). Zones of especially high ant species turnover can be identified along rainfall gradients, and these are likely to be especially sensitive to future climate change (Andersen et al. 2015). The ranges of invasive ants, which can displace native species, are likely to expand under global warming (Roura-Pascual et al. 2004; Fitzpatrick et al. 2007). Finally, climate change could further intensify the negative effects of disturbance; there is increasing evidence that climate change and disturbance can have complex and sometimes synergistic effects on biodiversity (Travis 2003; Ponce-Reyes et al. 2013; García-Valdés et al. 2015), including for ant communities (Gibb et al. 2015).

Most areas of the Caatinga are subject to high levels of chronic anthropogenic disturbance (CAD) (Singh 1998) due to ongoing extraction of forest products and overgrazing by livestock (Ribeiro et al. 2015). Human population density is very high (i.e., 26 inhabitants per km^2; Ab'Saber 1999; Medeiros et al. 2012) and mostly poor (Ab'Saber 1999) in the Caatinga, and the people are highly dependent on forest resources for their livelihoods (Leal et al. 2005; Sunderland et al. 2009; Gariglio et al. 2010). Recent studies have demonstrated that CAD results in taxonomic and phylogenetic impoverishment of woody plant species (Ribeiro et al. 2015; Ribeiro et al. 2016), biotic homogenization (Ribeiro-Neto et al. 2016), disruptions of plant–animal interactions (Leal et al. 2014b, 2015b), and reduction of soil nutrient stocks (Schulz et al. 2016). The Caatinga biota is also threatened by climate change, with the International Panel of Climate Change forecasting an increase in temperature of 1.8–4 °C, and a reduction in rainfall of 22% by 2100 from a 2000 baseline (Magrin et al. 2014). The range of climatic variation is also predicted to increase (Schär et al. 2004), including a higher frequency of extreme weather events, which might have greater ecological consequences than just the predicted shift in average conditions (Jentsch et al. 2009).

Despite the ecological dominance of ants and their importance as bio-indicators globally, systematic efforts to describe ant diversity in the Caatinga started only during the 1990s, and most available information is from research conducted during the last decade. In this chapter, we present an overview of the diversity, taxonomy, biogeography, and functional composition of the Caatinga ant fauna, along with a synthesis of its response to increased CAD and aridity. We conclude with some future directions for ant research in Caatinga.

3.2 The Caatinga Ant Fauna

The first effort to catalogue the Caatinga ant fauna was by C. R. F. Brandão, who documented 243 ant species occurring in six municipalities of the semiarid northeastern Brazil (Brandão 1995; Ministério do Meio Ambiente 2002). These data were subsequently included in a government initiative for biodiversity conservation, The Caatinga Workshop, in Petrolina, Pernambuco State (Ministério do Meio Ambiente 2002), which became a benchmark for conservation policies in the Caatinga. A decade later, Ulysséa and Brandão (2013) conducted extensive ant sampling in the Caatinga, analyzed wet material from collections, performed additional literature surveys, revised synonyms, and reported a total of 151 ant species from 63 genera and 11 subfamilies. We thus build on this list by adding species collected from recently published ant surveys (Sosa-Calvo et al. 2013; Leal et al. 2014b; Leal et al. 2015a; Ribeiro-Neto et al. 2016; Oliveira et al. 2017) and the specimens in our ant collection (Laboratório de Interação Planta-Animal from the Universidade Federal de Pernambuco) from Parnamirim and Buíque municipalities, both in Pernambuco state.

The database consists of 572 presence–absence records and 276 species/morphospecies from 37 localities in the Caatinga region (Table 3.1). The 276 ant species/morphospecies represent 62 genera and ten subfamilies. The inconsistencies in numbers of genera and subfamilies relative to Ulysséa and Brandão (2013) are due to the following: (1) *Cheliomyrmex morosus*, a species that does not occur in Brazil, has been recognized as a misidentification; and (2) the subfamily Ecitoninae is now included in the subfamily Dorylinae (Brady et al. 2014). The most species-rich genera are *Pheidole* (36 species/morphospecies), *Camponotus* (26), *Cephalotes* (22), *Crematogaster* (21), and *Pseudomyrmex* (20), and 25 genera were each represented by a single species (Table 3.1). Species accumulation has not achieved an asymptote (Fig. 3.1a), and about 80% of the species have been recorded in only one or two localities (Fig. 3.1b). All this indicates that many Caatinga ant species remain to be collected.

The great majority of ant species recorded in the Caatinga are widely distributed in other biomes. For example, the two most frequently recorded species, *Cephalotes pusillus* (Klug 1824) (17 localities) and *Ectatomma muticum* Mayr, 1870 (15), occur in Cerrado, Amazonian forest, and Atlantic Forest. Many of the rarer species, from the genera *Atta*, *Pachycondyla*, and *Strumigenys*, are most characteristic of tropical wet forests (Azevedo-Filho et al. 2003; Gomes et al. 2010), and in the Caatinga are restricted to moister sites, especially in its wetter fringes that border savanna or forest. One of the few known species endemic to the Caatinga is the giant ant *Dinoponera quadriceps* Kempf, 1970 (Fig. 3.2). It is one the most commonly recorded Caatinga species (occurring at 13 of our 37 localities) and is the most

Table 3.1 Ant species of the Caatinga

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
AMBLYOPONINAE			
Fulakora armigera (Mayr, 1887)	Ba6	Native	Ulysséa and Brandão (2013)
Fulakora elongata (Santschi, 1912)	Ba6	Native	Ulysséa and Brandão (2013)
Prionopelta punctulata Mayr, 1866	Mg1	Native	Ulysséa and Brandão (2013)
DOLICHODERINAE			
Azteca alfari Emery, 1893	Ba4, Mg1	Native	Ulysséa and Brandão (2013)
Azteca sp.1	Pe8	Native	LIPA collection
Azteca sp.3	Pe8	Native	LIPA collection
Azteca sp.2	Pe8	Native	LIPA collection
Dolichoderus attelaboides Fabricius, 1775	Ba6	Native	Ulysséa and Brandão (2013)
Dolichoderus diversus Emery, 1894	Ba12	Native	Ulysséa and Brandão (2013)
Dolichoderus germaini Emery, 1894	Pb2	Native	Ulysséa and Brandão (2013)
Dolichoderus lutosus (F. Smith, 1858)	Ba6, Rn	Native	Ulysséa and Brandão (2013)
Dolichoderus quadridenticulatus (Roger, 1862)	Pe8	Native	LIPA collection
Dolichoderus voraginosus Mackay, 1993	Mg1	Native	Ulysséa and Brandão (2013)
Dorymyrmex brunneus (Forel, 1908)	Se	Native	Ulysséa and Brandão (2013)
Dorymyrmex goeldi Forel, 1912	Pe8	Native	LIPA collection
Dorymyrmex pyramicus Forel, 1912	Ba4, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Dorymyrmex sp.1	Pe8	Native	LIPA collection
Dorymyrmex sp.2	Pe8	Native	LIPA collection
Dorymyrmex sp.3	Pe8	Native	LIPA collection
Dorymyrmex sp.4	Pe8	Native	LIPA collection
Dorymyrmex sp.5	Pe8	Native	LIPA collection
Dorymyrmex sp.6	Pe8	Native	LIPA collection
Dorymyrmex spurius Santschi, 1929	Pe7	Native	LIPA collection
Dorymyrmex thoracicus Gallardo, 1916	Ba10, Ba11, Ba5, Ba6, Ba9, Ce1, Pe4, Pe7, Pe8, Se	Native	Ulysséa and Brandão (2013) and LIPA collection

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Forelius brasiliensis (Forel, 1908)	Ba6, Mg1, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Forelius pusillus Santschi, 1922	Mg1	Native	Ulysséa and Brandão (2013) and LIPA collection
Linepithema humile (Mayr, 1868)	Ba6	Native	Ulysséa and Brandão (2013)
Linepithema sp.1	Pe8	Native	LIPA collection
Linepthema neotropicum Wild, 2007	Pe8	Native	LIPA collection
Tapinoma melanocephalum Fabricius, 1793	Al, Ba6, Ba11, Ce1, Mg1, Se	Introduced	Ulysséa and Brandão (2013)
Tapinoma sp.1	Pe8	Native	LIPA collection
Tapinoma sp.2	Pe7	Native	LIPA collection
DORYLINAE			
Acanthostichus serratulus F. Smith, 1858	Mg1	Native	Ulysséa and Brandão (2013)
Acanthostichus sp.1	Pe8	Native	LIPA collection
Eciton hamatum Fabricius, 1782	Ba11	Native	Ulysséa and Brandão (2013)
Labidus coecus (Latreille, 1802)	Ba10, Ba11, Ba6, Ce1, Mg1	Native	Ulysséa and Brandão (2013)
Labidus mars Forel, 1912	Ba6	Native	Ulysséa and Brandão (2013)
Labidus praedator (F. Smith, 1858)	Ba11, Ba6	Native	Ulysséa and Brandão (2013)
Neivamyrmex carettei (Forel, 1913)	Ba11, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Neivamyrmex diana (Forel, 1912)	Ce2	Native	Ulysséa and Brandão (2013)
Neivamyrmex minensis Borgmeier, 1928	Ce1	Native	Ulysséa and Brandão (2013)
Neivamyrmex orthonotus Borgmeier, 1933	Pe7	Native	LIPA collection
Nomamyrmex esenbeckii Westwood, 1842	Ce1	Native	Ulysséa and Brandão (2013)
Nomamyrmex sp.1	Pe7	Native	LIPA collection
ECTATOMMINAE			
Ectatomma brunneum F. Smith, 1858	Ba1, Ba11, Ba2, Ba4	Native	Ulysséa and Brandão (2013)

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Ectatomma edentatum Roger, 1863	Ba10, Ba11, Ba2, Ba3, Ba4, Ba6, Ce1, Mg1, Pe1	Native	Ulysséa and Brandão (2013)
Ectatomma muticum Mayr, 1870	Pe8, Pe8, Pe7, Se, Pi1, Ce1, Ba1, Ba4, Ba6, Ba8, Pi2, Al, Ba15, Ba3, Ba10	Native	Ulysséa and Brandão (2013) and LIPA collection
Ectatomma opaciventre Roger, 1861	Ba4	Native	Ulysséa and Brandão (2013)
Ectatomma suzanae Almeida, 1986	Ba6, Ce2, Mg1	Native	Ulysséa and Brandão (2013)
Ectatomma tuberculatum Olivier, 1792	Ba2	Native	Ulysséa and Brandão (2013)
Gnamptogenys concinna (F. Smith, 1858)	Ba6	Native	Ulysséa and Brandão (2013)
Gnamptogenys moelleri (Forel, 1912)	Ba6, Ba7, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Gnamptogenys regularis Mayr, 1870	Ba6	Native	Ulysséa and Brandão (2013)
Gnamptogenys striatula (Mayr, 1884)	Ba4, Ce1, Ce2, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Gnamptogenys sulcata (F. Smith, 1858)	Ce1, Mg1, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
FORMICINAE			
Brachymyrmex coactus Mayr, 1887	Mg1	Native	Ulysséa and Brandão (2013)
Brachymyrmex patagonicus Mayr, 1868	Mg1, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Brachymyrmex sp.1	Pe8	Native	LIPA collection
Brachymyrmex sp.2	Pe8	Native	LIPA collection
Brachymyrmex sp.3	Pe8	Native	LIPA collection
Brachymyrmex sp.4	Pe8	Native	LIPA collection
Brachymyrmex sp.5	Pe7	Native	LIPA collection
Camponotus (*Myrmaphaenus*) sp.2	Pe7	Native	LIPA collection
Camponotus (*Tanaemyrmex*) sp.1	Pe7	Native	LIPA collection
Camponotus arboreus F. Smith, 1858	Ba4, Ba6, Ce2, Mg1, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Camponotus atriceps F. Smith, 1858	Ba10, Ba6, Ce2, Mg1, Pe1, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Camponotus blandus F. Smith, 1858	Ba10, Ba11, Ba4, Ba6, Ce1, Pe4, Pe7, Pe8, Se	Native	Ulysséa and Brandão (2013) and LIPA collection
Camponotus cameranoi Santschi, 1922	Ba6	Native	Ulysséa and Brandão (2013)
Camponotus cingulatus Mayr, 1862	Ba4, Mg1, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Camponotus crassus Santschi, 1922	Ba10, Ba4, Ba6, Ba9, Ce1, Ce2, Mg1, Pe1, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Camponotus fastigatus Roger, 1863	Ba4, Ce1, Ce2, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Camponotus genatus Santschi, 1922	Ba11, Ba6	Native	Ulysséa and Brandão (2013)
Camponotus germaini Emery, 1903	Mg1	Native	Ulysséa and Brandão (2013)
Camponotus lespesii Forel, 1886	Ba6	Native	Ulysséa and Brandão (2013)
Camponotus melanoticus Santschi, 1939	Ba10, Ba11, Ba6, Mg1, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Camponotus novogranadensis Mayr, 1870	Ba11, Mg1	Native	Ulysséa and Brandão (2013)
Camponotus pallescens Mayr, 1887	Al, Pe4	Native	Ulysséa and Brandão (2013)
Camponotus nr. *Balzani*	Pe7	Native	LIPA collection
Camponotus renggeri Emery, 1894	Ba11, Ba2, Ba3, Mg1, Pi2	Native	Ulysséa and Brandão (2013)
Camponotus rufipes Fabricius, 1775	Ba1, Ba2, Ba6, Ba7	Native	Ulysséa and Brandão (2013)
Camponotus sericeiventris Guérin-Méneville, 1838	Mg1	Native	Ulysséa and Brandão (2013)
Camponotus sp.1	Pe8	Native	LIPA collection
Camponotus sp.2	Pe8	Native	LIPA collection

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Camponotus sp.3	Pe8	Native	LIPA collection
Camponotus sp.4	Pe8	Native	LIPA collection
Camponotus sp.5	Pe8	Native	LIPA collection
Camponotus substitutus Emery, 1894	Ba10, Ce2, Mg1	Native	Ulysséa and Brandão (2013)
Camponotus vittatus Forel, 1904	Ce2, Mg1, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Myrmelachysta sp.1	Ce1, Mg1	Native	Ulysséa and Brandão (2013)
Myrmelachysta sp.2	Pe8	Native	LIPA collection
Myrmelachysta sp.3	Pe7	Native	LIPA collection
Myrmelachysta nodigera Mayr, 1887	Pe8	Native	LIPA collection
Nylanderia sp.1	Ba11, Ba6, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Paratrechina longicornis Latreille, 1802	Ba4	Introduced	Ulysséa and Brandão (2013)
HETEROPONERINAE			
Acanthoponera mucronata Roger, 1860	Ba6, Mg1, Pe8	Native	Ulysséa and Brandão (2013)
MYRMICINAE			
Acromyrmex balzani Emery, 1890	Ba10, Ba15, Ba4, Mg1	Native	Ulysséa and Brandão (2013)
Acromyrmex landolti Forel, 1885	Pe8	Native	LIPA collection
Acromyrmex octospinosus Reich, 1793	Mg1	Native	Ulysséa and Brandão (2013)
Acromyrmex rugosus (F. Smith, 1858)	Ba4, Mg1, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Acromyrmex subterraneus (Forel, 1893)	Ce1, Mg1, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Apterostigma gr. *Pilosum*	Ba6	Native	Ulysséa and Brandão 2013
Atta laevigata F. Smith, 1858	Al, Pe1, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Atta opaciceps Borgmeier, 1939	Ba11, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Atta sexdens Linnaeus, 1758	Ba6, Mg1, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Basiceros scambognathus (Brown, 1949)	Ba2	Native	Ulysséa and Brandão 2013
Blepharidatta conops Kempf, 1967	Ce1	Native	Ulysséa and Brandão (2013)
Carebara sp.	Ce1	Native	Ulysséa and Brandão (2013)
Cephalotes angustus Mayr, 1862	Ba6	Native	Ulysséa and Brandão (2013)
Cephalotes atratus (Linnaeus, 1758)	Ba2, Ba6, Mg1	Native	Ulysséa and Brandão (2013)
Cephalotes betoi (De Andrade & Baroni-Urbani, 1999)	Ba3, Mg1, Pi1	Native	Ulysséa and Brandão (2013)
Cephalotes christopherseni Forel, 1912	Mg1	Native	Ulysséa and Brandão (2013)
Cephalotes clypeatus Fabricius, 1804	Ba1, Ba14, Ba4, Ba6, Pe8, Pi2	Native	Ulysséa and Brandão (2013) and LIPA collection
Cephalotes cordatus F. Smith, 1853	Ba4	Native	Ulysséa and Brandão (2013)
Cephalotes depressus Klug, 1824	Ba6, Pe6	Native	Ulysséa and Brandão (2013)
Cephalotes eduarduli Forel, 1921	Ba1, Mg1	Native	Ulysséa and Brandão (2013)
Cephalotes fiebrigi Forel, 1906	Ba1	Native	Ulysséa and Brandão (2013)
Cephalotes grandinosus (F. Smith, 1860)	Ba6, Mg1	Native	Ulysséa and Brandão (2013)
Cephalotes maculatus (F. Smith, 1876)	Pe3	Native	Ulysséa and Brandão (2013)
Cephalotes minutus (Fabricius, 1804)	Ba11, Ba2, Ba4, Ba6, Pi1, Pi2	Native	Ulysséa and Brandão (2013)
Cephalotes nilpiei De Andrade, 1999	Mg1	Native	Ulysséa and Brandão (2013)
Cephalotes pallens (Klug, 1824)	Ba1, Ba11, Ba4, Ba6, Ce1	Native	Ulysséa and Brandão (2013)

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Cephalotes pavonii Latreille, 1809	Ba4, Ba7, Mg1, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Cephalotes pellans De Andrade, 1999	Ce2, Mg1	Native	Ulysséa and Brandão (2013)
Cephalotes persimilis De Andrade, 1999	Ba13, Mg2, Pe8, Pi1, Pi2	Native	Ulysséa and Brandão (2013) and LIPA collection
Cephalotes pilosus Emery, 1896	Ba1, Ba6	Native	Ulysséa and Brandão (2013)
Cephalotes pinelii Guérin-Méneville, 1844	Pe7	Native	LIPA collection
Cephalotes nr. Cordatus	Pe8	Native	LIPA collection
Cephalotes pusillus (Klug, 1824)	Ba1, Ba10, Ba11, Ba2, Ba3, Ba6, Ce1, Ce2, Ce3, Ce4, Mg1, Pb1, Pe6, Pe8, Pi1, Pi2	Native	Ulysséa and Brandão (2013) and LIPA collection
Cephalotes ustus Kempf, 1973	Ba2, Ba6	Native	Ulysséa and Brandão (2013)
Crematogaster abstinens (Forel, 1899)	Ba10, Ba6, Mg1, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Crematogaster acuta (Fabricius, 1804)	Ba10, Ba8	Native	Ulysséa and Brandão (2013)
Crematogaster ampla Forel, 1912	Mg1	Native	Ulysséa and Brandão (2013)
Crematogaster brasiliensis (Mayr, 1887)	Ba6	Native	Ulysséa and Brandão (2013)
Crematogaster crinosa (Mayr, 1862)	Pe8	Native	LIPA collection
Crematogaster distans (Mayr, 1870)	Ce2	Native	Ulysséa and Brandão (2013)
Crematogaster erecta (Mayr, 1866)	Ba11, Mg1	Native	Ulysséa and Brandão (2013)
Crematogaster evallans (Forel, 1907)	Ba6, Mg1	Native	Ulysséa and Brandão (2013)
Crematogaster montezumia (F. Smith, 1858)	Ba15	Native	Ulysséa and Brandão (2013)
Crematogaster obscurata (Emery, 1895)	Mg1	Native	Ulysséa and Brandão (2013)
Crematogaster nr. Evallans	Pe8	Native	LIPA collection
Crematogaster nr. Obscurata	Pe8	Native	LIPA collection

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Crematogaster rochai (Forel, 1903)	Ce2	Native	Ulysséa and Brandão (2013)
Crematogaster sp.1	Pe8	Native	LIPA collection
Crematogaster sp.2	Pe8	Native	LIPA collection
Crematogaster sp.3	Pe8	Native	LIPA collection
Crematogaster sp.4	Pe8	Native	LIPA collection
Crematogaster sp.5	Pe7	Native	LIPA collection
Crematogaster sp.6	Pe7	Native	LIPA collection
Crematogaster torosa Mayr, 1870	Mg1	Native	Ulysséa and Brandão (2013)
Crematogaster victima F. Smith, 1858	Ba11, Ce2, Mg1, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Cyatta abscondita Sosa-Calvo, Schultz, Brandão, Klingenberg, Feitosa, Rabeling, Bacci, Lopes & Vasconcelos 2013	Ce1	Native	Sosa-Calvo et al. (2013)
Cyphomyrmex gr. rimosus sp. B	Pe8	Native	LIPA collection
Cyphomyrmex olitor Forel, 1893	Ba11	Native	Ulysséa and Brandão (2013)
Cyphomyrmex peltatus (Kempf, 1966)	Ba15	Native	Ulysséa and Brandão (2013)
Cyphomyrmex rimosus (Spinola, 1851)	Ce2, Se	Native	Ulysséa and Brandão (2013)
Cyphomyrmex sp.1	Pe7	Native	LIPA collection
Cyphomyrmex transversus Emery, 1894	Ba2, Ba4, Mg1, Pe7, Pe8, Pi2	Native	Ulysséa and Brandão (2013) and LIPA collection
Eurhopalothrix bruchi (Santschi, 1922)	Ba6	Native	Ulysséa and Brandão (2013)
Hylomyrma balzani Emery, 1894	Ba11, Ba6, Ce1	Native	Ulysséa and Brandão (2013)
Kalathomyrmex emeryi Forel, 1907	Ba12, Pe2, Pe8, Pi1	Native	Ulysséa and Brandão (2013) and LIPA collection
Kalathomyrmex sp.1	Pe8	Native	LIPA collection
Megalomyrmex drifti Kempf, 1961	Ba6	Native	Ulysséa and Brandão (2013)
Megalomyrmex silvestrii (Wheeler, 1909)	Pe3	Native	Ulysséa and Brandão (2013)

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Monomorium floricola Jerdon, 1851	Ba6, Pe7	Introduced	Ulysséa and Brandão (2013); LIPA collection
Myrmicocrypta sp.1	Ba2, Ba4, Ce1, Pi1	Native	Ulysséa and Brandão (2013)
Nesomyrmex sp.1	Ba1, Ba2, Ce2, Pi2	Native	Ulysséa and Brandão (2013)
Ochetomyrmex sp.1	Ba6	Native	Ulysséa and Brandão (2013)
Octostruma rugifera (Mayr, 1887)	Ba2, Ba6	Native	Ulysséa and Brandão (2013)
Oxyepoecus browni Albuquerque & Brandão, 2004	Ba6	Native	Ulysséa and Brandão (2013)
Oxyepoecus regularis Ulysséa & Brandão, 2012	Ba11, Ba6	Native	Ulysséa and Brandão (2013)
Oxyepoecus vezenyii Forel, 1907	Ba6, Ce2	Native	Ulysséa and Brandão (2013)
Pheidole diligens F. Smith, 1858	Ce2, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Pheidole fallax Mayr, 1870	Ba4	Native	Ulysséa and Brandão (2013)
Pheidole fera Santschi, 1925	Pe8	Native	LIPA collection
Pheidole fowleri Wilson, 2003	Mg1	Native	Ulysséa and Brandão (2013)
Pheidole obscurithorax Naves, 1985	Ba11, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Pheidole pr. Fracticeps	Pe8	Native	LIPA collection
Pheidole pr. Jelskii	Pe7	Native	LIPA collection
Pheidole radoszkowskii (Mayr, 1884)	Ba11, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Pheidole rochai Forel, 1912	Ba11	Native	Ulysséa and Brandão (2013)
Pheidole rufipilis Forel, 1908	Mg1	Native	Ulysséa and Brandão (2013)
Pheidole sp.1	Pe8	Native	LIPA collection
Pheidole sp.10	Pe8	Native	LIPA collection
Pheidole sp.11	Pe8	Native	LIPA collection
Pheidole sp.12	Pe8	Native	LIPA collection

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Pheidole sp.13	Pe8	Native	LIPA collection
Pheidole sp.14	Pe8	Native	LIPA collection
Pheidole sp.15	Pe8	Native	LIPA collection
Pheidole sp.16	Pe8	Native	LIPA collection
Pheidole sp.17	Pe8	Native	LIPA collection
Pheidole gr. *diligens* sp.18	Pe7	Native	LIPA collection
Pheidole gr. *flavens* sp.19	Pe7	Native	LIPA collection
Pheidole sp.2	Pe8	Native	LIPA collection
Pheidole sp.20	Pe7	Native	LIPA collection
Pheidole sp.21	Pe7	Native	LIPA collection
Pheidole sp.22	Pe7	Native	LIPA collection
Pheidole sp.23	Pe7	Native	LIPA collection
Pheidole sp.24	Pe7	Native	LIPA collection
Pheidole sp.3	Pe8	Native	LIPA collection
Pheidole sp.4	Pe8	Native	LIPA collection
Pheidole sp.5	Pe8	Native	LIPA collection
Pheidole sp.6	Pe8	Native	LIPA collection
Pheidole sp.7	Pe8	Native	LIPA collection
Pheidole sp.8	Pe8	Native	LIPA collection
Pheidole sp.9	Pe8	Native	LIPA collection
Pheidole triconstricta Forel, 1886	Pe8	Native	LIPA collection
Pogonomyrmex naegelii Emery, 1878	Ba6	Native	Ulysséa and Brandão (2013)
Procryptocerus goeldii Forel, 1899	Ba6	Native	Ulysséa and Brandão (2013)
Rogeria alzatei Kugler, 1994	Ba6	Native	Ulysséa and Brandão (2013)
Rogeria blanda (Smith, 1858)	Ba6, Ce2, Mg1	Native	Ulysséa and Brandão (2013)
Solenopsis geminata (Fabricius, 1804)	Ba2, Ba4, Mg1, Pe7, Pi2	Native	Ulysséa and Brandão (2013) and LIPA collection
Solenopsis globularia (Smith, 1858)	Ba4, Ba5, Ce2, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
Solenopsis invicta Buren, 1972	Pe5	Native	Ulysséa and Brandão (2013)
Solenopsis saevissima (Smith, 1855)	Ba3, Mg1, Pi2	Native	Ulysséa and Brandão (2013)
Solenopsis sp.1	Pe8	Native	LIPA collection
Solenopsis sp.2	Pe8	Native	LIPA collection

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Solenopsis sp.3	Pe8	Native	LIPA collection
Solenopsis sp.4	Pe8	Native	LIPA collection
Solenopsis sp.5	Pe8	Native	LIPA collection
Solenopsis sp.6	Pe8	Native	LIPA collection
Solenopsis tridens Forel, 1911	Ba16, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Solenopsis virulens (Smith, 1858)	Pe8	Native	LIPA collection
Strumigenys elongata Roger, 1863	Ce2	Native	Ulysséa and Brandão (2013)
Strumigenys lilloana (Brown, 1950)	Ba6, Mg1, Pi2	Native	Ulysséa and Brandão (2013)
Strumigenys louisianae Roger, 1863	Ba6	Native	Ulysséa and Brandão (2013)
Strumigenys schmalzi Emery, 1906	Ba6	Native	Ulysséa and Brandão (2013)
Tetramorium bicarinatum Nylander, 1846	Pi1	Introduced	Ulysséa and Brandão (2013)
Tetramorium sp.1	Pe8	Native	LIPA collection
Trachymyrmex sp.1	Al, Ba1, Ba2, Ba6, Ce1, Se	Native	Ulysséa and Brandão (2013)
Trachymyrmex sp.2	Pe8	Native	LIPA collection
Wasmannia auropunctata (Roger, 1863)	Ba11, Ba5, Ba6, Ce2, Mg1, Pe1	Native	Ulysséa and Brandão (2013)
Wasmannia lutzi Forel, 1908	Ba6, Mg1	Native	Ulysséa and Brandão (2013)
Wasmannia rochai (Forel, 1912)	Mg1	Native	Ulysséa and Brandão (2013)
Wasmannia sigmoidea Mayr, 1884	Ba11	Native	Ulysséa and Brandão (2013)
PONERINAE			
Anochetus emarginatus Fabricius, 1804	Ce1	Native	Ulysséa and Brandão (2013)
Anochetus gr. Inermis	Ba6	Native	Ulysséa and Brandão (2013)
Centromyrmex brachycola Roger, 1861	Pi2	Native	Ulysséa and Brandão (2013)
Dinoponera quadriceps Kempf, 1971	Ba1, Ba10, Ba15, Ba4, Ba5, Ba6, Ce1, Ce2, Pe7, Pe8, Pi1, Pi2, Se	Native	Ulysséa and Brandão (2013) and LIPA collection
Hypoponera sp.1	Ba2, Ba4, Ba6, Pi1	Native	Ulysséa and Brandão (2013)

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Leptogenys sp.1	Pe7	Native	LIPA collection
Odontomachus bauri Emery, 1892	Ba4, Ba5, Ce1, Ce2, Mg1	Native	Ulysséa and Brandão (2013)
Odontomachus brunneus Patton, 1894	Ba6	Native	Ulysséa and Brandão (2013)
Odontomachus chelifer Latreille, 1802	Ba6	Native	Ulysséa and Brandão (2013)
Odontomachus haematodus Linnaeus, 1758	Ba4, Ba6, Se	Native	Ulysséa and Brandão (2013)
Odontomachus sp.1	Pe8	Native	LIPA collection
Neoponera bucki Borgmeier, 1927	Ba6	Native	Ulysséa and Brandão (2013)
Neoponera magnifica Borgmeier, 1929	Ba6	Native	Ulysséa and Brandão (2013)
Neoponera venusta Forel, 1912	Ba6	Native	Ulysséa and Brandão (2013)
Neoponera villosa Fabricius, 1804	Ba6, Mg1	Native	Ulysséa and Brandão (2013)
Pachycondyla striata F. Smith, 1858	Ba6	Native	Ulysséa and Brandão (2013)
Platythyrea sp.1	Ce2	Native	Ulysséa and Brandão (2013)
Platythyrea sp.2	Pe7	Native	LIPA collection
Thaumatomyrmex atrox Weber, 1939	Ba2, Ba6	Native	Ulysséa and Brandão (2013)
Thaumatomyrmex contumax Kempf, 1975	Ba2, Pe2	Native	Ulysséa and Brandão (2013)
Thaumatomyrmex mutilatus Mayr, 1887	Ce1, Ce2, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection
PROCERATIINAE			
Discothyrea sexarticulata Borgmeier, 1954	Ba6	Native	Ulysséa and Brandão (2013)
PSEUDOMYRMICINAE			
Pseudomyrmex acanthobius Santschi, 1922	Ce2, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Pseudomyrmex elongatulus Forel, 1912	Ba6	Native	Ulysséa and Brandão (2013)
Pseudomyrmex elongatus Mayr, 1870	Pe7, Pe8	Native	LIPA collection
Pseudomyrmex flavidulus F. Smith, 1858	Ba4, Ba6, Mg1	Native	Ulysséa and Brandão (2013)

(continued)

Table 3.1 (continued)

SUBFAMILY Ant species	Code for sampling municipality	Origin	Data source
Pseudomyrmex gr. pallidus sp.1	Pe8	Native	LIPA collection
Pseudomyrmex gr. pallidus sp.2	Pe8	Native	LIPA collection
Pseudomyrmex gr. pallidus sp.3	Pe8	Native	LIPA collection
Pseudomyrmex gr. pallidus sp.4	Pe8	Native	LIPA collection
Pseudomyrmex gr. pallidus sp.5	Pe8	Native	LIPA collection
Pseudomyrmex gracilis (Fabricius, 1804)	Ba4, Ba6, Ce1, Mg1, Pe7, Pe8	Native	Ulysséa and Brandão (2013) and LIPA collection
Pseudomyrmex laevifrons Ward, 1989	Pe8	Native	LIPA collection
Pseudomyrmex oculatus F. Smith, 1855	Ba4	Native	Ulysséa and Brandão (2013)
Pseudomyrmex pisinnus Ward, 1989	Ce1	Native	Ulysséa and Brandão (2013)
Pseudomyrmex nr. Acanthobius	Pe8	Native	LIPA collection
Pseudomyrmex schuppi Forel, 1901	Ba6, Mg1	Native	Ulysséa and Brandão (2013)
Pseudomyrmex simplex (F. Smith, 1877)	Ba4	Native	Ulysséa and Brandão (2013)
Pseudomyrmex sp.6	Pe8	Native	LIPA collection
Pseudomyrmex sp.7	Pe8	Native	LIPA collection
Pseudomyrmex tenuis Fabricius, 1804	Ba6	Native	Ulysséa and Brandão (2013)
Pseudomyrmex termitarius F. Smith, 1855	Al, Ba6, Ba7, Ba9, Mg1, Pe7	Native	Ulysséa and Brandão (2013) and LIPA collection

The list was based on Ulysséa and Brandão 2013 and in the ant collection of the Plant-Animal Interactions Lab, Botany Department, Universidade Federal de Pernambuco, Recife, PE, Brazil totaling 37 localities

Legend for sampling municipality code: *Al* Olho D'Água do Casado, Piranhas and Delmiro Gouveia (Alagoas), *Ba1* Itaberaba, *Ba2* Maracás, *Ba3* Santa Rita de Cássia, *Ba4* Itatim, *Ba5* Contendas do Sincorá and Tanhaçú, *Ba6* Milagres, *Ba7* Euclides da Cunha, *Ba8* Mucururé, *Ba9* Rodelas, *Ba10* Tucano, *Ba11* Boa Vista do Tupim, *Ba12* Juazeiro da Bahia, *Ba13* Feira de Santana, *Ba14* Ipirá, *Ba15* Paulo Afonso, *Ba16* Senhor do Bonfim (Bahia), *Ce1* Crateús, *Ce2* Pentecoste, *Ce3* Barbalha, *Ce4* Chapada do Araripe, Ceará state, *Mg1* Manga, *Mg2* Januária (Minas Gerais), *Pb1* Coremas, *Pb2* Guarabira (Paraíba), *Pe1* Bezerros, Caruaru, Gravatá, and Pombos, *Pe2* Araripina, *Pe3* Caruaru, *Pe4* Serra Talhada, *Pe5* Santa Cruz da Baixa Verde, *Pe6* Floresta, *Pe7* Parnamirim, *Pe8* Buíque (Pernambuco), *Pi1* Canto do Buriti, *Pi2* Oeiras, Piauí state, *Rn* João Câmara (Rio Grande do Norte), *Se* Canindé do São Francisco (Sergipe)

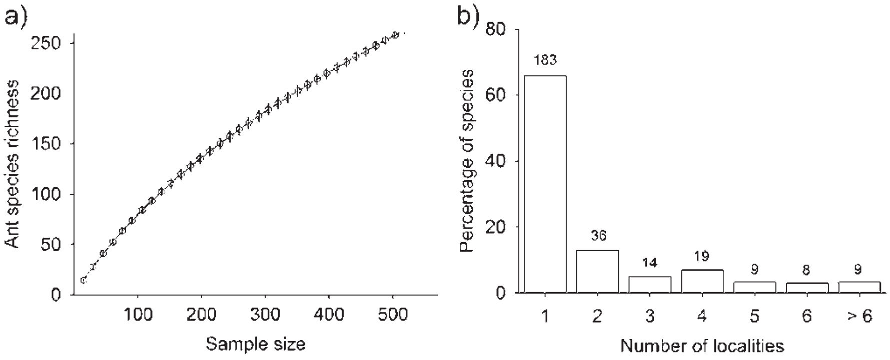
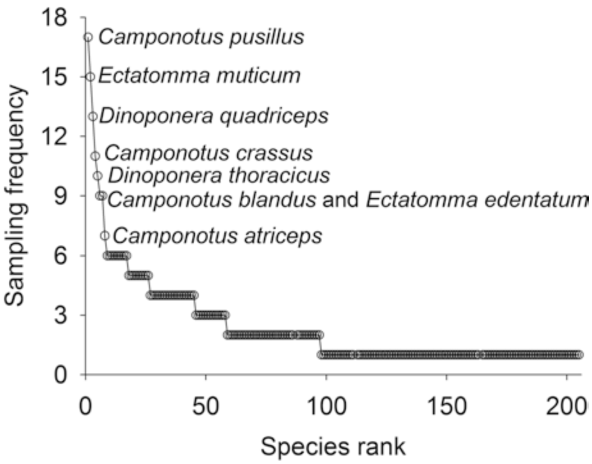


Fig. 3.1 (**a**) Ant species accumulation curve for 37 localities in the Caatinga, based on 571 species records. Vertical lines depict 95% confidence intervals. (**b**) Occurrence distribution of the 276 ant species across 37 localities in the Caatinga. Numbers above bars depict the number of species in each category

Fig. 3.2 Rank frequency plot of 204 ant species from 37 localities in the Caatinga. Data refer to the number of localities where a species has been sampled. The eight most frequently recorded species are indicated



important disperser of myrmecochorous seeds in the Caatinga (Leal et al. 2014b, c). Another notable Caatinga endemic is the leaf-cutter *Atta opaciceps*. This is the most abundant leaf-cutting ant in Catimbau, and its colonies can consume more than 20% of leaf biomass in their foraging areas (Siqueira et al. 2017).

3.3 Functional Composition

Ants are often classified in different functional groups schemes, according to their responses to the environment (e.g., Andersen 1995, 1997; Arnan et al. 2012). The most successful and widely used is the global model of ant functional groups

Table 3.2 Ant functional-group classification in relation to stress and disturbance (Andersen 1995, 1997, 2000), modified for the neotropical region

Functional group	Most common taxa
Dominant Dolichoderinae (DD)	*Azteca*, *Dorymyrmex*, *Forelius*, *Linepithema*
Subordinate Camponotini (SCa)	*Camponotus*
Generalized Myrmicinae (GM)	*Crematogaster*, *Monomorium*, *Pheidole*, *Solenopsis* (subgenus *Diplorhoptrum*)
Opportunists (Op)	*Brachymyrmex*, *Dinoponera*, *Ectatomma*, *Gnamptogenys*, *Nesomyrmex*, *Nylanderia*, *Odontomachus*, *Tapinoma*, *Tetramorium*
Cryptic species (CS)	*Acanthostichus*, *Rogeria*, *Strumigenys*, *Wasmannia*
Specialized predators (SP)	*Leptogenys*, *Thaumatomyrmex*
Army ants (Aa)	*Eciton*, *Labidus*, *Neivamyrmex*, *Nomamyrmex*
Fire ants (Fa)	*Solenopsis* (subgenus *Solenopsis*)
Higher Attini (HA)	*Acromyrmex*, *Atta*
Lower Attini (LA)	*Apterostigma*, *Cyphomyrmex*, *Kalathomyrmex*, *Mycetophylax*, *Trachymyrmex*
Tree specialists (TS)	*Cephalotes*, *Myrmelachista*, *Pseudomyrmex*

proposed by Australian myrmecologists (Andersen 1995, 1997, 2000; Hoffmann and Andersen 2003) that classifies ants according to biogeographical scale responses to environmental stress and disturbance. This model has been adapted for the Caatinga (Oliveira et al. 2017) and other neotropical regions in general (Leal et al. 2012; Paolucci 2016) (Table 3.2), as follows.

Dominant Dolichoderinae are those species at the top of dominance hierarchies in the most productive environments, which in the case of ants, are hot, open, and structurally simple environments; they exert a strong competitive influence on other ants. They are often absent from heavily shaded habitats. **Subordinate Camponotini** (exclusively species of *Camponotus* in the neotropics) are species competitively subordinate in the presence of Dominant Dolichoderinae, but can be competitively dominant in their absence. They are ubiquitous and very species rich; however, their relative abundance in any community is generally low. They have large body size, and often display nocturnal foraging. **Generalized Myrmicinae** have a much broader distribution in relation to environmental stress and disturbance than Dominant Dolichoderinae, and tend to predominate in moderately, rather than highly, productive environments for ants (Andersen 1995). They are often the most abundant ants in warm environments where Dominant Dolichoderinae are absent. In the Caatinga this group includes species of *Solenopsis* subgenus *Diplorhoptrum*, which behave like species of *Monomorium* elsewhere in the world (A.N. Andersen, personal observation), in addition to species of *Pheidole* and *Crematogaster*. **Opportunists** are unspecialized, behaviorally submissive species, often with wide habitat distributions. They predominate only at sites where stress or disturbance severely limits ant productivity and diversity, and consequently where behavioral dominance is low. The most common genus in the Caatinga is *Ectatomma*. **Cryptic species** are small to minute ants, predominantly from the subfamilies Myrmicinae and Ponerinae, which nest and forage almost exclusively within soil and litter, and therefore probably have little interaction with other ants. **Specialist predators** are medium- to large-sized species that are specialist predators of other arthropods. They tend to have little competitive interaction with other ants due to their specialized diets and typically low population densities. **Army ants** are highly aggressive, nomadic species with legionary recruitment. *Fire ants* are ferocious species of *Solenopsis* subgenus *Solenopsis* that have their origin in South America and become pests worldwide. **Higher Attini** are highly active and aggressive, polymorphic, species with large colony sizes that use fresh leaves to cultivate a symbiotic fungus; they are often favored by disturbance. **Lower Attini** are monomorphic, non-aggressive species with small colony sizes that use dead plant material and insect feces and corpses to cultivate a symbiotic fungus. They usually are highly sensitive to disturbance. Finally, **Tree specialists** nest exclusively in trees, and forage primarily there.

Here we quantify patterns of functional group composition at three locations where ants have been intensively surveyed: Pentecoste municipality (3°48′S, 39°20′W; Nunes et al. 2011) in Ceará state, Parnamirim municipality in Pernambuco (8°5′S, 39°34′W; Ribeiro-Neto et al. 2016; Oliveira et al. 2017), and Catimbau National Park also in Pernambuco (8.61667°S, 37.15°W, Arcoverde et al. unpublished data). These localities differ in rainfall pattern, soil type, vegetation structure, and disturbance history. Pentecoste has the highest rainfall (~1400 mm per year), which is uniform throughout the area, soils are mostly clay, and the vegetation is a dry forest, with a dense tree layer up to 8 m. Human pressure is apparently lower than at the other two localities (Nunes et al. 2011). Annual rainfall is a uniform 550 mm at the Parnamirim locality, where there is a mix of both sandy and clay soils. The vegetation has a sparse tree layer (up to 6 m tall) in areas with sandy soils and a denser tree layer in clay soils. Shrubs and herbs are more common in sandy soils, and disturbance is more intense in areas with clay soils (Oliveira et al. 2017). Catimbau has a steep rainfall gradient (from 1100 to 480 mm per year), soils are predominantly sandy, and tree cover increases with increasing rainfall (Rito et al. 2017). Shrubs and herbs predominate in dryer areas, and human pressure is higher in Catimbau than in the other two localities.

Our results show Generalized Myrmicinae as the most common and species-rich functional group in the Caatinga, followed by Opportunists and Subordinate Camponotini (Fig. 3.3). These results are in agreement with the Andersen's global model that predicts Generalized Myrmicinae to be numerically dominant in warm environments where Dominant Dolichoderinae does not dominate. Although the high temperatures and generally open habitats of the Caatinga favor Dominant Dolichoderinae, such species require a high availability of liquid carbohydrates in the form of honeydew secretions to fuel their dominance (Davidson 1997; Blüthgen and Fiedler 2004; Blüthgen et al. 2006), which does not occur in Caatinga vegetation (Câmara et al. unpublished data). Our results also highlight the prominence of Tree specialists in the Caatinga, which contributed >10% of total species (Fig. 3.3b).

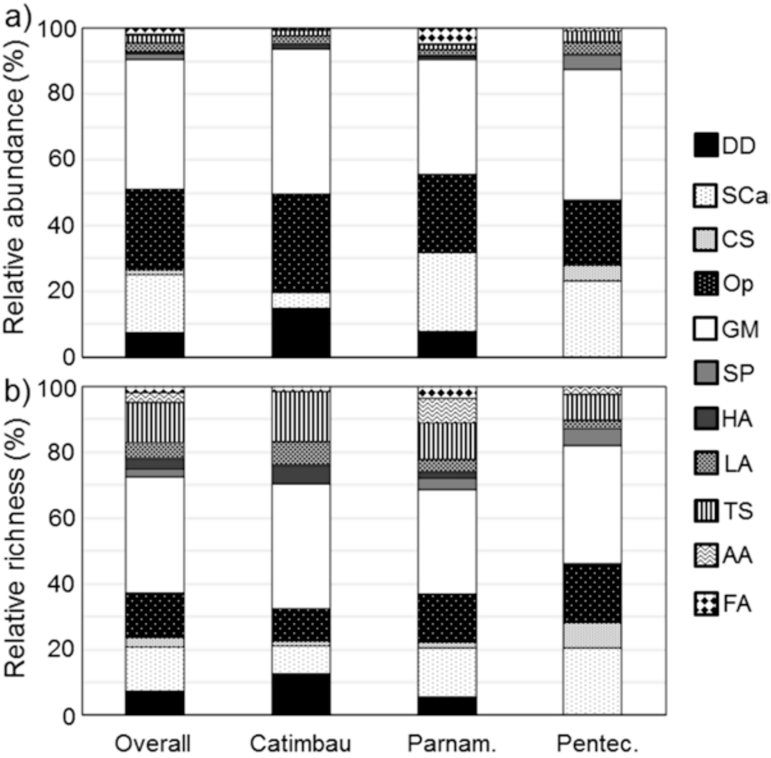


Fig. 3.3 Ant functional group composition (**a** relative abundance; and **b** relative species richness) at three Caatinga localities (Catimbau, Parnamirim [Parnam.], Pentecoste [Pentec.]), and considering the three localities together (Overall). The functional groups are: *AA* Army ants, *CS* Cryptic species, *DD* Dominant Dolichoderinae, *FA* fire ants, *GM* Generalized Myrmicinae, *HA* Higher Attini, *LA* Lower Attini, *Op* Opportunists, *SCa* Subordinate Camponotini, *SP* Specialist predators, *TS* Tree specialist

Their very low abundance (Fig. 3.3a) is likely an artefact of sampling based on pitfall traps in the ground.

Functional-group composition varied markedly among localities in terms of abundance ($\chi^2 = 53.6$, $p < 0.0001$, d$f = 20$, Fig. 3.3a), but only marginally so with species richness ($\chi^2 = 30.3$, $p = 0.06$, d$f = 20$, Fig. 3.3b). Notably, the major functional groups Dominant Dolichoderinae, Fire ants, and Higher Attini were not recorded at all in Pentecoste, and no Specialist predators or Army ants were recorded in Catimbau (Fig. 3.3). Significantly, Cryptic species are most abundant at Pentecoste, likely because of a more-developed litter layer due to higher tree cover (Leal et al. 2012). The more shaded conditions in Pentecoste can also explain the absence of Dominant Dolichoderinae, Higher Attini species, and Fire ants, as they all require open habitats (Tschinkel and King 2013; Leal et al. 2014a). Variation in soil type also contributes to variation in functional group composition. For instance, ant functional composition varies markedly between sandy and clay soils in the Parnamirim locality (Oliveira et al. 2017).

3.4 Responses to Anthropogenic Disturbance

Activities such as firewood collection, exploitation of non-timber products, hunting, and grazing by livestock are considered the main sources of CAD in the Caatinga (Brasil-MMA 2013; Leal et al. 2015b; Ribeiro et al. 2015, 2016). Recent studies have addressed the issue of impacts of CAD on ant biodiversity in the Parnamirim (Oliveira et al. 2017) and Catimbau (Arcoverde et al. unpublished data) localities by assessing ants' responses to disturbance along CAD gradients. Oliveira et al. (2017) also considered the role of soil type as a modulator of ant responses to disturbances. Using five CAD surrogates (density of people and livestock, and proximity to urban center, houses, and roads) across two types of soil (sandy and clay), it was found that CAD surrogates influenced ant species richness and ant functional group abundance in very different ways, but only secondarily to the effect of soil type (Table 3.3). The different CAD surrogates appeared to influence ant species richness in different ways—some negatively and others positively. Ant species also varied in their responses to CAD, with some decreasing in abundance and others increasing. The abundances of Specialist predators and Fire ants consistently decreased with increasing CAD, whereas the abundance of Opportunists increased (Table 3.3).

Table 3.3 Relative importance of soil type and five chronic anthropogenic disturbance metrics as predictors of total ant species richness and ant functional group abundance in Caatinga

Response variable	Soil	People	Stock	Proximity to road	Proximity to farm	Proximity to city
Total species richness	0.36 (Sa)	−0.308	0.404	−0.332	0.651	−0.538
Army ants	0.28 (C/Sa)	0.297	−0.274	0.346	0.284	−0.819
Dominant Dolichoderinae	0.62 (Sa)	−0.333	−0.687	0.38	0.886	0.297
Fire ants	0.29 (Sa)	−0.421	−0.296	0.325	−0.927	−0.815
Generalized Myrmicinae	0.39 (C)	−0.316	−0.44	−0.292	−0.728	0.396
Lower Attini	0.39 (Sa)	−0.316	0.44	−0.292	−0.728	−0.396
Opportunists	0.98 (Sa)	0.532	0.507	0.296	−0.999	−0.966
Specialist predators	0.84 (Sa)	−0.318	−0.549	0.33	−0.569	−0.769
Subordinate Camponotini	0.27 (C)	−0.926	−0.282	0.93	−0.349	−0.997
Tree specialists	0.55 (C)	−0.372	0.348	−0.505	0.29	0.425

Relative importance varies between 0 and 1, with the higher the values, the higher their importance in predicting response variables, and the sign (+/−) indicates the direction of the effects. The letter (*C* clay soil, *Sa* sandy soil) depicts the soil type with higher functional group abundance. The functional groups Higher Attini and Cryptic Species have not been analyzed because they were represented by single species

Ant responses to CAD varied markedly with soil type (Fig. 3.4). On clay soil, variation in both taxonomic and functional-group composition were related to most CAD surrogates, while on sandy soil only density of people plus distance to city (taxonomic composition; Fig. 3.4c) and density of people (functional composition; Fig. 3.4d) were significant explanatory variables. Ant functional-group composition showed predictable winner–loser replacement on clay soils, with the abundance of Opportunists (disturbance winners) increasing with CAD, and that of Specialist predators (disturbance losers) decreasing (Fig. 3.4f). The stronger response of ant communities to CAD on clay soils is likely related to higher-intensity land use, and therefore greater disturbance, on clay than on sandy soils.

In the Catimbau study (Arcoverde et al. unpublished data) all sites were on sandy soil. Neither overall richness nor abundance varied with CAD, but community composition did. The abundances of Dominant Dolichoderinae and Subordinate Camponotini increased and decreased, respectively, with increasing CAD. Both studies therefore revealed significant change in the ant taxonomic and functional composition with disturbance, with predictable winner–loser replacement. Disturbance winners were highly generalized species with wide environmental tolerances (Opportunists) and species favoring open habitats (Dominant Dolichoderinae). In contrast, highly specialized species such as Specialist predators were disturbance losers. These patterns of winner–loser replacement in relation to disturbance occur throughout the world (Andersen 1997; Hoffmann and Andersen 2003; Leal et al. 2012).

3.5 Responses to Climate Change

As the world temperature rises and rainfall patterns change, concern about the impact of climate change on biodiversity increases. One way of investigating the ecological consequences of climate change is to examine ecological change over climate gradients, using an approach that substitutes space for time (Koch et al. 1995; Williams et al. 1995; Canadell et al. 2002; De Frenne et al. 2013). Catimbau is an ideal locality for such a study, given that mean annual rainfall varies from 1100 to 480 mm in an area of just 607 km^2, representing virtually the entire rainfall variation in the Caatinga.

Neither species richness nor abundance varied with rainfall at the Catimbau sites, but both species and functional-group composition did (Fig. 3.5). Changes in the community composition were driven by *Cephalotes pusillus*, *Pheidole* sp. C, *Pseudomyrmex* sp. B, *Pheidole* sp. L, and *Azteca* sp. A, rare species mainly associated with high rainfall areas. For functional groups, the abundance of Tree specialists and Opportunists declined and increased, respectively, with increasing aridity. These results suggest that aridity leads to a vulnerability of rare and specialized species and functional groups, and benefits more generalist ones, such as the Opportunists group. This study also investigates the potential impacts of CAD (for

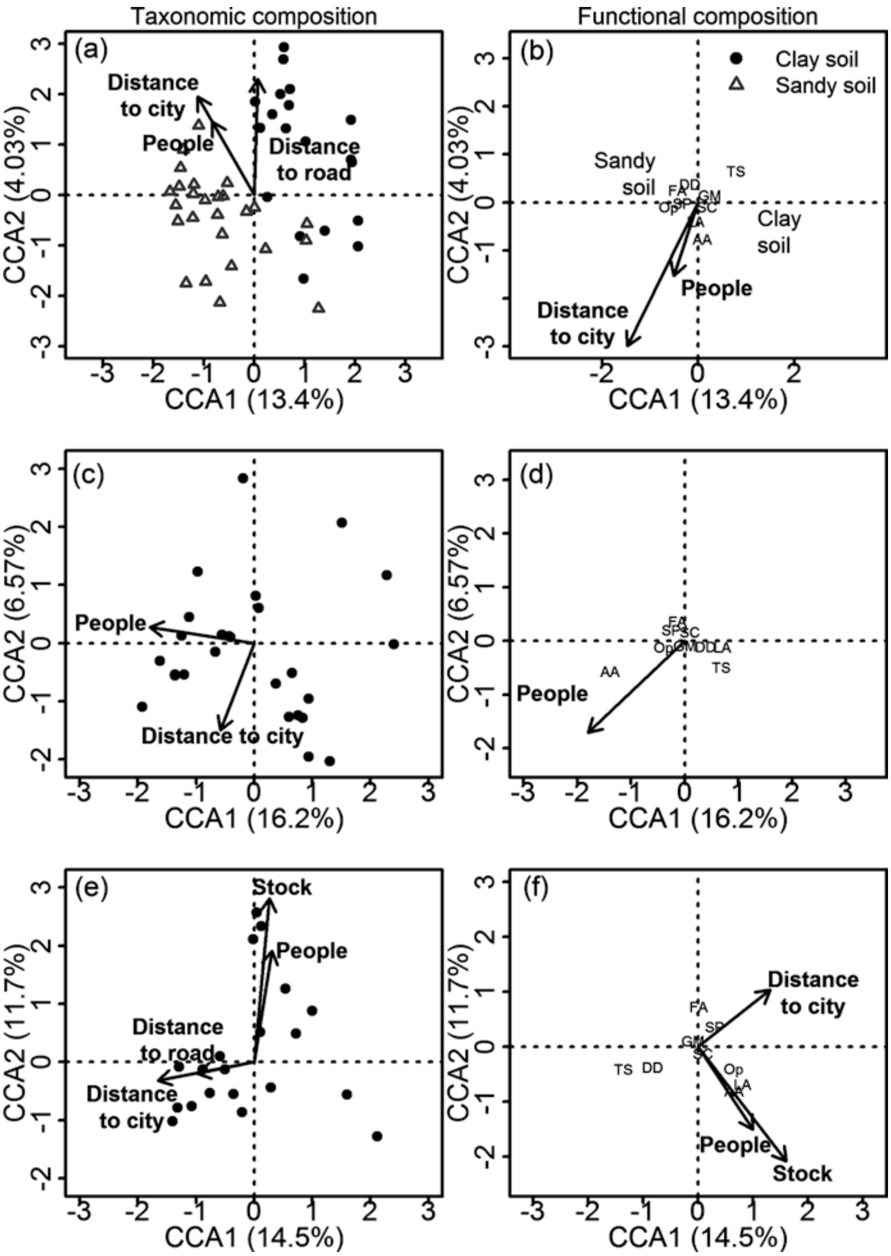


Fig. 3.4 Canonical correspondence analysis of 47 sites near Parnamirim based on taxonomic (**a**, **c**, **e**) and functional group (**b**, **d**, **f**) composition, with significant ($p < 0.05$ based on 10,000 aleatorizations) disturbance metrics shown as vectors. The different panels represent different soil types: (**a**, **b** both sand clay; **c**, **d** sand; **e**, **f** clay) (Adapted from Oliveira et al. 2017)

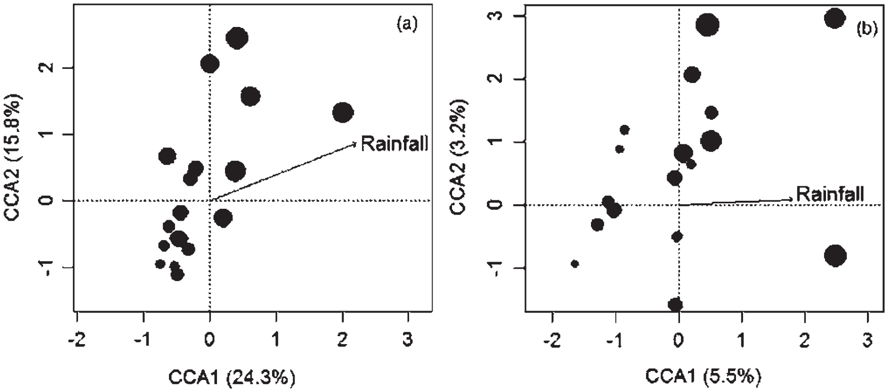


Fig. 3.5 Canonical correspondence analysis of 20 sites in Catimbau National Park based on taxonomic (**a**) and functional group (**b**) composition, with rainfall fitted as vectors. Circle size increases with increasing rainfall (Arcoverde et al. unpublished data)

disturbance results refer to Sect. 3.4) associated with climate change; however, the system failed to find an interaction between both factors.

Although Arcoverde et al. (unpublished data) did not find an interaction between rainfall and disturbance in Catimbau, this scenario might change in the future. Previous studies have shown the negative synergetic impact of disturbance and climate change on biodiversity (Travis 2003; García-Valdés et al. 2015) and the development of this project will help to shed some light in this matter for the Caatinga biome. Moreover, climate change can interact with disturbance in unexpected ways that affect the structure of ant communities. In this regard, ant communities from areas with hot, arid climates are more likely to be at greater risk (Gibb et al. 2015).

3.6 Conclusion

The true size of the Caatinga ant fauna is without doubt substantially higher than the 276 species that we have listed. The species accumulation curve shows no sign of approaching an asymptote. The great majority of the Caatinga has not been intensively sampled for ants, and the intensive sampling that has been conducted reveals high rates of species turnover between localities. For example, of the total 50 named species in the Parnamirim and Catimbau studies, only 11 (22%) occurred in both locations. The total Caatinga ant fauna is likely to approach or even exceed 400 species. However, this still makes it highly depauperate in a neotropical context, as illustrated by comparative data at a site scale. For example, the typical site species richness in the Caatinga of 15–25 (Oliveira et al. 2017; Arcoverde et al. unpublished data) is less than half that of the minimum values for Cerrado (Campos et al. 2011; Vasconcelos et al. unpublished data). The very low level of endemism of the ant fauna is also highly notable. Such low diversity and endemism is in stark contrast to the Caatinga flora (Queiroz 2006; Queiroz and Lavin 2011) and other faunal groups, including mammals (Gutiérrez and Marinho-Filho 2017), reptiles (Rodrigues 1996, 2003), and bees (Zanella and Martins 2003).

Intriguingly, the Caatinga ant fauna appears to have a very different biogeographic origin to that of the Caatinga flora. The great majority of Caatinga ant species also occur in Cerrado, such that the Caatinga ant fauna is essentially a subset of the far more diverse Cerrado fauna. It seems clear that the Caatinga ant fauna has been relatively recently derived from the Cerrado fauna. In contrast, the Caatinga flora is an ancient (ca. 30 million years old) arid-adapted one that has very few affinities with the Cerrado flora (Pennington et al. 2009). This raises the question, if Caatinga plants came from ancient arid-adapted vegetation, then why didn't comparable ants come as well? Perhaps they did, but were replaced by Cerrado elements during the wetter and cooler climate and associated humid vegetation that has been inferred for the Caatinga region during the Late Pleistocene and Early Holocene (Werneck 2011; Werneck et al. 2011).

Most of the endemic Caatinga flora is associated with sandy soils, which were far more widespread before the Early Quaternary (Werneck 2011; Werneck et al. 2011). This is also the case for snakes and lizards: for example, 27% of all Caatinga squamate species are restricted to the São Francisco sand dunes, which cover <1% of the total Caatinga area (Rodrigues 1996, 2003). The extent to which endemism within the Caatinga ant fauna is associated with sandy soils is unknown, but the São Francisco sand dunes are a priority for further sampling, and may throw important light on the biogeographic history of the Caatinga ant fauna.

The Caatinga biome suffers from extensive anthropogenic disturbance, and has only a very small proportion protected in conservation regions. We have shown that both the species and functional-group composition of the ant fauna is sensitive to disturbance. This has important implications for the many ecosystem services provided by ants. For example, the Caatinga is a global hotspot for myrmecochory, with a large proportion of species dependent on ants for seed dispersal (Leal et al. 2015a), and the ant species providing the highest-quality dispersal services, *Dinoponera quadriceps*, is highly sensitive to disturbance (Leal et al. 2014b, c). Seed removal by *D. quadriceps* has been shown to decrease with increasing levels of disturbance, with disturbance reducing mean dispersal distance four-fold (Leal et al. 2014b). From a conservation standpoint, the preservation of Caatinga areas with high biodiversity value, such as Catimbau National Park and other areas that currently hold significant areas of relatively undisturbed vegetation, are priorities for maintaining Caatinga biodiversity into the future.

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Chapter 4

Diversity, Distribution, and Conservation of the Caatinga Fishes: Advances and Challenges

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Abstract The Caatinga, located in the semiarid region of northeastern Brazil, is dominated by a seasonally dry tropical forest and encompasses a relatively modest hydrographic network, characterized by intermittent water courses. Even the major rivers which are perennial, such as the São Francisco and Parnaíba, have mostly intermittent tributaries within the Caatinga. Despite some early explorations dating back to sixteenth century and the systematic compilation of fish species which started in the beginning of the nineteenth century, until recently the fish fauna of the Caatinga biome has been considered poorly known due to the lack of adequate sampling. The present study assessed the current state of knowledge on this fish fauna, in terms of species richness, endemism, and conservation status, based on a literature review, recent field work, and collection records. Our major result was finding a considerable increment in the species richness in the biome when compared with previous estimates, totaling 386 fish species, 371 of which are native freshwater species, 203 are considered endemic to the hydrographic ecoregions where the Caatinga occurs, 15 are introduced from other basins, and 15 listed species have doubtful taxonomic status. Additionally, 32 species are currently recognized as undescribed. We also highlight that the 33 endangered fish species in the Caatinga are possibly not included in protected areas, and that the conservation units in the biome are not enough to ensure protection for endemic and endangered fish species.

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4.1 Introduction

The Caatinga is the only exclusively Brazilian ecological region (Drummond et al. 2010). Located in the semiarid region of northeastern Brazil, it is dominated by a seasonally dry tropical forest, from which it receives its name, and encompasses a relatively modest hydrographic network characterized by intermittent water courses (Rosa et al. 2003). Even the major rivers, such as the São Francisco and Parnaíba, which are perennial, have mostly intermittent tributaries within the Caatinga, and the scarcity of water resources is commonplace within the biome (Rosa et al. 2003).

The Caatinga's fish fauna have traditionally been treated as poor in terms of species diversity and endemism (Paiva and Campos 1995), but more recent reviews have shown that the earlier figures were greatly underestimated (e.g., Rosa et al. 2003, 2004). Nonetheless, those reviews considered the available knowledge to be essentially fragmentary, especially because of inadequate sampling of most river basins of the biome. This situation was a major concern for the conservation of the freshwater fishes, because many human impacts increasingly affected the aquatic biota, including water pollution, damming, and a major engineering project of inter-basin water transfer from the São Francisco River to the major drainages of four states in the Mid-Northeastern Caatinga ecoregion (Brasil 2004).

It was not until the present decade that a large sampling effort took place in the major drainages of the Caatinga biome (e.g., Nascimento et al. 2011, 2014; Ramos et al. 2014; Silva et al. 2014, 2015), thus permitting an updated view of its ichthyofauna composition. This chapter presents such an update, including data on fish species richness and endemism of the freshwater ecoregions encompassing the Caatinga biome, based on a robust review of the literature and collection records. The resulting body of information, although not viewed as definitive, is far more complete than previous assessments and will certainly guide future decisions on development planning, management, and conservation of fish species and their habitats.

4.2 Aquatic Ecoregions in the Caatinga

The typical fish fauna of the Brazilian northeast is mostly adapted to the semiarid conditions. Vari (1988) recognized the endemism in the fish species of the region and proposed an ecoregion ("Northeastern") corresponding to the northeast region of Brazil. Menezes (1996) also recognized the region's identity by including the northeastern rivers in what he called "Northeastern Small Drainages."

Rosa et al. (2003) reviewed the composition of the fish fauna of the Caatinga and proposed four hydrographic regions that conformed to the geographic distribution of species: Maranhão-Piauí, Mid-Northeastern (‘*Nordeste Médio-Oriental*’), São Francisco, and Eastern Basins (‘*Bacias do Leste*’). Abell et al. (2008) proposed a global definition of freshwater ecoregions, according to major biogeographic landscapes and similarity in the composition of freshwater fishes. According to these authors, the South American continent comprises 52 ecoregions, four of which are partially or fully within the semiarid region: Parnaiba, Northeastern Caatinga and Coastal Drainages (between the São Francisco and Parnaíba Rivers), São Francisco, and the Northeastern Mata Atlantica (south of the São Francisco River). Later, Albert et al. (2011) used the ecoregions of Maranho Piauí (sic), Mid-Northeastern Caatinga, São Francisco, and Mata Atlantica, which were essentially the same as those in the previous studies. These aquatic ecoregions are under the influence of three biomes: Cerrado in the west, the Caatinga in the middle, and the Atlantic Forest to the east.

In this chapter, we propose a standardized nomenclature for these ecoregions, considering the original names and the ones that best describe them: Maranhão-Piauí (MAPE), Mid-Northeastern Caatinga (MNCE), São Francisco (SFRE), and Northeastern Atlantic Forest (NAFE) (Fig. 4.1). Highlands act as drainage divides between the Caatinga’s ecoregions and harbor humid forested enclaves due to orographic rainfalls, favoring the maintenance of aquatic systems throughout the year (Rosa et al. 2003; Rosa and Groth 2004).

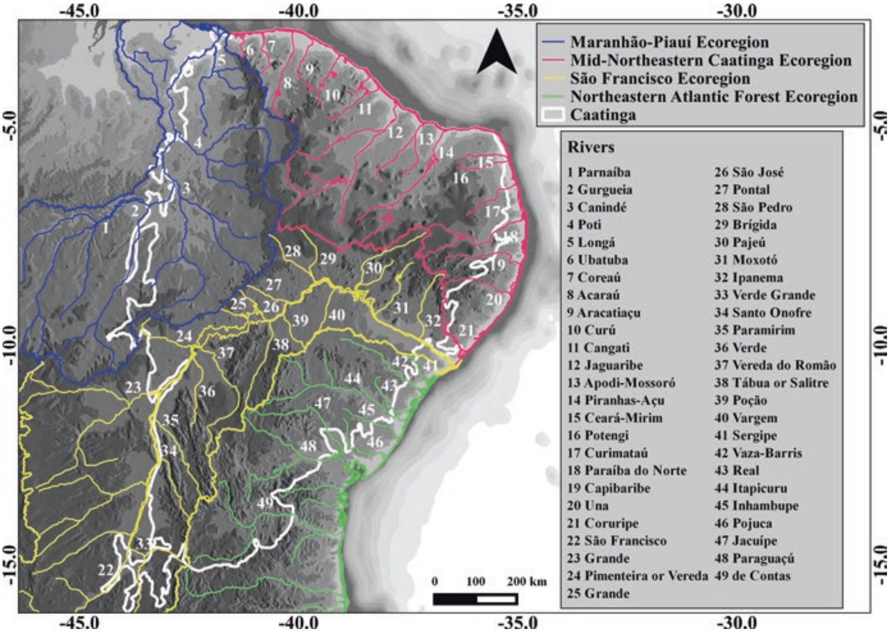

Fig. 4.1 Major river drainages of the four Caatinga freshwater ecoregion: Maranhão-Piauí (1–5), Mid-Northeastern Caatinga (6–21), São Francisco (22–40), and Northeastern Atlantic Forest (41–49). Highlands in dark gray

In the case of the river basins of the Caatinga, a major ongoing development project, which involves the construction of two large channels and pumping stations, will result in inter-basin water transfer from the São Francisco River to the main temporary drainages in the MNCE (Jaguaribe, Apodi-Mossoró, Piranhas-Açu and Paraíba do Norte rivers). The aquatic biota are likely to be the most affected, of which the fishes are the best-known group (Brasil 2004). In addition to changing the seasonal regime of the receptor drainages, this project may also modify their aquatic fauna composition, including the introduction of species from the donor drainage. The effects of the connection between basins on fish populations are still poorly understood (Moreira-Filho and Buckup 2005); however, among the most likely negative effects is the homogenization of the aquatic biota (Vitule and Pozenato 2012, Berbel-Filho et al. 2015). This possibility becomes even more worrisome because conservation units protect only 7.45% of the Caatinga (see Chap. 17).

4.3 History of Ichthyology in the Caatinga

Early explorations in South American ichthyology reported on the fish fauna of the Caatinga using native or Portuguese vernacular names for the species, such as Gabriel Soares de Sousa in his *Tratado Descritivo do Brasil em 1587* (Paiva 1985) and Halfeld (1860), who listed the commercially important species of the São Francisco River. The scientific exploration of fishes of the Caatinga started with the expedition of Johann Baptiste von Spix and Carl Friedrich Philipp von Martius, who collected specimens during the years 1818 and 1819 in many locations of Bahia, Pernambuco, Ceará, Piauí, and Maranhão states (Papavero 1971; Paiva and Campos 1995). Fishes obtained in this expedition were later studied by Spix and Agassiz (*Selecta Genera et Species Piscium Brasiliensium*, 1829–1831) (Paiva and Campos 1995). However, with few exceptions, the localities of the described species are not clearly indicated, as noted in the original publication and its translation (Pethiyagoda and Kottelat 1998).

The Thayer Expedition in Brazil (1865–1866), organized by Louis Agassiz, obtained fish specimens from the São Francisco and Parnaíba rivers, collected by Orestes Saint-John and John Allen (Myers 1943; Agassiz and Agassiz 1975; Higuchi 1996). These specimens were deposited in the Museum of Comparative Zoology, Harvard University (Cambridge, MA, USA). Part of that material has been used in the context of systematic reviews and for the description of new species (e.g., Garman 1913). Based on the preliminary review of this material, Louis Agassiz pointed out the similarity between the fauna of northeastern Brazil and the Amazon region (Agassiz and Agassiz 1975).

At the beginning of the twentieth century, during the year 1903, Franz Steindachner collected fishes in the São Francisco and Parnaíba rivers, some of which he described later (Steindachner 1906, 1915). John Haseman visited the São Francisco River in 1907 and 1908, from where he obtained fish collections that he sent to Stanford University in California, USA. Other authors described fish species from Ceará (Ihering 1907; Fowler 1915), Rio Grande do Norte (Starks 1913), and Bahia states (Ihering 1911; Eigenmann 1914, 1916, 1917; Miranda-Ribeiro 1918).

During the first half of the twentieth century there were additional contributions by Miranda-Ribeiro (1937), who studied vertebrate collections from northeastern Brazil, by his son (Miranda-Ribeiro 1939), who described one species found in Paraíba and Ceará states, and by Fowler (1941). The latter made the broadest taxonomic study of the freshwater fish fauna of northeastern Brazil, and described 38 species from Piauí, Ceará, Rio Grande do Norte, Paraíba, and Pernambuco states. However, his work included taxonomic errors, such as misidentifications, species described in misplaced genera or in synonymy, and inaccuracies in the reported localities of several species (Rosa et al. 2003, Ramos et al. 2017).

The second half of the twentieth century witnessed a strong development of neotropical ichthyology, and many papers were published, including descriptions of new species and systematic reviews of groups occurring in the Caatinga biome (e.g., Nijssen and Isbrucker 1976; Costa and Brazil 1990; Ploeg 1991; Vari 1991).

Following a major workshop held in 2000 by the Brazilian Ministry of the Environment at Petrolina, Pernambuco, which aimed to define priority areas for conservation in the Caatinga, a group of ichthyologists published a compilation of the state of knowledge on the fish fauna (Rosa et al. 2003). Their paper listed a total of 240 fish species occurring in the ecoregions encompassing the biome, 136 of which were recognized as possibly endemic and nine as introduced from other basins.

4.4 Advances in Terms of Fish Diversity

Despite the seminal works of the early 2000s (Rosa et al. 2003, 2004; Rosa 2004; Rosa and Groth 2004), few later papers focused on the diversity and conservation of fishes in the Caatinga (Langeani et al. 2009; Albert et al. 2011; Albuquerque et al. 2012). Although these studies have highlighted the degree of endemism and the intensity of human impacts in the region, the fish fauna of the Caatinga still lacked an updated comprehensive characterization. Langeani et al. (2009) evaluated the state of the art of freshwater ichthyology in northeastern Brazil, using a geographical division (coastal northern basins, including the Parnaíba, northeast, east, and the São Francisco). However, while their study presented the main research groups, recent advances, and gaps in knowledge, it lacked a species list.

Rosa et al. (2003) recognized the difficulty of establishing the fish fauna of the Caatinga, as several drainages are only partially located in the biome, and thus chose to present and analyze the data by aquatic ecoregions. Such an approach, which uses the geographical distribution and composition of freshwater fish species, as well as ecological and evolutionary patterns, has been proven effective, and, following the study of Abell et al. (2008) which delimited the freshwater ecoregions in the world, has been widely used. Albert et al. (2011) developed a comprehensive study on the patterns of freshwater fish species richness in the neotropical ecoregions. For the ecoregions comprising the Caatinga biome, they indicated the species richness and the number of endemic species, respectively, as 95 and 20 (21%) in MAPE, 88 and 38 (43%) in MNCE, 181 and 106 (59%) in SRFE, and 180 and 109 (61%) in NAFE. Nonetheless, their compilation did not provide lists of species composition.

Albuquerque et al. (2012) are the only recent authors to have approached the fauna and flora of the Caatinga as a whole, and presented a brief review of the main studies on the fishes of the biome. According to them, the studies of vertebrates and plants have insufficient samples, usually restricted to small areas. Regarding the fish fauna of the biome, they recognized the incomplete knowledge but pointed out recent advances, many in gray literature. In addition, they listed some specific studies and descriptions of new species of the Caatinga, which, nonetheless, do not allow a general view of the biome's fish fauna. Albuquerque et al. (2012) added six species to the former list of 240 species created by Rosa et al. (2003): *Platydoras brachylecis* in the Parnaíba River (MAPE), four in SRFE (*Aspidoras psammatides*, *Pimelodus pohli*, *Simpsonichthys harmonicus*, and *Salminus franciscanus*), and *Rhamdiopsis krugi*, a troglobic catfish of the Chapada Diamantina National Park (NAFE).

Endemism in the present analysis is indicated for the biome considering only the fish species recorded within the Caatinga limits. We used only strictly freshwater species of primary, secondary, and vicarious (Potamotrygonidae only) (sensu Myers 1949) fish families. Introduced species and those with uncertain taxonomic status (*species inquirendae*) were excluded from endemism calculations. The species belonging to mostly marine families, of the vicarious and complementary divisions of Myers (1949), such as Engraulidae, Pristigasteridae, Belonidae, Sciaenidae, and Gobiidae species, were also excluded from the endemism analysis, although they are listed in order to provide a broader view of the Caatinga's fish composition.

To compile the current taxonomic list of freshwater fishes of the Caatinga we used all occurrence records available in the digital portal Species Link (http://www.splink.org.br/) and all records with geographic coordinates in the fish collections of the Universidade Federal da Bahia (UFBA), Universidade Federal da Paraíba (UFPB), Universidade Federal do Rio Grande do Norte (UFRN), and Universidade Federal de Sergipe (UFS), which are not available online but are the most representative of the biome. In the case of river basins partially inserted in the Caatinga, the occurrence of the species in the biome was checked by geographic coordinates whenever possible. Thus, some species that occur in these drainages, but not within the Caatinga limits, were excluded from the species list [*Hemigrammus unilineatus* (Gill 1858), *Hyphessobrycon itaparicensis* Lima & Costa 2001, *Kryptolebias hermaphroditus* Costa 2011, and *Leporinus melanopleurodes* Birindeli, Britski & Garavello 2011]. In some doubtful cases, due to the lack of geographic coordinates or conflicting information, species were retained in the list pending confirmation of their occurrence in the Caatinga (e.g., *Apteronotus* sp., *Brachyhypopomus* sp., *Cetopsorhamdia* sp., *Corydoras* sp. 2, *Hemigrammus ora* Zarske, Le Bail & Géry 2006, *Phenacorhamdia* sp., and *Serrapinnus* cf. *lucindai* Jerep & Malabarba 2014).

The current taxonomic compilation of the fish fauna of the Caatinga (Table 4.1) includes 386 species, 146 more than the survey conducted by Rosa et al. (2003), representing a 60.8% increment. Of this total, 15 species (3.9%) are introduced and 203 (52.9%) are possibly endemic to the aquatic ecoregions encompassing the Caatinga. Among the new records, 32 are putative undescribed species and 77 spe-

Table 4.1 Taxonomic list of fish species of the Caatinga following Eschmeyer (2016), with indications of taxonomic/biogeographic status, species occurrence by ecoregion, endemism in the biome, and conservation status.

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
MYLIOBATIFORMES		**2**	**0**	**0**	**0**		
Potamotrygonidae	VI						
Potamotrygon orbignyi (Castelnau 1855)		X				No	
Potamotrygon signata Garman 1913		X				Yes	
OSTEOGLOSSIFORMES		**1**	**1**	**0**	**0**		
Arapaimidae	PR						
Arapaima gigas (Valenciennes 1847)	NN	X	X			No	
CLUPEIFORMES		**6**	**0**	**1**	**0**		
Engraulidade	VI						
Anchovia surinamensis (Bleeker 1865)		X				No	
Anchoviella guianensis (Eigenmann 1912)		X				No	
Anchoviella lepidentostole (Fowler 1911)		X				No	
Anchoviella vaillanti (Steindachner 1908)				X		No	
Lycengraulis batesii (Günther 1868)		X				No	
Pterengraulis atherinoides (Linnaeus 1766)		X				No	
Pristigasteridae	VI						
Pellona flavipinnis (Valenciennes 1837)		X				No	
CYPRINIFORMES		**0**	**1**	**1**	**0**		
Cyprinidae	PR						
Cyprinus carpio Linnaeus 1758	NN		X	X		No	
CHARACIFORMES		**59**	**39**	**64**	**52**		
Crenuchidae	PR						
Characidium aff. *zebra* Eigenmann 1909		X		X	X	No	
Characidium bahiense Almeida 1971		X		X	X	No	DD
Characidium bimaculatum Fowler 1941			X			Yes	
Characidium fasciatum Reinhardt 1867				X		No	DD
Characidium deludens Zanata & Camelier 2015	NR				X	Yes	
Characidium sp.1	UN	X				Yes	
Characidium sp.2	UN	X				Yes	
Erythrinidae	PR						
Erythrinus erythrinus (Bloch & Schneider 1801)			X			No	
Hoplerythrinus unitaeniatus (Spix & Agassiz 1829)		X	X	X	X	No	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Hoplias brasiliensis (Spix & Agassiz 1829)				X	X	No	
Hoplias intermedius (Günther 1864)				X		No	
Hoplias malabaricus (Bloch 1794)		X	X	X	X	No	
Parodontidae	PR						
Apareiodon davisi Fowler 1941			X			Yes	EN
Apareiodon hasemani Eigenmann 1916				X		Yes	
Apareiodon itapicuruensis Eigenmann & Henn 1916					X	Yes	
Apareiodon sp.1	UN	X				Yes	
Apareiodon sp.2	UN	X				Yes	
Parodon hilarii Reinhardt 1867				X		No	
Serrasalmidae	PR						
Colossoma macropomum (Cuvier 1816)	NN	X	X	X		No	
Metynnis lippincottianus (Cope 1870)		X	X			No	
Metynnis maculatus (Kner 1858)	NN			X	X	No	
Myleus altipinnis (Valenciennes 1850)				X		Yes	DD
Myleus micans (Lütken 1875)			X	X		No	
Myloplus asterias (Müller & Troschel 1844)		X				No	
Mylossoma aureum (Spix & Agassiz 1829)		X				No	
Pygocentrus nattereri Kner 1858		X	X			No	
Pygocentrus piraya (Cuvier 1819)				X		No	
Serrasalmus brandtii Lütken 1875				X		No	
Serrasalmus rhombeus (Linnaeus 1766)		X	X			No	
Hemiodontidae	PR						
Hemiodus parnaguae Eigenmann & Henn 1916		X				Yes	
Anostomidae	PR						
Hypomasticus garmani (Borodin 1929)					X	No	
Hypomasticus mormyrops (Steindachner 1875)					X	No	
Leporellus cartledgei Fowler 1941	SI			X		No	
Leporellus pictus (Kner 1858)	SI			X		No	
Leporellus vittatus (Valenciennes 1850)				X		No	
Leporinus bahiensis Steindachner 1875					X	No	
Leporinus friderici (Bloch 1794)		X	X	X		No	
Leporinus piau Fowler 1941		X	X	X	X	No	
Leporinus taeniatus Lütken 1875			X	X		Yes	
Megaleporinus brinco (Birindelli, Britski & Garavello 2013)	NR				X	Yes	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Megaleporinus obtusidens (Valenciennes 1836)		X		X	X	No	
Megaleporinus reinhardti (Lütken 1875)		X		X	X	Yes	
Schizodon dissimilis (Garman 1890)		X				Yes	DD
Schizodon fasciatus Spix & Agassiz 1829			X			Yes	
Schizodon knerii (Steindachner 1875)		X		X		Yes	
Schizodon rostratus (Borodin 1931)		X				Yes	
Chilodontidae	PR						
Caenotropus labyrinthicus (Kner 1858)		X				No	
Curimatidae	PR						
Curimata macrops Eigenmann & Eigenmann 1889		X				Yes	
Curimatella immaculata (Fernández-Yépez 1948)		X				No	
Curimatella lepidura (Eigenmann & Eigenmann 1889)			X	X	X	No	
Cyphocharax gilbert (Quoy & Gaimard 1824)				X	X	No	
Cyphocharax pinnilepis Vari, Zanata & Camelier 2010	NR				X	Yes	
Psectrogaster rhomboides Eigenmann & Eigenmann 1889		X	X			No	
Psectrogaster saguiru Eigenmann & Eigenmann 1889			X			Yes	
Steindachnerina elegans (Steindachner 1875)				X	X	No	
Steindachnerina notonota (Miranda Ribeiro 1937)		X	X			Yes	
Prochilodontidae	PR						
Prochilodus argenteus Spix & Agassiz 1829				X		Yes	
Prochilodus brevis Steindachner 1875			X	X	X	Yes	
Prochilodus costatus Valenciennes 1850				X	X	No	
Prochilodus lacustris Steindachner 1907		X				Yes	
Lebiasinidae	PR						
Nannostomus beckfordi Günther 1872			X		X	No	
Triportheidae	PR						
Lignobrycon myersi (Miranda Ribeiro 1956)					X	Yes	
Triportheus guentheri (Garman 1890)				X		Yes	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Triportheus signatus (Garman 1890)		X	X	X		Yes	
Bryconidae	PR						
Brycon orthotaenia Günther 1864				X	X	No	
Salminus franciscanus Lima & Britski 2007	NR			X		No	NT
Salminus hilarii Valenciennes 1850				X	X	No	
Iguanodectidae	PR						
Bryconops sp.				X		No	
Bryconops melanurus (Bloch 1794)		X				No	
Acestrorhynchidae	PR						
Acestrorhynchus britskii Menezes 1969				X		No	
Acestrorhynchus falcatus (Bloch 1794)		X			X	No	
Acestrorhynchus lacustris (Lütken 1875)				X	X	No	
Characidae	PR						
Astyanax bimaculatus (Linnaeus 1758)			X		X	No	
Astyanax epiagos Zanata & Camelier 2008	NR				X	Yes	DD
Astyanax fasciatus (Cuvier 1819)		X	X	X	X	No	
Astyanax hamatilis Camelier & Zanata 2014	NR				X	Yes	
Astyanax jacobinae Zanata & Camelier 2008	NR				X	Yes	DD
Astyanax lacustris (Lütken 1875)		X		X	X	No	
Astyanax rivularis (Lütken 1875)				X	X	No	
Brachychalcinus parnaibae Reis 1989		X				Yes	
Bryconamericus sp.	UN	X				Yes	
Bryconamericus stramineus Eigenmann 1908				X		No	
Cheirodon jaguaribensis Fowler 1941			X			Yes	DD
Compsura heterura Eigenmann 1915		X	X	X	X	No	
Creagrutus sp.	UN	X				Yes	
Ctenobrycon hauxwellianus (Cope 1870)		X				No	
Gymnocorymbus thayeri Eigenmann 1908		X				No	
Hasemania nana (Lütken 1875)		X		X		Yes	
Hasemania piatan Zanata & Serra 2010	NR				X	Yes	EN
Hemigrammus brevis Ellis 1911		X		X	X	No	
Hemigrammus gracilis (Lütken 1875)				X		No	
Hemigrammus guyanensis Géry 1959		X	X			No	
Hemigrammus marginatus Ellis 1911		X	X	X	X	No	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Hemigrammus ora Zarske, Le Bail & Géry 2006	NR	X				No	
Hemigrammus rodwayi Durbin 1909		X	X			No	
Hyphessobrycon bentosi Durbin 1908		X	X			No	
Hyphessobrycon brumado Zanata & Camelier 2010	NR				X	Yes	
Hyphessobrycon diastatos Dagosta, Marinho & Camelier 2014	NR			X		No	
Hyphessobrycon micropterus (Eigenmann 1915)				X	X	No	
Hyphessobrycon negodagua Lima & Gerhard 2001					X	Yes	DD
Hyphessobrycon parvellus Ellis 1911			X	X	X	Yes	
Hyphessobrycon piabinhas Fowler 1941			X			Yes	DD
Hyphessobrycon santae (Eigenmann 1907)				X		Yes	
Hyphessobrycon vinaceus Bertaco, Malabarba & Dergam 2007	NR				X	Yes	
Hysteronotus megalostomus Eigenmann 1911				X		No	NT
Jupiaba polylepis (Günther 1864)		X				No	
Knodus victoriae (Steindachner 1907)		X				No	
Kolpotocheirodon figueiredoi Malabarba, Lima & Weitzman 2004	NR				X	Yes	CR
Lepidocharax diamantina Ferreira, Menezes & Quagio-Grassiotto 2011	NR				X	Yes	EN
Moenkhausia costae (Steindachner 1907)			X	X		Yes	
Moenkhausia diamantina Benine, Castro & Santos 2007	NR				X	Yes	
Moenkhausia dichroura (Kner 1858)		X				No	
Moenkhausia intermédia Eigenmann 1908			X			No	
Moenkhausia lepidura (Kner 1858)		X				No	
Moenkhausia sanctaefilomenae (Steindachner 1907)		X		X		No	
Myxiops aphos Zanata & Akama 2004	NR				X	Yes	
Nematocharax venustus Weitzman, Menezes & Britski 1986					X	No	
Orthospinus franciscensis (Eigenmann 1914)				X		No	
Phenacogaster calverti (Fowler 1941)		X	X			Yes	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Phenacogaster franciscoensis Eigenmann 1911				X		No	
Piabarchus stramineus (Eigenmann 1908)				X		No	
Piabina argentea Reinhardt 1867				X	X	No	
Poptella compressa (Günther 1864)		X				No	
Psellogrammus kennedyi (Eigenmann 1903)			X	X	X	No	
Roeboides margareteae Lucena 2003	NR	X				Yes	
Roeboides sazimai Lucena 2007	NR	X				Yes	
Roeboides xenodon (Reinhardt 1851)				X		No	
Serrapinnus cf. *lucindai* Jerep & Malabarba 2014	NR	X				No	
Serrapinnus heterodon (Eigenmann 1915)		X	X	X	X	No	
Serrapinnus piaba (Lütken 1875)		X	X	X	X	No	
Serrapinnus potiguar Jerep & Malabarba 2014	NR		X			Yes	
Stygichthys typhlops Brittan & Böhlke 1965				X		Yes	EN
Tetragonopterus argenteus Cuvier 1816		X	X			No	
Tetragonopterus chalceus Spix & Agassiz 1829				X		No	
SILURIFORMES		**49**	**37**	**44**	**29**		
Aspredinidae	PR						
Aspredo aspredo (Linnaeus 1758)		X				No	
Auchenipteridae	PR						
Ageneiosus inermis (Linnaeus 1766)		X				No	
Ageneiosus sp.	UN	X				Yes	
Auchenipterus menezesi Ferraris & Vari 1999		X				Yes	
Centromochlus bockmanni (Sarmento-Soares & Buckup 2005)	NR			X		Yes	
Pseudotatia parva Mees 1974				X		Yes	DD
Trachelyopterus cratensis (Miranda Ribeiro 1937)	SI		X			No	DD
Trachelyopterus galeatus (Linnaeus 1766)		X	X	X	X	No	
Trachelyopterus striatulus (Steindachner 1877)					X	No	
Doradidae	PR						
Franciscodoras marmoratus (Lütken 1874)				X		Yes	
Hassar affinis (Steindachner 1881)		X				Yes	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Kalyptodoras bahiensis Higuchi, Britski & Garavello 1990					X	Yes	EN
Platydoras brachylecis Piorski, Garavello, Arce H. & Sabaj Pérez 2008	NR	X				Yes	
Heptapteridae	PR						
Cetopsorhamdia iheringi Schubart & Gomes 1959				X		No	
Cetopsorhamdia sp.	UN	X				Yes	
Imparfinis sp.	UN	X				Yes	
Phenacorhamdia sp.	UN	X				Yes	
Pimelodella cf. *steindachneri* Eigenmann 1917		X				No	
Pimelodella dorseyi Fowler 1941			X			Yes	
Pimelodella enochi Fowler 1941			X			Yes	
Pimelodella itapicuruensis Eigenmann 1917					X	No	
Pimelodella laurenti Fowler 1941				X		Yes	
Pimelodella papariae (Fowler 1941)	SI		X			No	DD
Pimelodella parnahybae Fowler 1941		X				Yes	
Pimelodella robinsoni (Fowler 1941)				X		Yes	
Pimelodella vittata (Lütken 1874)				X		No	
Pimelodella witmeri Fowler 1941	SI		X			No	
Pimelodella wolfi (Fowler 1941)	SI		X			No	DD
Rhamdia enfurnada Bichuette & Trajano 2005	NR			X		Yes	
Rhamdia quelen (Quoy & Gaimard 1824)		X	X	X	X	No	
Rhamdiopsis krugi Bockmann & Castro 2010	NR				X	Yes	
Rhamdiopsis sp.	UN			X		Yes	
Pimelodidae	PR						
Bergiaria westermanni (Lütken 1874)				X		No	
Brachyplatystoma filamentosum (Lichtenstein 1819)		X				No	
Brachyplatystoma vaillantii (Valenciennes 1840)		X				No	
Conorhynchos conirostris (Valenciennes 1840)				X		No	EN
Duopalatinus emarginatus (Valenciennes 1840)				X		No	
Hemisorubim platyrhynchos (Valenciennes 1840)		X				No	
Hypophthalmus cf. *edentatus* Spix & Agassiz 1829		X				No	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Pimelodus blochii Valenciennes 1840		X				No	
Pimelodus fur (Lütken 1874)				X		No	
Pimelodus maculatus Lacepède 1803		X		X		No	
Pimelodus ornatus Kner 1858		X				No	
Pimelodus pohli Ribeiro & Lucena 2006	NR			X		No	
Pimelodus sp.1	UN	X				Yes	
Pimelodus sp.2	UN	X				Yes	
Pseudoplatystoma corruscans (Spix & Agassiz 1829)				X		No	NT
Pseudoplatystoma fasciatum (Linnaeus 1766)		X				No	
Sorubim lima (Bloch & Schneider 1801)		X				No	
Pseudopimelodidae	PR						
Cephalosilurus fowleri Haseman 1911				X		Yes	
Lophiosilurus alexandri Steindachner 1876				X		Yes	VU
Microglanis leptostriatus Mori & Shibatta 2006	NR			X		No	
Pseudopimelodus charus (Valenciennes 1840)				X		No	
Trichomycteridae	PR						
Copionodon lianae Campanario & de Pinna 2000					X	Yes	NT
Copionodon orthiocarinatus de Pinna 1992					X	Yes	NT
Copionodon pecten de Pinna 1992					X	Yes	NT
Glaphyropoma rodriguesi de Pinna 1992					X	Yes	DD
Glaphyropoma spinosum Bichuette, de Pinna & Trajano 2008	NR				X	Yes	VU
Ituglanis agreste Lima, Neves & Campos-Paiva 2013	NR				X	Yes	DD
Ituglanis paraguassuensis Campos-Paiva & Costa 2007	NR				X	Yes	DD
Trichomycterus itacarambiensis Trajano & de Pinna 1996				X		Yes	CR
Trichomycterus payaya Sarmento-Soares, Zanata & Martins-Pinheiro 2011	NR				X	Yes	DD
Trichomycterus rubbioli Bichuette & Rizzato 2012	NR			X		Yes	VU

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Trichomycterus tete Barbosa & Costa 2011	NR				X	Yes	
Callichthyidae	PR						
Aspidoras carvalhoi Nijssen & Isbrücker 1976			X			Yes	DD
Aspidoras depinnai Britto 2000			X			Yes	
Aspidoras maculosus Nijssen & Isbrücker 1976					X	Yes	DD
Aspidoras menezesi Nijssen & Isbrücker 1976			X			Yes	DD
Aspidoras psammatides Britto, Lima & Santos 2005	NR				X	Yes	
Aspidoras raimundi (Steindachner 1907)		X				Yes	
Aspidoras rochai Ihering 1907			X			Yes	DD
Aspidoras sp.	UN			X		Yes	
Aspidoras spilotus Nijssen & Isbrücker 1976			X			Yes	
Callichthys callichthys (Linnaeus 1758)		X	X	X	X	No	
Corydoras garbei Ihering 1911				X		No	
Corydoras julii Steindachner 1906		X				No	
Corydoras lymnades Tencatt, Vera-Alcaraz, Britto & Pavanelli 2013	NR			X		No	
Corydoras multimaculatus Steindachner 1907				X		Yes	
Corydoras sp.1	UN		X			Yes	
Corydoras sp.2	UN	X				Yes	
Corydoras treitlii Steindachner 1906		X				Yes	
Corydoras vittatus Nijssen 1971		X				Yes	
Hoplosternum littorale (Hancock 1828)		X		X	X	No	
Megalechis thoracata (Valenciennes 1840)			X			No	
Loricariidae	PR						
Ancistrus damasceni (Steindachner 1907)		X				Yes	
Ancistrus sp.	UN	X				Yes	
Aphanotorulus gomesi (Fowler 1942)			X			Yes	
Harttia longipinna Langeani, Oyakawa & Montoya-Burgos 2001				X		Yes	DD
Hisonotus vespuccii Roxo, Silva & Oliveira 2015	NR			X		Yes	
Hypostomus alatus Castelnau 1855				X		No	
Hypostomus brevicauda (Günther 1864)					X	Yes	DD

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Hypostomus carvalhoi (Miranda Ribeiro 1937)	SI		X			No	DD
Hypostomus chrysostiktos Birindelli, Zanata & Lima 2007	NR				X	Yes	
Hypostomus eptingi (Fowler 1941)	SI		X			No	DD
Hypostomus francisci (Lütken 1874)				X		No	
Hypostomus jaguar Zanata, Sardeiro & Zawadzki 2013	NR				X	Yes	
Hypostomus jaguribensis (Fowler 1915)	SI		X			No	
Hypostomus johnii (Steindachner 1877)		X				No	
Hypostomus lima (Lütken 1874)				X		Yes	
Hypostomus macrops (Eigenmann & Eigenmann 1888)				X		Yes	
Hypostomus nudiventris (Fowler 1941)	SI		X			No	
Hypostomus papariae (Fowler 1941)	SI		X			No	
Hypostomus pusarum (Starks 1913)			X			Yes	
Hypostomus salgadae (Fowler 1941)	SI		X			No	
Hypostomus sertanejo Zawadzki, Ramos & Sabaj 2017	NR		X			Yes	
Hypostomus sp.1	UN	X				Yes	
Hypostomus sp.2	UN	X				Yes	
Hypostomus sp.3	UN	X				Yes	
Hypostomus sp.4	UN	X				Yes	
Hypostomus unae (Steindachner 1878)					X	Yes	
Hypostomus vaillanti (Steindachner 1877)		X		X		Yes	DD
Hypostomus wuchereri (Günther 1864)					X	No	DD
Limatulichthys griseus (Eigenmann 1909)		X				No	
Loricaria parnahybae Steindachner 1907		X				Yes	
Loricaria sp.	UN	X				Yes	
Loricariichthys derbyi Fowler 1915		X	X			Yes	
Loricariichthys sp.	UN		X			Yes	
Megalancistrus barrae (Steindachner 1910)				X		Yes	
Otocinclus hasemani Steindachner 1915		X				No	
Otocinclus xakriaba Schaefer 1997				X		Yes	
Pareiorhaphis lophia Pereira & Zanata 2014	NR				X	No	
Parotocinclus bahiensis (Miranda Ribeiro 1918)					X	Yes	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Parotoncinclus cabessadecuia Ramos, Lima & Ramos 2017	NR	X				No	
Parotocinclus cearensis Garavello 1977		X	X			Yes	DD
Parotocinclus cesarpintoi Miranda Ribeiro 1939			X			Yes	
Parotocinclus cristatus Garavello 1977					X	No	
Parotocinclus haroldoi Garavello 1988		X				Yes	
Parotocinclus jimi Garavello 1977					X	Yes	
Parotocinclus jumbo Britski & Garavello 2002	NR		X	X		Yes	
Parotocinclus minutus Garavello 1977					X	Yes	
Parotocinclus seridoensis Ramos, Barros-Neto, Britski & Lima 2013	NR		X			Yes	
Parotocinclus spilosoma (Fowler 1941)			X			Yes	
Parotocinclus spilurus (Fowler 1941)			X			Yes	EN
Parotoncinclus sp.1	UN		X			Yes	
Parotoncinclus sp.2	UN		X			Yes	
Pseudancistrus genisetiger Fowler 1941			X			Yes	
Pseudancistrus papariae Fowler 1941	SI		X			No	DD
Pterygoplichthys etentaculatus (Spix & Agassiz 1829)				X		No	
Pterygoplichthys parnaibae (Weber 1991)		X				Yes	
Rhinelepis aspera Spix & Agassiz 1829				X		No	NT
Rineloricaria sp.1	UN	X				Yes	
Rineloricaria sp.2	UN			X		Yes	
Spatuloricaria nudiventris (Valenciennes 1840)				X		No	
GYMNOTIFORMES		**7**	**2**	**5**	**1**		
Gymnotidae	PR						
Gymnotus carapo Linnaeus 1758		X	X	X	X	No	
Rhamphichthyidae	PR						
Rhamphichthys marmoratus Castelnau 1855		X				No	
Hypopomidae	PR						
Brachypopomus sp.	UN	X				No	
Sternopygidae	PR						
Eigenmannia besouro Peixoto & Wosiacki 2016				X		No	
Eigenmannia macrops (Boulenger 1897)		X				No	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Eigenmannia virescens (Valenciennes 1836)		X	X	X		No	
Sternopygus macrurus (Bloch & Schneider 1801)		X		X		No	
Apteronotidae	PR						
Apteronotus brasiliensis (Reinhardt 1852)				X		No	
Apteronotus sp.	UN	X				Yes	
CYPRINODONTIFORMES		**8**	**9**	**45**	**10**		
Rivulidae	SE						
Anablepsoides cearensis (Costa & Vono 2009)	NR		X			Yes	CR
Cynolebias altus Costa 2001				X		Yes	DD
Cynolebias attenuatus Costa 2001				X		Yes	DD
Cynolebias gibbus Costa 2001				X		Yes	
Cynolebias gilbertoi Costa 1998				X		Yes	
Cynolebias itapicuruensis Costa 2001					X	Yes	DD
Cynolebias leptocephalus Costa & Brasil 1993				X		Yes	CR
Cynolebias microphthalmus Costa & Brasil 1995			X			Yes	
Cynolebias obscurus Costa 2014	NR			X		Yes	
Cynolebias ochraceus Costa 2014	NR			X		Yes	
Cynolebias oticus Costa 2014	NR			X		Yes	
Cynolebias paraguassuensis Costa, Suzart & Nielsen 2007	NR				X	Yes	DD
Cynolebias parietalis Costa 2014	NR			X		Yes	
Cynolebias parnaibensis Costa, Ramos, Alexandre & Ramos 2010	NR	X				Yes	DD
Cynolebias perforatus Costa & Brasil 1991				X		Yes	
Cynolebias porosus Steindachner 1876				X		Yes	DD
Cynolebias rectiventer Costa 2014	NR			X		Yes	
Cynolebias roseus Costa 2014	NR			X		Yes	
Cynolebias vazabarrisensis Costa 2001					X	Yes	DD
Hypsolebias adornatus (Costa 2000)				X		Yes	VU
Hypsolebias antenori (Tulipano 1973)			X			Yes	
Hypsolebias caeruleus Costa 2013	NR			X		Yes	
Hypsolebias carlettoi (Costa & Nielsen 2004)	NR			X		Yes	CR
Hypsolebias coamazonicus Costa, Amorim & Bragança 2014	NR	X				Yes	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Hypsolebias faouri Britzke, Nielsen & Oliveira, 2016	NR		X			Yes	
Hypsolebias flagellatus (Costa 2003)	NR			X		Yes	
Hypsolebias flavicaudatus (Costa & Brasil 1990)				X		Yes	CR
Hypsolebias fulminantis (Costa & Brasil 1993)				X		Yes	CR
Hypsolebias ghisolfii (Costa, Cyrino & Nielsen 1996)				X		Yes	CR
Hypsolebias gilbertobrasili Costa 2012	NR			X		Yes	NT
Hypsolebias guanambi Costa & Amorim 2011	NR			X		Yes	VU
Hypsolebias harmonicus (Costa 2010)	NR			X		Yes	VU
Hypsolebias hellneri (Berkenkamp 1993)				X		Yes	EN
Hypsolebias igneus (Costa 2000)				X		Yes	CR
Hypsolebias janaubensis (Costa 2006)	NR			X		Yes	CR
Hypsolebias longignatus (Costa 2008)	NR		X			Yes	VU
Hypsolebias lopesi (Nielsen, Shibatta, Suzart & Martín 2010)	NR			X		Yes	VU
Hypsolebias macaubensis (Costa & Suzart 2006)	NR			X		Yes	CR
Hypsolebias magnificus (Costa & Brasil 1991)				X		Yes	EN
Hypsolebias martinsi Britzke, Nielsen & Oliveira, 2016	NR			X		Yes	
Hypsolebias mediopapillatus (Costa 2006)	NR			X		Yes	VU
Hypsolebias nitens Costa 2012	NR			X		Yes	
Hypsolebias nudiorbitatus Costa 2011	NR				X	Yes	DD
Hypsolebias picturatus (Costa 2000)				X		Yes	VU
Hypsolebias pterophyllus Costa 2012	NR			X		Yes	
Hypsolebias radiseriatus Costa 2012	NR			X		Yes	DD
Hypsolebias sertanejo Costa 2012	NR			X		Yes	
Hypsolebias shibattai Nielsen, Martins, de Araujo & dos Reis Suzart 2014	NR			X		Yes	
Hypsolebias similis (Costa & Hellner 1999)				X		Yes	VU
Hypsolebias stellatus (Costa & Brasil 1994)				X		Yes	EN
Hypsolebias trifasciatus Nielsen, Martins, de Araujo & dos Reis Suzart 2014	NR			X		Yes	
Melanorivulus decoratus (Costa 1989)				X		Yes	NT

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Melanorivulus parnaibensis (Costa 2003)	NR	X				No	
Pituna schindleri Costa 2007	NR	X				Yes	
Poeciliidae	SE						
Pamphorichthys hollandi (Henn 1916)		X		X	X	Yes	
Phalloptychus eigenmanni Henn 1916					X	Yes	CR
Poecilia latipinna (Lesueur 1821)	NN				X	No	
Poecilia reticulata Peters 1859	NN	X	X	X	X	No	
Poecilia sarrafae Bragança & Costa 2011	NR	X	X			Yes	
Poecilia sphenops Valenciennes 1846	NN			X	X	No	
Poecilia vivipara Bloch & Schneider 1801		X	X	X	X	No	
Xiphophorus helleri Heckel 1848	NN		X			No	
SYNBRANCHIFORMES		**1**	**1**	**1**	**1**		
Synbranchidae	SE						
Synbranchus sp.1	UN	X				Yes	
Synbranchus sp.2	UN		X	X	X	No	
PERCIFORMES		**13**	**13**	**16**	**8**		
Sciaenidae	VI						
Pachyurus francisci (Cuvier 1830)				X		No	NT
Pachyurus squamipennis Agassiz 1831				X		No	DD
Plagioscion squamosissimus (Heckel 1840)		X	X	X	X	No	
Cichlidae	SE						
Aequidens tetramerus (Heckel 1840)		X				No	
Apistogramma piauiensis Kullander 1980		X				Yes	DD
Astronotus ocellatus (Agassiz 1831)	NN	X	X	X		No	
Cichla kelberi Kullander & Ferreira 2006	NN		X	X		No	
Cichla monoculus Spix & Agassiz 1831	NN	X	X	X		No	
Cichla ocellaris Bloch & Schneider 1801	NN		X			No	
Cichlasoma orientale Kullander 1983		X	X	X		No	
Cichlasoma sanctifranciscense Kullander 1983		X	X	X		No	
Coptodon rendalli (Boulenger 1897)	NN	X	X	X	X	No	
Crenicichla lepidota Heckel 1840				X	X	No	
Crenicichla menezesi Ploeg 1991		X	X	X		No	
Crenicichla sp.	UN			X		Yes	
Geophagus brasiliensis (Quoy & Gaimard 1824)			X	X	X	No	

(continued)

Table 4.1 (continued)

ORDER/Family/*Species*	TBS	MAPE	MNCE	SFRE	NAFE	E	C
Geophagus diamantinensis Mattos, Costa & Santos 2015	NR				X	Yes	
Geophagus itapicuruensis Haseman 1911	SI				X	No	DD
Geophagus obscurus (Castelnau 1855)	SI				X	No	DD
Geophagus parnaibae Staeck & Schindler 2006	NR	X				Yes	
Oreochromis niloticus (Linnaeus 1758)	NN	X	X	X	X	No	
Parachromis managuensis (Günther 1867)	NN		X	X		No	
Satanoperca jurupari (Heckel 1840)		X				No	
Gobiidae	VI						
Awaous tajasica (Lichtenstein 1822)		X	X	X		No	
BELONIFORMES		**1**	**0**	**0**	**0**		
Belonidae	VI						
Pseudotylosurus microps (Günther 1866)		X				No	
Total (386)		**147**	**103**	**178**	**101**		

Numbers indicate total number of species in their respective orders for each ecoregion
Conservation status taken from Brasil (2014); DD and NT, taken from ICMBio (2014), were included to pinpoint research priorities
C conservation status in Brazil, *CR* critically endangered, *DD* data deficient, *E* endemism in the Caatinga biome, *EN* endangered, *MAPE* Maranhão-Piauí ecoregion, *MNCE* Mid-Northeastern Caatinga ecoregion, *NAFE* Northeastern Atlantic Forest ecoregion, *NN* non-native species, *NR* new species records, *NT* nearly threatened, *PR* primary freshwater group (sensu Myers 1949), *SE* secondary freshwater group (sensu Myers 1949), *SFRE* São Francisco ecoregion, *SI species inquirendae*, *TBS* taxonomic/biogeographic status, *UN* undescribed species, *VI* vicarious taxa of marine origin, *VU* vulnerable

cies were described as new from 2001 to June 2017. A significant part of such an increment in the knowledge of the fishes of the Caatinga resulted from the research carried out in the Parnaíba River basin (Ramos et al. 2014; Silva et al. 2015).

The 371 native species recorded in the Caatinga are distributed in 137 genera, 34 families, and seven orders, following the taxonomic arrangement of Eschmeyer (2016). The largest number of species was recorded in the order Siluriformes (143 species, representing 38.5% of the native fish fauna of the Caatinga), followed by the orders Characiformes, with 132 species (35.5%), and Cyprinodontiformes, with 58 (15.6%). The most speciose families among the Siluriformes were Loricariidae (59), Callichthyidae (20), and Heptapteridae (19). Within the Characiformes the most diverse family was Characidae, with 62 species, which is also the most speciose fish family in the Caatinga. Other diverse characiform families were the Anostomidae, Curimatidae, and Serrasalmidae, with 16, nine, and nine species, respectively. Within the order Cyprinodontiformes, the family Rivulidae of annual fishes was the most diverse, with 54 species. Of these, 32 belong to the genus *Hypsolebias*, 18 to *Cynolebias*, two to *Melanorivulus*, one to *Anablepsoides*, and one to *Pituna*. The other orders are represented by the following numbers of species: Perciformes, 17 (4.6%); Gymnotiformes, nine (2.4%); Myliobatiformes and Synbranchiformes, two species each (0.5%).

Taking the work of Rosa et al. (2003) as a baseline, 77 new species described since 2001 were included in the present study (Table 4.1). These species belong to 16 families, especially the annual fish family Rivulidae, genera *Hypsolebias* and *Cynolebias*, with 21 and eight species described, respectively. Compared to Rosa et al. (2003) some new genera were established as including already described taxa (e.g., *Hypsolebias*, *Megaleporinus*, and *Melanorivulus*), while 11 other genera represent new records in the biome: *Anablepsoides*, *Centromochlus*, *Hisonotus*, *Ituglanis*, *Kolpotocheirodon*, *Lepidocharax*, *Microglanis*, *Myxiops*, *Pareiorhaphis*, *Pituna*, and *Rhamdiopsis*, mostly in NAFE. By ecoregion, 33 species were described from SRFE, 26 from NAFE, 12 from MAPE, and eight from MNCE. Two of the new species originally described from one ecoregion have been recorded in at least two ecoregions: *Parotocinclus jumbo* (MNCE and SRFE) and *Poecilia sarrafae* (MAPE and MNCE) (Table 4.1).

The early systematics of freshwater fishes from northeastern Brazil were mainly based on short descriptions, incorrect identifications, and confusing taxonomy, with some taxa established in synonymy with previously described species (Rosa et al. 2003; Barros et al. 2011). Among these studies, Fowler (1941) should be highlighted; in this study, 38 alleged new species were described from material collected in the Parnaíba, Jaguaribe, and Piranhas-Açu rivers, and Papari Lake. However, most of these descriptions do not provide diagnostic characteristics for distinguishing among species described in the same study or earlier. Other problems of the study are misidentifications, inaccuracies, and possible mistakes in locality data, including in type localities, and overlooking of previous literature. These aspects may have led to doubts about the real identity and distribution of species. For instance, Fowler (1941) mentioned three specimens of *Platydoras* allegedly collected by von Ihering in Fortaleza, Ceará State in 1937, and identified as *P. costatus*. However, such specimens along with recently collected material were used to describe *P. brachylecis* Piorski, Garavello, Arce H. & Sabaj Pérez 2008, which is endemic to MAPE. Similar errors occurred with several others of Fowler's reported species, for which the geographic origin of the type material remains uncertain.

Locality errors in the study of Fowler (1941) may also have occurred in the species assigned to Papari Lake, in Rio Grande do Norte State. Among the presumed errors were two new species (*Pimelodella papariae* and *Pseudancistrus papariae*). Other species recorded by Fowler in Papari Lake also do not seem to occur there currently. However, the occurrence of *Pseudancistrus* is the one that draws the most attention. Representatives of this genus in northeastern Brazil have only been collected in the basins of the Jaguaribe and Piranhas-Açu rivers, currently identified as *P. genisetiger*. It is possible that species lots assigned to Papari Lake had been collected in one of these two basins, which were also sampled by von Ihering. Thus, it is possible that the described species from Papari Lake are not valid, but are rather junior synonyms of others already described, including by Fowler himself. Exploratory molecular studies (DNA barcode) of the freshwater fish fauna of

MNCE, including topotypes of some species described by Fowler (1941), suggest that the species richness of *Hypostomus* and *Pimelodella* is lower than the number of nominal species (Ramos et al. 2017).

Due to taxonomic uncertainties, 15 (3.9%) species were listed as *species inquirendae* (Table 4.1). These species belong to six genera (*Leporellus*, *Trachelyopterus*, *Pimelodella*, *Hypostomus*, *Pseudancistrus*, and *Geophagus*), ten of which were described by Fowler (1915, 1941)—most from the MNCE—which may result in a decrease in the species diversity known for that ecoregion.

4.5 Distribution Patterns

Knowing the geographical distribution and the environments in which species occur is a fundamental guideline for understanding the biogeographic patterns, in addition to providing support for conservation strategies and environmental licensing (Lanés et al. 2014). According to Rosa et al. (2003), many areas of Caatinga, especially those away from the main course of the rivers and in headwaters, lacked surveys. In addition to the unprecedented efforts in the basin of Parnaíba River (Ramos et al. 2014), including its headwaters (Silva et al. 2015), several basins of the MNCE have been widely sampled, especially those included in the São Francisco Inter-basin Water Transfer project (SFIWT) (Silva et al. 2017). Such data will allow further evaluation of changes in the specific composition of the receptor drainages (Jaguaribe, Apodi-Mossoró, Piranhas-Açu, and Paraíba do Norte river basins).

Other compilatory studies or ichthyological surveys were also important in verifying the geographic distribution of the species among ecoregions. Recent inventories have been made in the basins of the Curimataú (Ramos et al. 2005), Piranhas-Açu (Nascimento et al. 2011; Silva et al. 2014, 2017), and Mundaú rivers (Teixeira et al. 2017), all in the MNCE. The freshwater fish fauna of Rio Grande do Norte State, involving eight river basins of the MNCE, was compiled by Nascimento et al. (2014). For the SFRE, Luz et al. (2012) provided a study of the fishes of the marginal environments and tributaries of the middle and lower basin, which is predominantly composed of small-sized species. The ichthyofauna of the humid forest enclaves of Ibiapaba (between MAFE and MNCE) and Araripe (MNCE and SFRE) plateaus was studied by Rodrigues-Filho et al. (2016).

A study on the diversity and conservation of the fishes of Serra do Espinhaço provided an overview of the drainages of the southern Caatinga in the NAFE (Alves et al. 2008). Additionally, a detailed biogeographic study with data from 25 basins in the same ecoregion was prepared by Camelier and Zanata (2014), but this focused mainly on the fishes associated with the Atlantic Forest in the lower stretches of the coastal rivers.

According to the current list, and considering only the 371 native species, fish species distribution according to ecoregion includes 140 species in MAPE, 91 in MNCE, 166 in SRFE, and 95 in NAFE. Of these, only 14 (*Hoplerythrinus unitaeniatus*, *Hoplias malabaricus*, *Leporinus piau*, *Astyanax fasciatus*, *Compsura heter-*

ura, *Hemigrammus marginatus*, *Serrapinnus heterodon*, *S. piaba*, *Trachelyopterus galeatus*, *Rhamdia quelen*, *Callichthys callichthys*, *Gymnotus carapo*, *Poecilia vivipara*, and *Plagioscion squamosissimus*) occur in the four ecoregions, showing the ichthyofauna heterogeneity of the biome. Some of these species with wide distribution possibly represent species complexes (Albert et al. 2011).

Other recently revised taxa have been recognized as distinct species, both using traditional morphological characters and integrated molecular data. For instance, the annual fish group *Hypsolebias antenori*, present in areas of Caatinga in MNCE and SRFE, is currently composed of 18 species: nine in the complex *H. flavicaudatus*, three in the complex *H. ghisolfii*, and five in the complex *H. antenori*, as well as *H. nudiorbitatus*. Thus, species previously considered to be of least concern for conservation purposes have gradually been separated into several species with restricted geographical ranges, some already endangered (Costa 2003, 2006; Costa and Amorim 2011; Costa et al. 2012; Britzke et al. 2016).

A biogeographical analysis of the Caatinga's fish species using the Jaccard similarity index indicates greater similarity in the species shared between MAPE and MNCE (19.6%) and between SRFE and NAFE (18.8%), but low similarity values among the ecoregions (mean = 15.9%), suggesting the vicariant role of the water dividers between them. While MAPE and the main drainages of MNCE on the north coast and SRFE and NAFE on the eastern coast are adjacent ecoregions with their estuaries flowing in the same direction, we may infer the role of sea-level changes in the faunal exchange between adjacent basins in periods of marine regressions. The lowest level of shared species is between MAPE and NAFE (11.7%), the ecoregions that are most distant from each other. However, some species shared among ecoregions inhabiting the upper or middle courses of drainages (e.g., *Parotocinclus jumbo* in MNCE and SRFE) would be better explained by tectonic adjustments and capture of headwaters.

These results corroborate the proposal of Albert and Carvalho (2011), who also found few species in common among the ecoregions of northeastern Brazil; they suggested more affinities between Parnaíba (MAPE) and the Amazon, the SFRE and the Paraná lowlands, and the NAFE and the southeastern region. However, their analyses included all freshwater species of the tropical South American ecoregions.

According to Rosa et al. (2003), the NAFE basins can be divided into two groups: coastal basins north of the Chapada Diamantina, including the Sergipe, Vaza-Barris, Real, and Itapicuru river basins; and the basins of the eastern slope of the Chapada Diamantina, which include the Paraguaçu and de Contas drainages (Rosa et al. 2003). Ichthyological surveys recently conducted in these basins resulted in the description of several species, mainly from the inland headwaters (Langeani et al. 2009; Lima et al. 2013), and corroborate the high number of endemic species of the coastal basins located south of the mouth of the São Francisco River (Buckup 2011).

Some authors (Menezes 1972; Bizerril 1994; Ribeiro 2006) have suggested that the fish fauna of the river basins of the NAFE received a strong contribution from the Paraná and São Francisco river basins. Camelier and Zanata (2014) also found shared species between the NAFE and adjacent ecoregions. Most species were shared with the SFRE, mainly with the North Group, rather than with the Paraíba do Sul and Upper Paraná (UPAE) ecoregions. Indeed, the UPAE seems to share more species with the upper SFRE than with the other stretches of this basin. However, the limited number of studies on the phylogeny of taxons from the NAFE precludes the understanding of the relationships among these drainages from a biogeographical perspective (Camelier and Zanata 2014).

Currently, the São Francisco River, after running parallel to the coast towards the north, turns abruptly to the eastern coast of Brazil before flowing into the Atlantic Ocean between the states of Alagoas and Sergipe. However, geological evidence suggests that its course changed during the Mindel glaciation (approximately 400,000 years before present [bp]), from a previous north-flowing direction into what today is the Parnaíba River basin in Piauí State (Mabesoone 1994). Some studies involving molecular markers of terrestrial organisms have found evidence that corroborates the past course of the São Francisco River being to the north (Coutinho-Abreu et al. 2008; Nascimento et al. 2013). Although molecular studies of freshwater fishes are ideal for reconstructing the geomorphological history of a region, since their occurrence along river basins depends on the connection between them (Jones and Johnson 2009), no study has yet been performed involving samples of the São Francisco and Parnaíba River basins. However, the 11 species shared between MAPE and SRFE (*Schizodon kneri*, *Hasemania nana*, *Moenkahausia sanctafilomenae*, *Pimelodus maculatus*, *Hypostomus vaillanti*, *Sternopygus macrurus*) may represent examples of the ichthyofauna involved in this vicarious event.

On the other hand, species present in three ecoregions of Caatinga, excluding MNCE (*Characidium* aff. *zebra*, *C. bahiense*, *Megaleporinus obtusidens*, *M. reinhardti*, *Astyanax lacustris*, *Hemigrammus brevis*, *Hoplosternum littorale*, and *Pamphorichthys hollandi*), may represent taxa that have not adapted to the temporary river regime of this particular ecoregion. Some taxa that occur in the basins of the NAFE or in other drainages further south have not yet been recorded in the basins of the MNCE, such as representatives of the genera *Atlantirivulus*, *Mimagoniates*, *Microglanis*, and *Pareiorhaphis*. Besides the peculiar water regime of the MNCE, the narrow continental shelf in the northern portion of NAFE may have prevented the dispersion of these lineages into the coastal basins north of the São Francisco River. According to Roxo et al. (2014), *Parotocinclus* aff. *spilurus* belongs to a clade of Otothyrinae, corroborating the polyphyletic status of the genus, which had its origin in the eastern coastal drainages and later dispersed into the SRFE, MNCE, and MAPE between 19.3 and 43.2 million years ago, suggesting the influence of several river-capture events to explain some biogeographic patterns.

Elements of Amazonian origin also occur in the ichthyofauna of the Caatinga, especially in the coastal drainages of the MAFE and MNCE. The fish fauna of the Parnaíba River basin (as well as that of the Tocantins River) shows more affinity with the Amazon basin than with those of the SRFE and MNCE (Albert and Carvalho 2011; Ramos et al. 2014). Thus, the fish fauna composition of MAPE may have originated in dispersive events through the coastal plain during Pleistocene sea-level regressions. With the exposure of the continental shelf, paleochannels could have connected the drainages of the MAPE with the Amazon basin to the west and the western rivers of the MNCE. This dispersive coastal route has already been suggested by Hubert and Renno (2006) to explain the high number of freshwater fish species shared among the drainages of northern South America.

Five species recorded in the MNCE (*Hemigrammus guyanensis*, *H. rodwayi*, *Hyphessobrycon bentosi*, *Nannostomus beckfordi*, and *Metynnis lippincottianus*) had been treated in the literature as present only in the Amazon region (Reis et al. 2003, Buckup et al. 2007). With the exception of *Hemigrammus rodwayi*, the other typically Amazonian species have been collected mainly in small coastal basins of the MNCE, which can also be explained by the preterit connections of the Atlantic Forest with the Amazon reported by authors such as Menezes et al. (2007). The presence of *Pseudancistrus* species in the major drainages of the MNCE (Jaguaribe and Piranhas-Açu rivers) also indicates a relationship with the Amazon–Orinoco–Guiana Core (Armbruster and Tafforn 2008), although some studies suggest that *P. genisetiger* is the sister group of *Hemipsilichthys gobio* from the Paraiba do Sul river basin, and may belong to an undescribed genus within the Delturinae (Covain and Fisch-Muller 2012).

The same dispersive process could have occurred between the basins of the MNCE as evidenced by the presence of paleo-rivers in the estuary of the Apodi-Mossoró and Piranhas-Açu rivers (Gomes and Vital 2010). Thus, it is possible that the headwater regions have become more isolated, which may have contributed to the higher species richness of *Aspidoras* and *Parotocinclus*. These genera are more speciose in the MNCE than in other ecoregions, and are represented by five and seven valid species, respectively, which usually exhibit small geographic range, often restricted to a single basin.

On the other hand, Costa (2010) suggested that the diversification of the annual fish tribe Cynolebiasini originated by vicariant events in the area of Paranã-Urucuia-São Francisco, followed by dispersal to the northeastern basins (Jaguaribe and adjacent basins, MNCE) of Brazil during Miocene. Such dispersal may have occurred in the area of headwaters of the Salgado River, in the upper Jaguaribe river basin (MNCE), and in the sub-middle section of the São Francisco River, between the Brigida and Pajeú tributary rivers. Berbel-Filho et al. (2015), in a study integrating morphological and molecular data to compare lineages of two cichlid species of the basins included in the SFIWT, also found evidence of past connectivity between the SRFE and some MNCE basins.

4.6 Conservation

Aquatic environments are among the most threatened in the world due to accelerated habitat degradation, eutrophication, and the introduction of exotic species (Lévêque et al. 2005). Other impacts directly affecting the Brazilian freshwater fish fauna are the destruction of riparian vegetation and river damming (Rosa and Menezes 1996). Although freshwater ecosystems are in rapid decline, recent studies have shown that freshwater biodiversity has been neglected by conservation assessments (Nogueira et al. 2010) and has a low priority in conservation initiatives both by the government agencies and non-governmental organizations (Lévêque et al. 2005).

The Caatinga includes 30 protected areas (13 of Integral Protection: four Ecological Stations [EEs], one Biological Reserve, seven National Parks [NP], one Natural Monument; and 15 of Sustainable Use: three Environmental Protection Areas [EPAs], two Areas of Relevant Ecological Interest, six National Forests, and six Private Reserves of Natural Patrimony) (ICMBio 2016). Most of these protected areas face problems such as unresolved land ownership and lack of funds for their operation and maintenance (Tabarelli and Silva 2003). These deficiencies in the protected areas are further aggravated by a lack of management plans, which compromises their implementation and management (Tabarelli and Silva 2003).

One atlas of the Brazilian endangered fauna in federal conservation units did not record any fish species in the protected areas of the Caatinga (Nascimento and Campos 2011). In fact, few studies have focused on freshwater fishes in protected areas. The only extensive fish inventory in the Caatinga's conservation units are from the Aiuaba EE (14 species), Seridó EE (13 species), Catimbau NP (14 species), and Ubajara NP (16 species) (Botero et al. 2014, 2017; Ávila et al. 2017; Silva et al. 2017). In addition to these data, there is a record in the literature of three generalist species in the Serra das Confusões NP (Silva et al. 2015) and some records in the Serra da Ibiapaba and Chapada do Araripe EPAs (Rodrigues-Filho et al. 2016). Although the Caatinga conservation units have been designed without taking into account the drainage network and aquatic biota, and often include a few water bodies (Silva et al. 2015, 2017), they eventually protect a significant portion of the fish species in the Caatinga ecoregions. Nonetheless, many endangered, endemic, and habitat-specialized species are apparently not protected in conservation units. Water bodies in protected areas are often landlocked and non-natural, may dry out due to damming upstream, and usually serve as drinking sources for cattle. It is noteworthy that no endangered species has been recorded so far in the protected areas of the Caatinga (Silva et al. 2017).

The significant advances in sampling the river drainages of the Caatinga made by regional research groups, which are associated with taxonomic studies and data from ichthyological collections, enabled the assessment of the conservation status of several species of the Caatinga, resulting in an increase in the number of endangered species in this biome (Brasil 2014). Currently, there are 33 endangered fish species in the Caatinga, none in the MAPE, four in the MNCE, 23 in the SFRE, and six in the NAFE.

At state level, only Bahia has a list of endangered species created following the same criteria adopted in the national assessments, and this was followed by workshops to identify priority areas for conservation (SEMA-BA 2015). The results of these workshops are being compiled into articles, official documents, and educational materials.

A similar dataset as the one presented herein was also used for the reevaluation of priority areas for conservation, sustainable use, and sharing of benefits for

Brazilian biodiversity (Caatinga, Cerrado, and Pantanal biomes) (Brasil 2016). This exercise involved a review of the fish fauna in the drainages of the Caatinga, which database included more than 1,100 locations in the four Caatinga ecoregions. From the taxonomic list of 333 native species, 144 target species belonging to 19 families were selected, using criteria such as settled taxonomy, extinction risk, ecoregion endemism, unique life cycles or habitats (e.g., temporary or permanent wetlands, caves), and fishery importance.

4.7 Challenges

The data compiled herein show that knowledge of the Caatinga fish fauna has advanced considerably since the seminal works of the early twenty-first century (Rosa et al. 2003, 2004; Rosa 2004), supported mainly by the records of recently described species, undescribed species, and new records in the biome basins. However, as pointed by Albuquerque et al. (2012), the biodiversity of the Caatinga still remains poorly documented, and, among the challenges to the knowledge of the biome, studies on the effective composition of species of the fish fauna and systematic revisions of ambiguous groups are necessary.

Our study used data from the fish collections of federal universities in northeastern Brazil, which are considered the most representative for the Caatinga. Nonetheless, most of the records from these collections are not yet available online on digital platforms. Therefore, a major recommendation is that of digitalizing and making such data public, as well as that restricted to gray literature in the universities.

Although much of the Caatinga has already been inventoried, some areas need to be better sampled while others remain virtually unexplored. Among the areas that need further sampling, we highlight the coastal rivers that make up part of the Caatinga, especially those of the MNCE. Among the under-sampled areas are tributaries of the SRFE in Bahia and the north of Minas Gerais, an area under the influence of the Caatinga that remains understudied, as pointed out by Langeani et al. (2009).

Many fish species are widely distributed in the basins of the ecoregions of the Caatinga and are under the influence of other biomes, especially the Cerrado to the west (MAPE, SRFE, and NAFE) and the Atlantic Forest to the east (MNCE, SRFE, and NAFE). While some species have a known geographic distribution fully inserted in the Caatinga biome, even in basins that extend into other biomes, and can be considered endemic to the Caatinga. Nonetheless, more macro-ecological studies are recommended to identify this typical semiarid fauna and the ecological factors that are more important for their geographical distribution.

Further studies are necessary to add information to the systematic knowledge of the freshwater fish fauna of the Caatinga ecoregions and of adjacent biomes, as more endemic species may be discovered. It is important to know the spatial distribution of the fish fauna of the Caatinga, especially of recently described species and those yet to be described, which may have a wider distribution than currently accepted. Also important are ecological studies of semiarid fishes, as only 7% of the articles on freshwater fish assemblages published in Brazil focused on the northeast (Dias et al. 2016).

The mosaic composition of the fish assemblages of South American drainages, as a result of the accumulation of diverse faunistic interchanges among adjacent basins, might hamper the approach of 'areas of endemism' in biogeographical studies (Lima and Ribeiro 2011). Thus, it would be better to identify distribution patterns of monophyletic taxa, and then to seek geomorphological evidence that might explain the elaborate scenarios of ichthyofaunal evolution through time (Lima and Ribeiro 2011).

Comparative phylogeographic studies could also be informative because they can detect demographic patterns related to climatic changes or make inferences of landscape evolution, such as geodispersion through river capture or range expansion due to riverine connections during marine regression periods. However, population genetics studies of neotropical freshwater fish are in their infancy and restricted to a few species (Albert and Reis 2011). Even considering other biological groups, the Caatinga is one of the least studied biomes of South America, even though it could provide useful information on how species responded to past changes and may help to predict how they might cope with the ongoing climatic changes (Turchetto-Zolet et al. 2012). Future inter-specific (biogeography) and intra-specific (phylogeography) molecular research could shed new light on the processes that generated and maintain the diverse fish fauna of the Caatinga.

For the conservation of the Caatinga fishes, there is an urgent need for preservation of the integrity of the temporary aquatic environments, which, besides representing important shelter and feeding areas for several fish species, also harbor the diverse Rivulidae annual fishes, mainly in the SFRE (Albuquerque et al. 2012). Additional studies should be performed to gather data on the biology and populational status of'data deficient' and 'nearly threatened' species (ICMBio 2014), as well as ecological studies to corroborate the role of the humid highland forest enclaves ('*brejos de altitude*') for the maintenance of fish populations in perennial headwaters, as suggested by Rosa et al. (2003). During the dry season fishes survive in deeper ponds along river channels, perennial springs and dams, and special attention should also be directed to these refuge areas for the Caatinga's fishes.

All of the recommendations made by Rosa (2004) aimed at increasing the knowledge on the fish fauna of the Caatinga and promoting its conservation are still valid: (1) ichthyofaunistic surveys; (2) systematics and biogeographic studies; (3) creation of new conservation units, considering the aquatic habitat diversity; (4) legal protection of special biotopes, such as temporary pools; (5) funding for recovering degraded aquatic habitats, through remediation programs and restoration of riparian forests; (6) promotion of environmental education programs for the conservation of aquatic habitats and species; (7) restriction on the introduction of exotic species in natural aquatic environments without previous studies of environmental impact; and (8) compliance with environmental legislation with respect to interventions in aquatic environments, such as in the construction of engineering works.

To this list, we should add the consolidation of regional ichthyological collections and hiring and retention of researchers in northeastern Brazil (Langeani et al. 2009). It is imperative that all recommendations are followed to ensure the preservation of the aquatic biota of the Brazilian semiarid region, which faces many impacts due to water scarcity. The Caatinga fishes epitomize the struggle for survival in harsh environments and may represent interesting models for the study of adaptation to climate change.

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Chapter 5
Ecology, Biogeography, and Conservation of Amphibians of the Caatinga

Adrian Antonio Garda, Mariana Garcez Stein, Ricardo Bonfim Machado, Marília Bruzzi Lion, Flora Acuña Juncá, and Marcelo Felgueiras Napoli

Abstract In this chapter, we review current knowledge on the ecology, biodiversity, biogeography, and conservation of amphibians of the Caatinga. We recorded 98 species belonging to 12 families, with 20 endemic species and 67% of the regional diversity concentrated in two families: Hylidae and Leptodactylidae. We generated a surface of potential anuran richness based on binary maps generated through niche modeling. Our resulting map corroborated most areas previously recognized as highly diverse, but also suggested others that must be further studied. A general pattern of higher richness areas on the east portion of the biome, associated with the Atlantic Forest, is evident, but central and western portions with higher richness values are also evident. The biodiversity of the Caatinga is just starting to be understood, with the vast majority of papers on amphibians published only in the last 20 years. A concerted effort is needed to fill information gaps regarding Caatinga amphibians, including geographic distribution and biogeography, community and population ecology, physiology, and taxonomic and phylogenetic appraisals that can adequately support conservation policies and practices for its fauna.

Keywords Amphibians • Caatinga • Richness • Endemism • Ecology • Conservation

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5.1 Introduction

Amphibians are terrestrial vertebrates that mostly depend on water for survival. They are intrinsically linked to the availability of water bodies for reproduction, growth, and survival (Wells 2007). Accordingly, although at a global scale salamanders are more diverse in temperate regions, most amphibians are found where water abounds, such as tropical rainforests (Wiens 2007). From proximal physiological mechanisms to final evolutionary and macroecological studies, water has been shown to be of major importance to amphibian communities' composition and richness at local, regional, and global scales (Pyron and Wiens 2013).

Nevertheless, savannas, semi-arid, and arid regions worldwide are also home to several amphibian species. Because of the limits imposed by such habitats on anurans' life histories, remarkable adaptations to these harsh habitats have been identified and described (Warburg 1997; Wells 2007). Indeed, although highly dependent on water, amphibians are also some of the most tolerant animals to dehydration (Hall 1922). From species that spend much of their lives buried underground, emerging only after heavy rains, to animals that are able to absorb water from dew condensed on their bodies, frogs, salamanders, and caecilians have thrived under the most drastic conditions.

Because of such physiological restrictions imposed by water availability, semi-arid and arid environments throughout the world have received less attention from amphibian biologists. Indeed, to our knowledge, no macroecology publication addresses the diversity and biogeography of amphibian faunas in arid and semi-arid regions of the world. The drivers of community assembly in such regions are likely related to environmental stress. However, because little information exists in the literature for most desert and semi-arid areas, analyses evaluating whether environmental filtering or competition drive the assembly of such communities worldwide currently do not exist, although some attempts in well-studied areas have been conducted (Schalk et al. 2015).

Some of the best-studied desert and semi-arid regions are found in North America. The Sonoran and Chihuahuan Deserts, for example, harbor 13 and 17 amphibian species, respectively (Duellman 1999). Other regions in the Intermontane Plateaus, which have low levels of mean annual precipitation (<750 mm), have species richness of fewer than 17 per region (Duellman and Sweet 1999). Tropical arid and semi-arid regions in South America, by contrast, are poorly studied and some, like the Caatinga, can be considered highly understudied.

5.2 Caatinga Amphibians

In this chapter we review the current knowledge on the ecology, biodiversity, biogeography, and conservation of amphibians of the Caatinga. First, we give an overview of the current knowledge of the taxonomy and ecology of Caatinga amphibians.

Second, we compile all species currently known to occur in the Caatinga and generate a richness surface based on species distribution modeling and the delimitation proposed for the Caatinga in this book. Lastly, we evaluate, based on the results, the conservation status of the Caatinga and point to future research on the ecology, evolution, and conservation of Caatinga amphibians.

The first compilation on the diversity of Caatinga amphibians listed 48 species occurring within the region (Rodrigues 2003). Because species from relictual forests and other mesic areas were not considered, this number was recognized as a sub-estimate of Caatinga amphibian diversity (Rodrigues 2003). Since then, many new species have been described not only for typical Caatinga areas such as the ones addressed by Rodrigues (2003), but many for mesic enclaves and contact zones between the Caatinga and Atlantic Forests and the Caatinga and Cerrado. More recent compilations listed 56 species for the region, but also did not incorporate mesic enclaves in the analysis (Albuquerque et al. 2012). In addition, many papers describing inventories and/or compiling information on whole states are now available. Likewise, a recent increase in the density of researchers in northeastern Brazil has also contributed to a deeper understanding of amphibian ecology in the region.

5.2.1 Taxonomy

Several new species have been described for the Caatinga in recent years (e.g., Napoli and Juncá 2006; Magalhães et al. 2014). Many of such descriptions are from species associated with moister areas, such as *brejos de altitude* in Ceará (Hoogmoed et al. 1994; Roberto et al. 2014) and portions of the Espinhaço range in Bahia, such as Chapada Diamantina (Napoli et al. 2011; Pombal-Jr et al. 2012; de Carvalho et al. 2013; Juncá et al. 2015). Furthermore, species once considered widespread across the open diagonal have been found actually to be species complexes (Narvaes and Rodrigues 2009; Caramaschi and Napoli 2012; de Sá et al. 2014). The description of species from such complexes (Stevaux 2002; Narvaes and Rodrigues 2009), along with new taxa from lowland areas (Magalhães et al. 2014), has also contributed to the increase in the recognized diversity of the Caatinga. Some of these new species are clearly identifiable through traditional amphibian taxonomy tools, such as external morphology and advertisement calls (Magalhães et al. 2014), while integrative taxonomy approaches have helped identify otherwise cryptic lineages (Andrade et al. 2016).

Likewise, phylogeography has also helped identify undescribed taxa in the open diagonal, such as lizards (Werneck et al. 2012; Oliveira et al. 2015). For instance, because many species once thought to be widespread across the open diagonal were described based on specimens from Chaco or Cerrado, strong structure, deep divergences, and lack of gene flux between populations from type localities and the Caatinga are now being used as evidence for the existence of cryptic lineages. Following this lineage species concept (de Queiroz 1998), several new species of frogs have been identified, such as *Leptodactylus* aff. *chaquensis* (A. A. Garda, unpublished data), *Dendropsophus* aff. *minutes* (Gehara et al. 2014), *Pseudopaludicola* aff. *mystacalis* (Andrade et al. 2016), *Phyllomedusa* aff. *nordestina* (São Pedro 2014), and *Dermatonotus* aff. *muelleri* (São Pedro 2014; Gehara et al. 2017). Most, however, still await formal taxonomic description.

Some species groups are notoriously problematic and can hamper appropriate analyses of regional biodiversity (even that conducted herein). For example, species complexes such as *Leptodactylus latrans* and *Scinaxx-signatus* demand not only taxonomic revisions but also thorough re-examination of museum specimens to appropriately identify species distribution limits. Such re-evaluations are especially important in contact zones between the Caatinga and Atlantic Forest, where at least two species, *L. latrans* and *L.* aff. *chaquensis*, can be found. Furthermore, poor sampling across most of the region is likely to severely influence biodiversity estimates. Enormous areas of the Caatinga have never been surveyed, and several others were visited outside the peak of reproductive periods. Low sampling in areas with high levels of endemism, such as Chapada Diamantina, are particularly troublesome.

5.2.2 Ecology

Ecological knowledge of the Caatinga's amphibians is still in its infancy; only a handful of papers on its population and community ecology have been published (Arzabe et al. 1998; Vieira et al. 2007; Xavier and Napoli 2011; Protázio et al. 2015b), and long-term ecological studies simply do not exist. Such an absence of studies is no surprise, considering that most major cities in northeastern Brazil are on the Atlantic coast and large areas of the Caatinga have never even been surveyed. For a long time, this precluded year-round population and community studies in which the strong seasonality of the region could be addressed. Furthermore, rainfall unpredictability made opportunistic studies nearly impossible for researchers living outside the Caatinga itself. This scenario started to change in the late 1990s, with pioneering work published by researchers who established themselves away from the capitals (Arzabe and de Almeida 1997; Arzabe 1999).

Such efforts were fuelled by government initiatives to map priority areas for research conservation (MMA 2007), followed by funding to conduct research in key areas. This automatically led to an increase in papers, book chapters, and books with species lists for areas previously unknown for herpetologists (Borges-Nojosa and Cascon 2005; Loebmann and Haddad 2010; Moura et al. 2010; Santana et al. 2015), and to population and community ecology papers (Arzabe 1999; Vieira et al. 2007, 2009; Xavier and Napoli 2011; Protázio et al. 2015b; Cascon and Langguth 2016), natural history studies (Kokubum et al. 2009; Jorge et al. 2015), and studies on the physiology of Caatinga frogs (Navas et al. 2002; Prates and Navas 2009; Prates et al. 2013; Madelaire and Gomes 2016). Such a proliferation of studies, however, only marginally increased our understanding of the ecology of Caatinga amphibians.

For example, there are surprisingly few papers on the population ecology of Caatinga frogs. Although some have addressed entire communities for more than 1 year (Vieira et al. 2007; Xavier and Napoli 2011; Protázio et al. 2015a, b; Ferreira-Silva et al. 2016), only three papers have focused on one population for longer periods (Jorge et al. 2015; Caldas et al. 2016b; Camurugi et al. in press). Yet, ecological information on some species is available in some classic papers on Caatinga frogs, such as that by Jared et al. (1999) which described natural history aspects of the emblematic *Corythomantis greeningi*. Also, nine reproductive modes have been reported for the region (Vieira et al. 2009), but only considering previous species richness reported for typical Caatinga vegetation sites (Rodrigues 2003; Albuquerque et al. 2012).

Community ecology papers, addressing temporal and spatial niches over time, have only been conducted in about ten sites at the Caatinga (Arzabe et al. 1998; Arzabe 1999; Vieira et al. 2007; Xavier and Napoli 2011; Protázio et al. 2015a, b; Ferreira-Silva et al. 2016). Most papers used more descriptive approaches, outlining yearly activity patterns and microhabitat use (Arzabe et al. 1998; Vieira et al. 2007; Cascon and Langguth 2016; Ferreira-Silva et al. 2016). As expected, rainfall is a major determinant of frogs' activity year round (Cascon and Langguth 2016; Ferreira-Silva et al. 2016). A few papers, in contrast, specifically tested hypotheses by addressing factors responsible for community structure (Xavier and Napoli 2011; Protázio et al. 2015a, b). For example, the spatial distribution of frog species at Chapada Diamantina was significantly related to vegetation structure (Xavier and Napoli 2011), while at a lowland Caatinga site in Paraíba, phylogeny, as opposed to recent competition, was shown to affect community structure (Protázio et al. 2015b).

Water economy is a central issue for amphibians living in xeric environments for obvious reasons, and has significantly affected their morphology, sensory systems and behavior, physiology, and ecology (Warburg 1997). Restrictions imposed by scarce water availability in arid and semi-arid regions may limit species diversity by selecting clades tolerant to such conditions while shaping their ecology, natural history, and behavior. Many traits related to water economy in xeric environments have been reported for Caatinga amphibians (Navas et al. 2004), including behavioral (Navas et al. 2002), thermal tolerance (Simon et al. 2015), physiological (Pereira et al. 2007), ecological (Maciel and Juncá 2009), and morphological adaptations (Navas et al. 2002; Prates and Navas 2009). Most papers, however, are restricted to a handful of model species for the region (e.g., *Rhinella granulosa*, *Rhinella jimi*, and *Pleurodema diplolister*).

5.2.3 Biogeography

No comprehensive compendium has been published on the diversity of frogs from the Caatinga. Previous book chapters and publications have listed 48 and 56 species for the region (Rodrigues 2003; Albuquerque et al. 2012). Such analyses are confounded by difficulties in establishing the limits to the Caatinga (Camardelli and

Napoli 2012) and by the lack of appropriate databases. Furthermore, no single analysis has evaluated amphibian richness throughout the entire Caatinga, mainly because of the complete lack of data for large portions of the region.

Biogeographically, the best analysis evaluated areas of amphibian endemism for the region using a comprehensive database of the best-sampled localities and identified 15 priority areas for conservation in the region based on a parsimony analysis of endemism (Camardelli and Napoli 2012). Herein, we use niche modeling to generate binary maps for species occurring in the Caatinga to produce a surface of potential richness for the region. We then discuss the results obtained in light of the priority areas proposed by Camardelli and Napoli (2012) and based on other idiosyncrasies of the region.

5.3 Potential Richness of Caatinga Amphibia

We constructed a database with species distribution records from online repositories (speciesLink [http://splink.cria.org.br/], GBIF [Global Biodiversity Information Facility; https://www.gbif.org/]), literature records, and information from scientific collections that kindly shared their records. We considered species to be present in the Caatinga when at least one locality was reported from within the Caatinga limits adopted in the present book.

As expected, the inclusion of species from mesic areas almost doubled the recognized diversity for the region compared to the most recent account (56; Albuquerque et al. 2012). In total, 98 species belonging to 12 families occur in the Caatinga, with Hylidae and Leptodactylidae harboring 67% of the region's diversity (66 species, Table 5.1, Fig. 5.1). Our results indicate 20 endemic species (one under description, *Pristimantis* sp., for Ceará), of which 14 are restricted to mesic enclaves (12 from the Chapada Diamantina in Bahia and four from *brejos* in Ceará, Table 5.1). Only *Ceratophrys joazeirensis*, *Proceratophrys caramaschi*, *P. aridus*, and *Chthonerpeton arii* are endemic species associated with lowland areas (Table 5.1). Another 13 species are mostly distributed within the Caatinga, despite entering neighbor regions (Cerrado and Atlantic Forest), some of which could be considered endemic if a less strict criterion is used.

We constructed a richness surface based on the juxtaposition of binary distribution maps for the 98 amphibians reported for the Caatinga. We used maps generated through modeling of potential distributions for species for which this was possible. Otherwise, we constructed 10 km buffers or convex polygons encompassing all occurrence points for species known from very few localities. For species with at least nine occurrence points we modeled potential distributions using the Maximum Entropy Modeling (MaxEnt) (Phillips et al. 2006) as follows: for each species we constructed ten replicate models using the bootstrap method and saved the consensus among all replicas as the final map. In each replica, we randomly selected 10% of each species records, which were later used to test the model generated. We

Table 5.1 Amphibian species reported for the Caatinga biome used to generate the surface of potential richness in the present study (Fig. 5.1)

Binary source	Species	Distribution
Bufonidae (6)		
Shape/buffer	*Rhinella casconi*[a]	E
Modeled	*Rhinella crucifer*	AF
Modeled	*Rhinella granulosa*	W
Modeled	*Rhinella hoogmoedi*	AF
Modeled	*Rhinella jimi*	AF/Ca
Modeled	*Rhinella rubescens*	Ce
Caeciliidae (3)		
Shape/buffer	*Siphonops annulatus*	W
Shape/buffer	*Chthonerpetonarii*	E
Modeled	*Siphonops paulensis*	W
Ceratophryidae (2)		
Modeled	*Ceratophrys aurita*	AF
Modeled	*Ceratophrys joazeirensis*	E
Craugastoridae (3)		
Modeled	*Haddadus aramunha*[b]	E
Modeled	*Pristimantis ramagii*	AF
Modeled	*Pristimantis* sp.[a]	E
Eleutherodactylidae (2)		
Shape/buffer	*Adelophryne baturitensis*[a]	E
Shape/buffer	*Adelophryne maranguapensis*[a]	E
Hylidae (39)		
Modeled	*Bokermannohyla alvarengai*	Ce/Ca
Modeled	*Bokermannohyla diamantina*[b]	E
Shape/buffer	*Bokermannohyla flavopicta*[b]	E
Modeled	*Bokermannohyla itapoty*[b]	E
Shape/buffer	*Bokermannohyla juiju*[b]	E
Modeled	*Bokermannohyla oxente*[b]	E
Modeled	*Corythomantis galeata*[b]	E
Shape/buffer	*Corythomantis greeningi*	Ce/Ca
Modeled	*Dendropsophus branneri*	W
Modeled	*Dendropsophus minusculus*	AM
Modeled	*Dendropsophus minutus*	W
Modeled	*Dendropsophus nanus*	W
Modeled	*Dendropsophus novaisi*	AF/Ca
Modeled	*Dendropsophus oliveirai*	AF
Modeled	*Dendropsophus rubicundulus*	Ce
Modeled	*Dendropsophus soaresi*	AF/Ca
Modeled	*Gastrotheca fissipes*	AF
Modeled	*Hypsiboas albomarginatus*	AF
Modeled	*Hypsiboas albopunctatus*	Ce

(continued)

Table 5.1 (continued)

Binary source	Species	Distribution
Modeled	*Hypsiboas crepitans*	W
Modeled	*Hypsiboas faber*	AF
Modeled	*Hypsiboas multifasciatus*	Ce
Modeled	*Hypsiboas raniceps*	W
Shape/buffer	*Phyllodytes acuminatus*	AF
Modeled	*Phyllomedusa bahiana*	AF
Modeled	*Phyllomedusa nordestina*	AF/Ca
Modeled	*Pseudis bolbodactyla*	Ce
Modeled	*Scinax auratus*	AF
Shape/buffer	*Scinax camposseabrai*	AF/Ca
Modeled	*Scinax eurydice*	AF
Modeled	*Scinax fuscomarginatus*	W
Shape/buffer	*Scinax montivagus*[b]	E
Modeled	*Scinax nebulosus*	W
Modeled	*Scinax pachycrus*	Ca
Modeled	*Scinax x-signatus*	Ca
Not included	*Trachycephalus atlas*	AF/Ca
Modeled	*Trachycephalus nigromaculatus*	AF
Modeled	*Trachycephalus typhonius*	Ce
Shape/buffer	*Xenohyla eugenioi*	AF/Ca
Hylodidae (1)		
Shape/buffer	*Crossodactylus* cf. *trachystomus*	?
Leptodactylidae (28)		
Not included	*Adenomera* cf. *andreae*	AM
Not included	*Adenomera* cf. *hylaedactyla*	AM
Modeled	*Leptodactylus* aff. *chaquensis*	Ca
Modeled	*Leptodactylus caatingae*	Ca
Modeled	*Leptodactylusfurnarius*	Ce
Modeled	*Leptodactylus fuscus*	W
Modeled	*Leptodactylus latrans*	AF
Modeled	*Leptodactylus mystaceus*	W
Modeled	*Leptodactylus mystacinus*	W
Modeled	*Leptodactylus natalensis*	AF
Shape/buffer	*Leptodactylus oreomantis*[b]	E
Modeled	*Leptodactylus podicipinus*	Ce
Modeled	*Leptodactylus pustulatus*	Ce
Modeled	*Leptodactylus syphax*	W
Modeled	*Leptodactylus troglodytes*	W
Modeled	*Leptodactylus vastus*	W
Modeled	*Physalaemus albifrons*	Ca
Modeled	*Physalaemus centralis*	W
Modeled	*Physalaemus cicada*	Ca

(continued)

Table 5.1 (continued)

Binary source	Species	Distribution
Modeled	*Physalaemus cuvieri*	W
Modeled	*Physalaemus kroyeri*	Ca
Modeled	*Pleurodema alium*	Ca
Modeled	*Pleurodema diplolister*	Ca
Shape/buffer	*Pseudopaludicola jaredi*	AF/Ca
Modeled	*Pseudopaludicola mystacalis*	W
Modeled	*Pseudopaludicola pocoto*	Ca
Modeled	*Rupirana cardosoi*[b]	E
Microhylidae (4)		
Shape/buffer	*Chiasmocleis cordeiroi*	AF
Modeled	*Dermatonotus muelleri*	W
Modeled	*Elachistocleis cesarii*	W
Modeled	*Elachistocleis piauiensis*	Ca
Odontophrynidae (8)		
Modeled	*Odontophrynus carvalhoi*	AF/Ca
Shape/buffer	*Odontophrynus* cf. *americanus*	AF/Ca
Shape/buffer	*Proceratophrys aridus*	E
Shape/buffer	*Proceratophrys caramaschii*	E
Modeled	*Proceratophrys cristiceps*	Ca
Shape/buffer	*Proceratophrys minuta*[b]	E
Shape/buffer	*Proceratophrys redacta*[b]	E
Modeled	*Proceratophrys renalis*	AF
Pipidae (2)		
Modeled	*Pipa carvalhoi*	W
Modeled	*Pipa pipa*	Am
Ranidae (1)		
Modeled	*Lithobates palmipes*	Am/AF

The source of binary maps produced for each species included niche model maps (modeled), buffers around single localities, and convex hulls for species with less than nine localities (see Sect. 3 for a description of the methods used). Species were categorized according to their distribution *AF* mostly Atlantic Forest, *Am* mostly Amazon Forest, *Ca* mostly the Caatinga, *Ce* mostly Cerrado, *E* endemic to the Caatinga, *W* widespread (common in ≥3 biomes)

[a] Species endemic to *brejos de altitude* (mesic enclaves) in Ceará State

[b] Species endemic to the Espinhaço Range (Chapada Diamantina) in central Bahia State

gathered climatic variables from the WordClim database at a resolution of 2.5 arcminutes (approximately 5 × 5 km) for the year 2000 (www.worldclim.org; Hijmans et al. 2005). To model species distributions we selected only variables that had correlation coefficients equal to or smaller than 90% for each group, resulting in nine variables from WorldClim being added to altitude. We reclassified environmental suitability values of average models according to a threshold to produce binary maps (0 for absence and 1 for potential presence). The threshold chosen was

Fig. 5.1 Sample of amphibians from the Caatinga biome, northeastern Brazil: (**a**) *Rhinella jimi*; (**b**) *Siphonops paulensis*; (**c**) *Ceratophrys joazeirensis*; (**d**) *Pristimantis ramagii*; (**e**) *Adelophryne baturitensis*; (**f**) *Corythomantis greeningi*; (**g**) *Dendropsophus nanus*; (**h**) *Hypsiboas raniceps*; (**i**) *Phyllomedusa nordestina*; (**j**) *Scinax pachycrus*; (**k**) *Pseudopaludicola pocoto*; (**l**) *Rupirana cardosoi*; (**m**) *Leptodactylus* aff. *chaquensis*; (**n**) *Physalaemus cicada*; (**o**) *Dermantonotus muelleri*; (**p**) *Proceratophrys cristiceps*; (**q**) *Pipa carvalhoi*; and (**r**) *Lithobates palmipes*

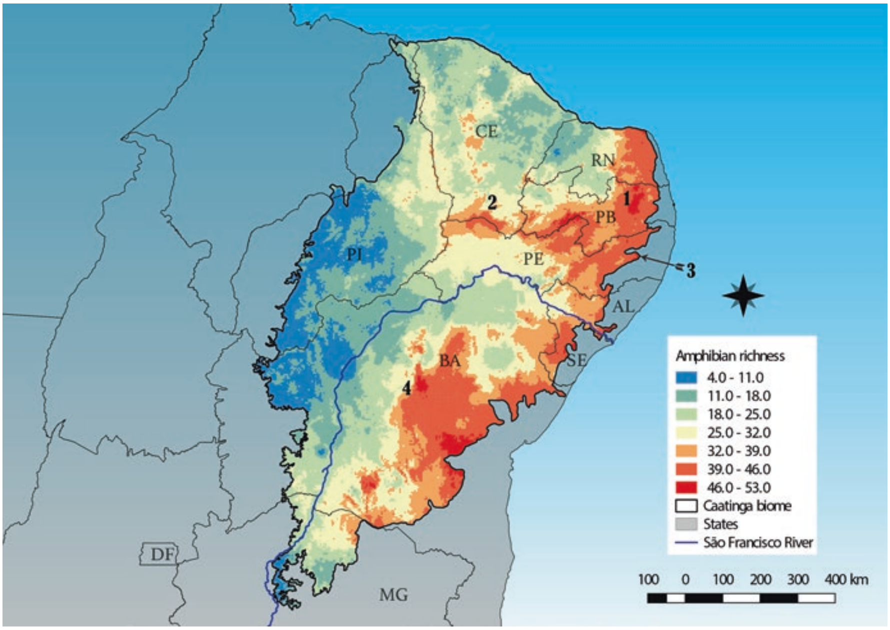

Fig. 5.2 Surface of potential amphibian richness for the Caatinga biome, northeastern Brazil, generated by the overlap of binary occurrence maps resulting from niche models and buffers (for species with low number of localities). Numbers indicate high diversity areas discussed in the text: (*1*) Borborema plateau; (*2*) Chapada do Araripe; (*3*) Caruaru; and (*4*) Chapada Diamantina. Brazilian states: *AL* Alagoas, *BA* Bahia, *CE* Ceará, *DF* Distrito Federal, *MG* Minas Gerais, *PE* Pernambuco, *PB* Paraíba, *PI* Piauí, *SE* Sergipe

based on the Maximum training sensitivity plus specificity parameter (Max SSS; Liu et al. 2013).

The juxtaposition of binary maps produced a surface of potential richness for Caatinga amphibia, with regions ranging from low to high numbers of species (<11–53, Fig. 5.2). The upper value recovered is higher than those reported for most local studies, where some of the best-surveyed lowland areas had richness ranging from 21 to 26 species (Garda et al. 2013). Even ecotone areas, such as the Caatinga/Atlantic Forest (35 species; Magalhães et al. 2013) and enclaves with influences of Cerrado, Caatinga, and Atlantic Forest (31 species; Ribeiro et al. 2012) have lower richness. The most diverse areas found by Camardelli and Napoli (2012), in comparison, ranged from 31 to 40 species.

Nevertheless, our results do not represent absolute richness values, but rather potential richness, and the general pattern is what should be compared instead. Indeed, many regions with the highest species diversity in the present analysis match hotspots and high richness areas previously reported for the Caatinga and semi-arid regions of Brazil (Camardelli and Napoli 2012). These include well-known high diversity areas in the Caatinga such as sites 3 and 4 (Fig. 5.2), which match Camardelli and Napoli's highest diversity sites (Camardelli and Napoli

2012). The correspondence between such analyses underscores an emerging general trend for Caatinga amphibian diversity.

Nevertheless, some areas with high potential richness found herein are new and deserve to be investigated. These include areas in Paraíba and Ceará (Fig. 5.2, sites 1 and 2—Brejo Paraibano and Chapada do Araripe, respectively), and the southwestern border between Paraíba and Pernambuco. Most other high richness values are found along the eastern portion of the region, near the contact zone with the Atlantic Forest, corresponding to Raso da Catarina and Planalto da Borborema ecoregions, as well as to transition areas in Bahia and *brejos de altitude* in Pernambuco and Paraíba (Fig. 5.2). Also, at the central portion, the Chapada Diamantina presented elevated richness, as well as Chapada do Araripe. Indeed, some of the most species-rich sites include transition areas in Bahia. Some areas of endemism for the semi-arid region of Brazil, although not figuring among the most diverse sites, also presented high overall potential diversities (Maranguape, 25–32 species).

Still, some regions have low richness, especially areas west of the region that have been less surveyed and are outside the influence of Atlantic Forest-related species. Again, these low diversity areas match those indicated by Camardelli and Napoli (2012), most of which are sites on the western portion of the region in Bahia and Piauí (denoted as Q13, Q28, Q31, and Q45 in Figure 1 in Camardelli and Napoli 2012). Sampling may cause bias in richness estimates for these low-species areas, given that it is rare to find a site in Brazil with fewer than 15 frog species. For example, only in 2016 was a list of amphibians for a Caatinga locality in Rio Grande do Norte, which occupies an area of 52,000 km^2 (equivalent to West Virginia in the USA, or to the Netherlands), published (Caldas et al. 2016a). The authors reported 19 species of amphibians for the region, which lies just west of two of the lowest-diversity areas identified by Camardelli and Napoli (2012) (Q4 and Q7 in Figure 1 of their article; <11 species). Our map, already including data from Caldas et al. (2016a), points to much higher potential richness for these two quadrats, indicating that some apparently low-diversity areas may be the result of sampling bias.

Indeed, although the modeling of potential distributions can help predict species ranges, a comprehensive database to generate such models is paramount for avoiding bias and incorrect results. Our map of potential richness must be interpreted with caution in respect to absolute numbers, as overestimation/underestimation of local richness is possible.

5.4 Conservation

Caatinga amphibians are subject to the same general problems affecting all of the Caatinga biota: high rates of degradation and deforestation, extremely small networks of protected areas, desertification, and climate change (Leal et al. 2005). Although according to IUCN (the International Union for Conservation of Nature and Natural Resources) most species in the Caatinga are not endangered, taxa with restricted distributions, such as those found in mesic areas, are of special concern. Indeed, the only frogs listed in an endangered category for the Caatinga are *Adelophryne baturitensis* and *A. maranguapensis* (vulnerable and endangered, respectively) are restricted to mesic areas (IUCN 2016). Because these areas are small, and most have been used heavily for agriculture and tourism (Ab'Sáber 2003), pressure on the environment tends to be higher as well as local diversity being high, with several species yet to be described. Indeed, 16 of 20 amphibian species endemic to the Caatinga were described only after 2006. Furthermore, many clearly distinguishable undescribed species await formal description or are currently being described, several of which are from mesic regions. Yet, new taxa from lowland areas have also been described recently (Magalhães et al. 2014), which along with several species whose distributions are highly dependent on the Caatinga ('Ca' in Table 5.1), indicate that conservation initiatives must also target these areas.

Because of higher recorded and potential richness and endemism, most conservation efforts and attention have been directed at mesic enclaves in the Caatinga (Camardelli and Napoli 2012; Xavier et al. 2015). Nevertheless, lowland areas harbor many species that, albeit not endemic to the Caatinga, have most of their distribution confined to this region (AF [mostly Atlantic Forest]/Ca, Ce [mostly Cerrado]/Ca, and Ca, in Table 5.1: 24 species). Future conservation efforts should also focus on better identifying priority areas outside or not solely restricted to mesic enclaves that ensure conservation of lowland taxa. Furthermore, expanding current areas within *brejos* and other humid areas is paramount for protecting currently recognized species and also the undescribed taxa they harbor.

Our superficial knowledge of Caatinga amphibians' population dynamics, drivers of community structure, and physiology severely hamper our ability to predict global warming effects on the region. Indeed, because of the imminent threat of climate change on the Caatinga (Salazar et al. 2007), increased aridity is likely to severely impact anurans, despite some analysis indicating that other endemic vertebrates (mammals and lizards) may increase their areas of climatic suitability (de Oliveira et al. 2012). Intuitively, increased aridity should impact more lowland taxa, which occupy drier areas. Still, better models are necessary to predict range contractions across the Caatinga, which, associated with better distribution data, will help predict more precisely global warming impacts on the region.

Protecting Caatinga amphibian biodiversity will require a concerted effort to fill large information gaps, despite the substantial increase shown here for the last two decades. Thorough taxonomic evaluation using integrative tools, field inventories to build solid databases for biogeographic and biodiversity analyses, support for long-term ecological studies, and research on physiological tolerances and adaptations to arid environments are vital. Finally, capacity building outside major urban centers is one of the most important steps to rapidly leverage our understanding of the region's biodiversity and the opportunities and needs for its long-term conservation.

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Chapter 6
Species Composition, Biogeography, and Conservation of the Caatinga Lizards

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Abstract The Caatinga is one of the few semiarid regions in the subtropical zone surrounded by humid areas. Its fauna was previously considered impoverished and with few endemics, but many surveys have been conducted in the last two decades and it is now possible to perform a more accurate and realistic analysis of Caatinga lizard diversity and biogeography. Our objectives in the present chapter are to (1) review the literature on the origin and diversification of Caatinga lizards; (2) provide an updated species list and categorize distribution patterns; (3) identify potential areas that could hold high species richness; and (4) evaluate whether the proposed division of the Caatinga into different ecoregions reflects patterns of lizard endemism. We found 79 lizard species belonging to 13 families. Among them, 49 are typical from the Caatinga, eight occur in forested habitats, nine are typical from Cerrado habitats, three are endemic to humid forest enclaves ('*brejos de altitude*') and eight occur only in rocky outcrops from the Espinhaço Mountain Range. The areas of endemism recovered corroborate most of the proposed ecoregions, and the most diverse areas are at the marginal portions of the Caatinga, with nuclear areas showing lower richness potentials. We identified 38 endemic species most from paleoclimatic dunes from São Francisco River and 'Raso da Catarina'. We can now confirm that previous suggestions about the Caatinga fauna being species poor and having low endemism are not correct. It is clear that the Caatinga shares part of its fauna with Cerrado, Atlantic Forest, and even with Chaco, but the number of endemics is relatively high and still rising as new data become available. With the results generated here we indicate some directions for future studies and conservation priorities.

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6.1 Introduction

The Caatinga is one of the few semiarid regions in the subtropical zone that is surrounded by humid areas (Ab'Saber 1970, 1974), occurring exclusively in northeastern Brazil (Ab'Saber 1974, 1977; Rizzini 1997; Prado 2003; see Chaps. 1 and 2). Despite centuries of inadequate soil use and uncontrolled exploration of its natural resources (see Chaps. 13 and 14), the Caatinga has been neglected in terms of research efforts and conservation policies (Chaps. 17 and 18). Only recently have governmental and non-governmental sectors focused conservation efforts in the region (Velloso et al. 2002), while also promoting an understanding of the distribution of phytophysiognomies within the Caatinga (Araújo et al. 2005), dividing it into eight distinct ecoregions (Velloso et al. 2002). However, these ecoregions were delimited without information on animal species distributions. Therefore, it is not clear to what extent they represent fauna elements, making their use in planning land use and developing conservation policy risky.

The Caatinga fauna (sensu Ab'Saber 1974, 1977) was previously considered impoverished and mostly lacking endemic species, comprising a large proportion of widely distributed species shared along the diagonal of open formations (DOF) in South America (Vanzolini 1974, 1988; Mares et al. 1981; Willig and Mares 1989). However, this description resulted from poor sampling coverage and lack of information on adjacent regions (Rodrigues 2005b; Albuquerque et al. 2012; Barbosa et al. 2013). When considering all the different vegetation types within the Caatinga, including mesic enclaves known as *brejos de altitude*, 79 lizard species are known in the region (present study). This number is similar to the adjacent Cerrado (76 species; Brites et al. 2009; Nogueira et al. 2011), but lower than the much larger Amazon Forest (132 species; Vogt and Bernhard 2003). Despite this high richness, the geographic distribution of most species is still poorly known, and new field surveys and taxonomic appraisals are likely to increase the known diversity.

The Caatinga and Cerrado were believed to share most of their lizard faunas as a result of a homogenization process promoted mainly by expansions and retractions of both regions during Quaternary (Vanzolini 1976, 1981; Vanzolini and Williams 1981). Habitat fluctuations would have led to a predominance of species with broad ecological requirements and widely distributed in both regions. However, recent papers have challenged the view that Quaternary events were the main drivers of lizard diversification in open areas of the Neotropical Region (Colli et al. 2002; Colli 2005; Werneck 2011; Werneck et al. 2011). Indeed, older events from the Tertiary seem to have been more important to species diversification in these regions (Silva 1995; Silva and Bates 2002; Colli 2005; Werneck et al. 2011).

Few studies on the Caatinga lizards were published during the 1970s and 1980s, and most were conducted in core areas, such as the 'Depressões Sertanejas'. Species diversity reported for these areas were lower than in marginal areas in contact with other regions, such as Cerrado and Atlantic Forest (Vanzolini 1974; Vanzolini et al. 1980; Vitt 1995). Studies from a particular region, the dunes along the São Francisco River, showed high richness and endemism (Rodrigues 1996). Rodrigues (2005b) reviewed information on distributions of Caatinga lizards and suggested that sandy soils were related to high speciation rates and levels of endemism. In addition, he provided a list of 150 sampled sites, but most had as few as three lizard species reported. By contrast, a typically well-sampled site in the Caatinga has more than 15 species (Vanzolini et al. 1980; Vitt 1995; Rodrigues 2005b; Garda et al. 2013; Cavalcanti et al. 2014). Likewise, the humid forest enclaves were also highlighted as important centers of diversity and endemism. The first zoogeographical studies evaluated these areas separately, not considering them part of the Caatinga, which led to an incomplete view of the region (Rodrigues 2005b). Indeed, many species from semiarid regions are intrinsically related to climatic and geological characteristics of these areas (Vanzolini 1981; Vanzolini and Williams 1981). The perception of the Caatinga as a region led to the inclusion of more areas in biogeographic studies and richness estimates, helping biologists to create a more precise picture of its local biodiversity.

Since the publication by Rodrigues (2005b), many surveys have been conducted in the Caatinga. These new studies significantly increased our knowledge on the composition and distribution of lizard species in the Caatinga (Arzabe et al. 2005; Delfim and Freire 2007; Freire et al. 2009; Garda et al. 2013; Pedrosa et al. 2013; Cavalcanti et al. 2014; Magalhães et al. 2015; Caldas et al. 2016). Furthermore, several new species were described and/or synonymized (Rodrigues and Santos 2008; Cassimiro and Rodrigues 2009; Rodrigues et al. 2009a, b; Arias et al. 2011a, b; Oliveira et al. 2015), whereas others were first recorded within the region. This caused the number of lizards species known to occur in the Caatinga to rise from 61 (Borges-Nojosa and Caramaschi 2005; Rodrigues 2005b) to 79 (present work) in one decade.

Because of the amount of information recently published, it is now possible to conduct a more accurate analysis of the distribution patterns of Caatinga lizards. Our objectives in this chapter are to (1) review the literature on the origin and diversification of Caatinga lizards; (2) provide an update of the species list and the distribution patterns of Caatinga lizards; (3) overlay species distributions within the Caatinga to understand how species richness varies geographically and identify areas that may hold high species richness; and (4) evaluate whether the proposed division of the Caatinga into different ecoregions (Velloso et al. 2002) reflects lizard patterns of endemism. With this general overview of lizard macroecology and biogeography in the Caatinga, we hope to contribute to a better understanding of the history of this region. We also expect to provide biological information that can be used in conservation studies and policies, which is now critical due to the high rates of habitat loss in the Caatinga (Leal et al. 2005; Rodrigues 2005a; Chap. 13).

6.2 The Origin and Diversification of Caatinga Lizards

Quaternary climatic fluctuations have been traditionally invoked to explain the origin and diversification of South America lizards (Vanzolini 1974; Heyer 1978; Duellman 1979). However, new data and new interpretations indicate that older events (Tertiary) may have been more important in shaping the diversity patterns we observe today (Colli et al. 2002; Colli 2005). During the Tertiary, South America remained isolated for a long period resulting in high diversification rates and an endemic biota (Heyer and Maxson 1982; Estes and Báez 1985; Bauer 1993). Initially, moisture increased, reaching a peak in the Eocene, after which the uplift of the Andes caused the climate to become progressively colder and drier, with an increased latitudinal differentiation (Webb 1978; Parrish 1993). The deepest divergences in South American lizards, including the main split separating savanna and forest dwellers, occurred during this period. In addition, plants also experienced great diversification rates during Tertiary (Romero 1993). This in turn influenced and modified the main floristic provinces of South America. One of these, the Mixed Microfloral Province, was characterized by a combination of temperate and tropical elements, including species adapted to dry environments (Romero 1993). The main open areas in South America probably originated from this province, including the Cerrado and the Caatinga (Romero 1993; Colli 2005).

From the Oligocene to the Pleistocene, South America had larger areas covered by open landscapes and dry climates (Pascual and Jaureguizar 1990; Colli 2005). Consequently, lizards adapted to open areas had a long time to diversify. Four main events could have been responsible for diversification during Tertiary (Colli 2005): (1) the establishment of a climatic gradient associated with the formation of three main floristic provinces at the end of Tertiary; (2) the great marine transgression in the Eocene; (3) the uplift of the Central Brazilian Plateau; and (4) the arrival of immigrants from North America at the end of Tertiary. These could have been the most important events for the origin of the shared fauna between Cerrado and Caatinga. The oldest fossil records from lizard families that occur today in the Caatinga belong to the families Iguanidae and Teiidae (Albino 1996; Colli 2005). Iguanidae probably originated during Gondwana (Bauer 1993) and Teiidae in North America. Teiids then dispersed to South America during Cretaceous, where they experienced an adaptive radiation during Tertiary (Vanzolini and Heyer 1985; Colli 2005). Scincidae also originated in Gondwana and fossils have been found in Africa (Vanzolini and Heyer 1985). Gekkonidae, Phyllodactylidae, and Sphaerodactylidae were first recorded in the Paleocene (Báez and Gasparini 1979; Estes and Báez 1985). There are no fossils for Gymnophthalmidae, Hoplocercidae, and Tropiduridae, but because they are endemic to South America (Guyer and Savage 1986; Frost and Etheridge 1989), they probably originated in this continent. The diversification of some species of *Iguana*, *Tupinambis*, *Cnemidophorus*, *Lygodactylus*, *Hemidactylus*, *Gymnodactylus*, and *Mabuya* appears to have occurred during Tertiary (Colli et al. 2002; Colli 2005; Werneck and Colli 2006), explaining why some Caatinga open areas species are shared with other environments, such as Chaco and Cerrado. In addition to Tertiary events, climatic changes during Quaternary appear to have influenced diversification of some groups, such as *Enyalius*, *Coleodactylus*, *Diploglossus*, and several gymnophthalmids associated with forested areas. The vanishing refuge theory posits that during glacial periods in Quaternary forested environments retracted and xeric areas expanded (Haffer 1969; Vanzolini and Williams 1970, 1981), and populations of these species possibly thrived by retreating to sites with tolerable conditions for them.

Pleistocene climatic cycles have also been shown have influenced the Caatinga fauna, even though major cladogenic events are older, usually dating back to the Miocene. Several researchers have recently evaluated the phylogeographic structure and recent demographic history of Caatinga lizards (Werneck et al. 2012, 2015; Recoder et al. 2014). Results have unveiled a hidden diversity of cryptic species under several widespread species (Werneck et al. 2012, 2015), gene flow and shallow diversity for morphologically different populations recently described as new species (Oliveira et al. 2015), and a general pattern of population expansion for several taxa (Werneck et al. 2012; Recoder et al. 2014; Oliveira et al. 2015; Gehara et al. 2017). Furthermore, the genetic structure of sister species and/or populations shared between the Caatinga and Cerrado is shallower and younger in the former. Based on coalescent simulations and Approximate Bayesian Computation analysis, Oliveira et al. (2015) showed that whiptail lizards (*Ameivula* gr. *ocellifera*) in the Caatinga diverged from Cerrado populations in the Miocene. This divergence was followed by a rapid expansion in a founder-effect fashion, with continuous gene flow among the Caatinga and Cerrado lineages throughout the Pleistocene. Processes such as this one could likely be shared by other taxa and may represent a general mechanism related to the divergence of the DOF fauna.

6.3 Species Composition and Distribution Patterns of Caatinga Lizards

We collected lizard distribution data from ten scientific collections: Coleção Herpetológica da Universidade Federal de Sergipe (CHUFS); Museu de História Natural da Universidade Federal de Alagoas (MUFAL); Coleção Herpetológica da Universidade Federal da Paraíba (CHUFPB); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Nacional do Rio de Janeiro (MNRJ); Núcleo de Ofiologia da Universidade Federal do Ceará (NUROF); Coleção Herpetológica da Universidade de Brasília (CHUNB); Coleção Herpetólogica da Universidade Federal da Bahia (CHUFBA); Coleção Herpetológica da Universidade Federal de Viçosa (CHUFV); and Coleção Herpetológica da Universidade Estadual de Feira de Santana (UE de Feira de Santana). We examined all specimens from CHUFS, MUFAL, CHUFPB, MNRJ, and NUROF. Curators from CHUNB, CHUFBA, CHUFV, and UE de Feira de Santana identified the specimens in their collections (G.R. Colli, M. Napoli, R.N. Feio, and F. Juncá), while one of us (F.R. Delfim) checked the identifications of the specimens of the remaining collections. Because MZUSP has a very large number of specimens, we reviewed up to five individuals per species per locality. In addition, we conducted field surveys at 18 different sites. At each site we sampled lizards for at least 20 days using 100 pitfall traps (25 arrays with four buckets). We sampled the following localities in Northeast Brazil: Paulo Afonso (Bahia); Quixadá, Santa Quitéria, São Gonçalo do Amarante, and Várzea da Conceição (Ceará); Areia (Paraíba); Arcoverde, Nascente, Trindade, and Serra Talhada (Pernambuco); Paulistana, Pavussu, Rio Grande do Piauí, and São Francisco de Assis do Piauí (Piauí); and Canindé do São Francisco, Poço Redondo, and Nossa Senhora da Glória (Sergipe).

We recorded 79 species from 13 families with at least one record within the Caatinga. Among them, 49 are typical from the Caatinga, eight live in forested habitats (Atlantic Forest, Amazon Forest, or humid forest enclaves), nine are typical from Cerrado habitats, three are endemic from humid forest enclaves, and eight are known to occur only in rocky outcrops from the Espinhaço Mountain Range, in Minas Gerais, and Bahia (Table 6.1). There was also an exotic species (*Hemidactylus mabouia*) and one typical from Argentinian Chaco (*Tropidurus etheridgei*).

We expand the Caatinga distribution patterns proposed by Rodrigues (2005b) to classify lizards in seven broad categories (Table 6.1): 1—wide distribution (WD; 14 species); 2—relictual distribution (RD; 15 species); 3—limited distribution in the Caatinga (L; three species); 4—paleoquaternary sandy dunes from São Francisco River (SF; 13 species); 5—rocky fields from the Espinhaço Mountain Range (ER; eight species); 6—species from adjacent open regions, such as Cerrado/Chaco/and coastal restingas (AA; nine species); and 7—Atlantic Forest and/or humid forest enclaves (FL; 11 species).

Based on our review of museum data and our field surveys, we now know that the Caatinga has 38 endemic species, most associated with sandy soils (Rodrigues 1996; 2005b), but also species restricted to forested environments and/or mesic Caatinga areas and rocky fields related to the Cerrado (Borges-Nojosa and Cascon 2005; Freitas and Silva 2007). Most species that inhabit these relicts are distinct from typical Caatinga species (Borges-Nojosa and Caramaschi 2005; Borges-Nojosa and Cascon 2005). The most diverse lizard families in the Caatinga are Tropiduridae (18 species) and Gymnophthalmidae (25 species). During Tertiary, a pronounced latitudinal temperature gradient promoted the separation of lizards into Meridional and Septentrional groups (Colli 2005). Tropidurids could have been affected by this compartmentalization, which matches the divergence observed among subfamilies: Liolaeminae (Meridional), Tropidurinae, and Leiocephalinae (Septentrional). In addition to Tertiary events, climatic cycles during Quaternary could also have influenced diversification. Isolation in open area enclaves probably resulted in the differentiation of the tropidurids *Eurolophosaurus* and *Tropidurus*, and of most of the Caatinga's gymnophthalmids (Rodrigues 1991a, 1991b, 1991c, 1991d, 1996). Gymnophthalmids from both sandy areas and mesic environments experienced most of their diversification during Quaternary (Rodrigues 2005b).

Table 6.1 Checklist of lizards from the Caatinga with ecological and zoogeographical information

Taxa	Ecological category	Activity	Preferred habitat type	Distribution Pattern	Typical region
Gekkonidae					
Hemidactylus agrius Vanzolini, 1978	T	N	G	?	Caat
Hemidactylus brasilianus (Amaral, 1935)	T	N	G	WD	Caat
Hemidactylus mabouia (Moreau de Jonnès, 1818)	T	N	G/Pa	WD	Ex
Lygodactylus klugei (Smith, Martin & Swain, 1977)	A	D	TB	WD	Caat
Phyllodactylidae					
Gymnodactylus geckoides Spix, 1825	T	D	G	WD	Caat
Gymnodactylus vanzolini Cassimiro & Rodrigues, 2009[a]	T	D	G	ER	RF
Phyllopezus periosus Rodrigues, 1986[a]	T/A	N	S	L	Caat
Phyllopezus pollicaris (Spix, 1825)	T/A	N	G/Pa	WD	Caat
Sphaerodactylidae					
Coleodactylus meridionalis (Boulenger, 1888)	T	D	LL	R	Caat
Mabuydae					
Asparonema aff. *dorsivittatum*	T	D	?	ER	RF
Brasilicincus heathi (Schmidt & Inger, 1951)	T	D	LL	WD	Caat
Copeoglossum arajara (Rebouças-Spieker, 1981)	T	D	LL	OD	Cer
Copeoglossum nigropunctatum (Spix, 1825)	T	D	SA	FC	FE
Psychosaura agmosticha (Rodrigues, 2000)	T	D	B	R	Caat
Psychosaura macrorhyncha (Hoge, 1946)	T	D	B	R	Caat
Dactyloidae					
Norops brasiliensis (Vanzolini & Williams, 1970)	SA	D	TB	OD	Cer
Norops fuscoauratus (D'Orbigny, 1837 *in* Duméril & Bibron, 1837)	A	D	TB	FC	FE

(continued)

Table 6.1 (continued)

Taxa	Ecological category	Activity	Preferred habitat type	Distribution Pattern	Typical region
Hoplocercidae					
Hoplocercus spinosus Fitzinger, 1843	T	D	AT	OD	Cer
Iguanidae					
Iguana iguana (Linnaeus, 1758)	A	D	TB	WD	Caat
Leiosauridae					
Enyalius bibronii Boulenger, 1885	SA	D	G	R	Caat
Enyalius catenatus (Wied, 1821)	SA	D	G	FC	FE
Enyalius erythroceneus Rodrigues, Freitas, Silva & Bertolloto, 2006[a]	SA	D	G	ER	RF
Enyalius pictus (Schinz, 1822)	SA	D	G	FC	FE
Polychrotidae					
Polychrus acutirostris Spix, 1825	A	D	TB	WD	Caat
Polychrus marmoratus (Linnaeus, 1758)	A	D	TB	FC	FE
Tropiduridae					
Eurolophosaurus amathites (Rodrigues, 1984)[a]	T	D	P	SFR	Caat
Eurolophosaurus divaricatus (Rodrigues, 1986)[a]	T	D	P	SFR	Caat
Eurolophosaurus aff. *divaricatus*[a]	T	D	P	SFR	Caat
Eurolophosaurus sp.[a]	T	D	P	ER	RF
Stenocercus squarrosus Nogueira & Rodrigues, 2006	T	D	?	OD	Cer
Strobilurus torquatus Wiegman, 1834	A	D	TB	FC	FE
Tropidurus cocorobensis Rodrigues, 1987[a]	T	D	P	R	Caat
Tropidurus erythrocephalus Rodrigues, 1987[a]	T	D	S	R	Caat
Tropidurus etheridgei Cei, 1982	T	D	S	OD	Ch
Tropidurus helenae (Manzani & Abe, 1990)[a]	T	D	S	R	Caat
Tropidurus hispidus (Spix, 1825)	T	D	G	WD	Caat

(continued)

Table 6.1 (continued)

Taxa	Ecological category	Activity	Preferred habitat type	Distribution Pattern	Typical region
Tropidurus jaguaribanus Passos, Lima & Borges-Nojosa, 2011[a]	T	D	S	L	Caat
Tropidurus montanus Rodrigues, 1987	T	D	G	OD	Cer
Tropidurus mucujensis Rodrigues, 1987[a]	T	D	S	ER	RF
Tropidurus pinima (Rodrigues, 1984)[a]	T	D	S	R	Caat
Tropidurus psammonastes Rodrigues, Kasahara & Yonenaga-Yassuda, 1988[a]	T	D	P	DSF	Caat
Tropidurus semitaeniatus (Rodrigues, 1825)	T	D	S	WD	Caat
Tropidurus sertanejo Carvalho, Sena, Peloso, Machado, Montesinos, Silva, Campbell & Rodrigues, 2016[a]	T	D	G	?	Caat
Anguidae					
Diploglossus lessonae Peracca, 1890	SF	D	LL	R	Caat
Ophiodes striatus (Spix, 1825)	SF	D	LL	OD	Cer
Gymnophthalmidae					
Acratosaura mentalis (Amaral, 1933)	F	D	LL	R	Caat
Acratosaura spinosa Rodrigues, Cassimiro, Freitas & Silva, 2009[a]	F	D	LL	ER	CR
Anotosaura collaris Amaral, 1933[a]	F	D	LL	R	Caat
Anotosaura vanzolinia Dixon, 1974[a]	F	D	LL	R	Caat
Calyptommatus confusionibus Rodrigues, Zaher & Curcio, 2001[a]	F	N	P	SFR	Caat
Calyptommatus leiolepis Rodrigues, 1991[a]	F	N	P	SFR	Caat
Calyptommatus nicterus Rodrigues, 1991[a]	F	N	P	SFR	Caat
Calyptommatus sinebrachiatus Rodrigues, 1991[a]	F	N	P	SFR	Caat

(continued)

Table 6.1 (continued)

Taxa	Ecological category	Activity	Preferred habitat type	Distribution Pattern	Typical region
Cercosaura ocellata Wagler, 1830	F	D	LL	OD	Cer
Colobosaura modesta (Reinhardt & Lütken, 1862)	F	D	LL	OD	Cer
Colobosauroides carvalhoi Soares & Caramaschi, 1998[a]	F	D	LL	R	Caat
Colobosauroides cearensis Cunha, Lima-Verde & Lima, 1991[a]	F	D	LL	R	Caat
Dryadosaura nordestina Rodrigues, Freire, Pellegrino & Sites Jr., 2005	F	D	LL	FC	FE
Heterodactylus septentrionalis Rodrigues, Freitas & Silva, 2009[a]	F	D	LL	ER	RF
Leposoma baturitensis Rodrigues & Borges (1997)[a]	F	D	LL	FC	BA
Micrablepharus maximiliani (Reinhardt & Lütken, 1862)	F	D	LL	WD	Caat
Notobachia ablephara Rodrigues, 1984[a]	F	D/N	P	SFR	Caat
Placosoma limaverdorum Borges-Nojosa, Caramaschi & Rodrigues, 2016[a]	F	D	LL	FC	BA
Procellosaurinus erythrocercus Rodrigues, 1991[a]	F	D	P	SFR	Caat
Procellosaurinus tetradactylus Rodrigues, 1991[a]	F	D	P	SFR	Caat
Psilops paeminosus Rodrigues, 1991[a]	F	D	P	SFR	Caat
Psilops mucugensis[a]	F	D	P	ER	RF
Scriptosaura Catimbau Rodrigues & Santos, 2008[a]	F	N	P	R	Caat
Stenolepis ridleyi Boulenger, 1887	F	D	LL	FC	FE
Vanzosaura multiscutata (Amaral, 1933)[a]	F	D	LL	WD	Caat
Teiidae					
Ameiva ameiva (Linnaeus, 1758)	T	D	G	WD	Caat
Ameivula confusioniba (Arias, Carvalho, Rodrigues & Zaher, 2011)[a]	T	D	G	L	Caat

(continued)

Table 6.1 (continued)

Taxa	Ecological category	Activity	Preferred habitat type	Distribution Pattern	Typical region
Ameivula nigrigula (Arias, Carvalho, Rodrigues & Zaher, 2011)[a]	T	D	G	L	Caat
Ameivula ocellifera (Spix, 1825)	T	D	G	WD	Caat
Glaucomastix cyanura (Arias, Carvalho, Rodrigues & Zaher, 2011)[a]	T	D	G	L	Caat
Glaucomastix venetacauda (Arias, Carvalho, Rodrigues & Zaher, 2011)[a]	T	D	G	L	Caat
Kentropyx calcarata Spix, 1825	T	D	G	FC	FE
Tupinambis teguixin (Linnaeu, 1758)	T	D	G	WD	FE
Salvator merianae (Duméril & Bibron, 1839)	T	D	G	WD	Caat

Based on Rodrigues (2005a, b)

Ecological category: *A* arboreal, *F* fossorial, *SA* semi-arboreal, *SF* semi-fossorial, *T* terrestrial

Activity: *D* diurnal, *N* nocturnal

Preferred habitat type: *AT* ant hills and termite mounds, *B* bromeliads, *G* general, *LL* litter leaf, *P* psammophilous, *Pa* periantropic, *S* saxicolous, *TB* trees and bushes

Distribution pattern: *ER* distribution limited to rocky fields from Espinhaço Range, *FC* related with remaining forest environments in altitude areas from the Caatinga, *L* limited distribution in the Caatinga, *OD* typical species from adjacent open regions, such as Cerrado/Chaco/tabuleiros and coastal restingas, *R* relictual distribution, *SFR* related with paleoquaternary sandy dunes from São Francisco River, *WD* widely distributed, *?* unknown distribution.

Typical region: *BA* endemic from humid forest enclaves (Brejos), *Caat* Caatinga, *Cer* Cerrado, *Ch* Chaco, *Ex* exotic, *FE* forested environments, such as Atlantic and Amazon Forest, *RF* rocky fields from Espinhaço Range

[a] Endemic species

The Caatinga shares numerous genera with the Cerrado, probably due to Tertiary events. However, another important portion of the fauna probably had its origin during climatic fluctuations in Quaternary (Vanzolini and Williams 1981; Colli 2005; Werneck and Colli 2006; Werneck 2011; Oliveira et al. 2015). The patterns cited here (Table 6.1) complement the ones detailed in Rodrigues (2005b). We expand the original proposal of three distributional patterns (WD, RD, and SF) by adding four other patterns (L, AA, FL, and ER) (Table 6.1). This preliminary categorization is a starting point in the attempt to reconstruct the biogeographical history of the Caatinga. In Table 6.1 we present an extended and updated checklist of distribution patterns of Caatinga lizards given in Rodrigues (2005b), with the position of each species according with these patterns.

6.3.1 Widely Distributed Species

We identified 16 widely distributed species, most of them very abundant, occurring in many Caatinga phytophysiognomies. *Ameiva ameiva, Iguana iguana*, and *Salvator merianae* are widely distributed in open areas as well as in forested environments (Werneck and Colli 2006). *Phyllopezus* spp., *Polychrus acutirostris*, and *Vanzosaura* spp. occur in the DOF in South America, from Chaco to the Caatinga (Vanzolini et al. 1980; Werneck and Colli 2006; Delfim and Freire 2007; Garda et al. 2012). *Gymnodactylus geckoides* and *Ameivula ocellifera* occur in the Caatinga and Cerrado, but may represent species complexes and need to have their geographic distributions re-evaluated after systematic revisions (Arias et al. 2011a, b; Domingos et al. 2014; Oliveira et al. 2015). *Hemidactylus brasilianus*, *Tropidurus hispidus*, and *Brasiliscincus heathi* are widely distributed in the Caatinga and also permeate neighboring regions such as the Cerrado and coastal restingas (Freitas and Silva 2007). *Tropidurus semitaeniatus* and *Lygodactylus klugei* are also widely distributed in the Caatinga but tend not to occur in transitional areas (Werneck and Colli 2006; Freitas and Silva 2007). For example, *L. klugei* was also recorded in seasonally dry tropical forest enclaves within the Cerrado (Werneck and Colli 2006). *Tropidurus semitaeniatus* is an aggressive colonizer but is specialized on rocky outcrops (Rodrigues 2005b). *Micrablepharus maximiliani* shows a distinct distribution, being widely distributed in Cerrado and also occurring in some areas in Caatinga (Werneck and Colli 2006; Nogueira et al. 2011). Its distribution in Caatinga appears to be restricted to two regions: one in the west margin, in contact areas with Cerrado, and in the coastal restingas, which could have been connected to Caatinga and Cerrado habitats during Quaternary. The species is usually absent in central Caatinga (except in some mesic enclaves), where conditions are more xeric (Vanzolini et al. 1980; Delfim and Freire 2007).

6.3.2 Species with Relictual Distribution

Enyalius bibronii, *Coleodactylus meridionalis*, *Diploglossus lessonae*, *Acratosaura mentalis*, *Anotosaura vanzolinia*, *Colobosauroides carvalhoi*, and *C. cearensis* have RDs in mesic environments in the Caatinga (Arzabe et al. 2005; Rodrigues 2005b). They are closely related to lineages intimately associated with forested environments (Rodrigues 2005b). It is likely that the environments where these species or their relatives originated are humid and shaded forests (Rodrigues 2005b). The distributions of these species corroborate the vanishing refuge theory (Haffer 1969; Vanzolini and Williams 1970, 1981), where the retraction of forested environments and expansion of xeric areas during Quaternary resulted in species being isolated in relictual patches of forested vegetation.

Similarly, but isolated in different types of habitats, other species also have isolated populations. For example, *Tropidurus cocorobensis* occurs exclusively in sandy soils (Rodrigues 2005b); *T. erythrocephalus*, *T. helenae*, and *T. jaguaribanus* in rocky outcrops (Rodrigues 2005b; Passos et al. 2011; Werneck et al. 2015); and *Psychosaura macrorhyncha* and *P. agmosticha* are usually associated with bromeliads (Rodrigues 2005b). In addition, *Anotosaura collaris* and *Scriptosaura catimbau* are known in only one or a few localities (Rodrigues 2005b; Rodrigues and Santos 2008; Rodrigues et al. 2013b). Most RD species are locally endemic (12 species) and occur in the 'Borborema plateau' and in marginal areas of the 'Depressões Sertanejas', where most mesic areas within the Caatinga are found.

6.3.3 Species with Limited Distribution in the Caatinga

There are six species in this category of species with limited distribution in the Caatinga. *Glaucomastix cyanura*, *G. venetacauda*, *Ameivula confusioniba*, and *A. nigrigula* were recently described and are known only from a few records (Arias et al. 2011a, b; Cavalcanti et al. 2014). They are likely not relictual, and their apparent restricted distributions may instead result from poor sampling coupled with taxonomic problems. In the case of *A. confusioniba* and *A. nigrigula*, a recent phylogeographic analysis showed very shallow divergences and unrestricted gene flow among these species and *A. ocellifera* (Oliveira et al. 2015). Similarly, *Phyllopezus periosus* and *T. jaguaribanus* were not long ago considered to be lizards with RDs due to the small number of records (Freire et al. 2000; Rodrigues 2005b; Passos et al. 2011; Carvalho 2013). Nowadays, with the increase in sampling efforts, it is clear that *P. periosus* is not relictual, but instead distributed throughout the oriental portion of Caatinga, from Rio Grande do Norte to Sergipe.

6.3.4 Species Related to Paleoquaternary Sandy Dunes from São Francisco River

The species described here are all related to paleoquaternary sandy dunes of São Francisco River or with sandy soil areas that were previously contacted with this region in the past. They are typically relictual, and because of their distinctive historical past, it is better to group them in their own biogeographic unit (Rodrigues 1996, 2005a).

Several endemic gymnophythalmids occur in SF, including *Calyptommatus* (four species), *Notobachia* (one species), and *Procellosaurinus* and *Psilophthalmus* (two species each) (Rodrigues 1996). In addition, some tropidurids have also diversified in the area: three *Eurolophosaurus* species, *Tropidurus pinima*, and *T. psammonastes* (Rodrigues 1996; Werneck et al. 2015). The species in the SF category occur mostly in the ecoregion with the same name, but some also occur south of the 'Ibiapaba-Araripe' ecoregion and in small portions of 'Raso da Catarina' and 'Depressão Sertaneja Meridional', but always associated with the SF (Delfim et al. 2006, 2011).

6.3.5 Species with Distributions Limited to Rocky Outcrops from Espinhaço Range

We recorded eight species from rocky fields of Espinhaço Range, in Bahia and Minas Gerais. Most species are closely related with Cerrado species. Only *Psilops mucugensis* and *Acratosaura spinosa* are typical from the Caatinga. However, *Acratosaura* is historically related to the Espinhaço Range (Freitas and Silva 2007; De-Carvalho et al. 2010), while one new species of *Psilops* was recently described from the Cerrado (Rodrigues et al. 2017). *Enyalius erythroceneus* belongs to the *E. catenatus* group, with species from the Caatinga and Atlantic Forest (Rodrigues et al. 2006; Freitas and Silva 2007).

Other species included in this category are *Tropidurus mucujensis*, *Gymnodactylus vanzolini*, and *Asparonema* aff. *dorsivittatum* (Rodrigues 1987; Freitas and Silva 2007; Cassimiro and Rodrigues 2009), which are related to the Cerrado. *Heterodactylus septentrionalis* and *Eurolophosaurus* sp. appear to be related to species from Espinhaço Range, but outside the Caatinga (Rodrigues 1981, 1986, 1996; Freitas and Silva 2007).

Despite the wide contact of the Espinhaço Range with the Caatinga, species from ER are more related to the Cerrado fauna (Nogueira et al. 2011; Oliveira et al. 2015). All species in the ER category occur in areas with typical Cerrado vegetation (Rodrigues 1987; Cassimiro and Rodrigues 2009; Rodrigues et al. 2009b). ER species occur in two ecoregions, the ‘Chapada Diamantina’ and a small portion of ‘Depressão Sertaneja Meridional’, in northern Minas Gerais.

6.3.6 Species from Adjacent Open Regions, Such as Cerrado/Chaco/Tabuleiros and Coastal Restingas

Nine species mainly distributed in Cerrado and/or Chaco and can be found in the Caatinga, in relictual highlands, transitional areas, and in Cerrado enclaves. One of the species, *Tropidurus etheridgei*, is typical from Chaco and also found in disjunct Cerrado populations (Nogueira et al. 2011). Similarly, *Stenocercus squarrosus*, *Hoplocercus spinosus*, and *Tropidurus montanus* are also found in isolated populations within the Caatinga (Rodrigues 2005b). It is probable that these species are now restricted to the few areas that still hold their specific ecological requirements, suggesting former wider distributions that retracted in response to climate change (Rodrigues 1996). Similarly, other typical Cerrado species, such as *Norops brasiliensis*, *Colobosaura modesta*, *Copeoglossum arajara*, and *Cercosaura ocellata*, occur dispersed in relictual populations, humid forest enclaves, and/or highlands covered by ‘*cerradões*’ (forested savannas), where the conditions are more favorable (Borges-Nojosa and Caramaschi 2005; Borges-Nojosa and Cascon 2005; Nogueira et al. 2011).

Finally, *Ophiodes striatus* is also closely related to Cerrado species and appears to have expanded its distribution in the Caatinga towards coastal restingas. The species is also recorded in humid forest enclaves, always along forest edges (Borges-Nojosa and Caramaschi 2005; Borges-Nojosa and Cascon 2005), and transitional areas between Caatinga and Atlantic Forest (Magalhães et al. 2015). In both regions, the species inhabits open areas with grasslands but is absent from more xeric Caatinga areas. AA species occur mainly on highlands of 'Depressão Sertaneja Setentrional' and 'Chapada Diamantina', but also in transitional areas with Cerrado and Atlantic Forest.

6.3.7 Species Related to Atlantic Forest and/or Humid Forest Enclaves

Eleven species from forested areas were recorded within the Caatinga. Four (*Norops fuscoauratus*, *Polychrus marmoratus*, *Kentropyx calcarata*, and *Copeoglossum nigropunctatum*) also occur in Atlantic Forest, Cerrado, and Amazon, and in the Caatinga they occur only in humid forest enclaves (Borges-Nojosa and Caramaschi 2005; Borges-Nojosa and Cascon 2005; Nogueira et al. 2011). *Enyalius catenatus*, *E. pictus*, *Strobilurus torquatus*, *Dryadosaura nordestina*, and *Stenolepis ridleyi* are typical from Atlantic Forest, but likewise also occur in humid forest enclaves (Borges-Nojosa and Caramaschi 2005; Rodrigues et al. 2005, 2013a; Garda et al. 2014).

Enyalius spp. from the Caatinga are related to their Atlantic Forest congeners, and like *Enyalius bibronii* appear to tolerate more xeric environments than the typical humid forests where they usually occur (Rodrigues et al. 2006; Freitas and Silva 2007). For example, *Enyalius catenatus* has been recorded in relictual forests from Bahia and Paraíba (Arzabe et al. 2005), and, at least in Paraíba, it occurs in areas dryer than the coastal forests typically found along its distribution (Arzabe et al. 2005). *Enyalius pictus* also occupies rock outcrops and Cerrado areas in Minas Gerais and Bahia (Freitas and Silva 2007). *Dryadosaura nordestina* was recorded in the same area where *E. catenatus* was recorded in Paraíba (Parque Estadual Pedra da Boca, Arzabe et al. 2005). This site is in a transitional area between the Caatinga and Atlantic Forest, and its peculiar climate helps retain more moisture and shadow than surrounding Caatinga areas (Araújo et al. 2005; Arzabe et al. 2005).

Two species are endemic from humid forest enclaves of Ceará: *Leposoma baturitensis* and *Placosoma limaverdorum* (Borges-Nojosa and Caramaschi 2005; Borges-Nojosa et al. 2016). *Leposoma* is typical from Atlantic Forest and Amazon (Rodrigues et al. 2002) and does not occur in coastal forests north of the São Francisco River (Rodrigues and Borges 1997). *Placosoma* occurs mainly in Atlantic Forest from southeast Brazil (Cunha 1966; Borges-Nojosa and Caramaschi 2005), but there is a record of *P. cordylinum* in Mato Grosso (Uetz and Hošek 2016). The record in the humid forest enclaves of Ceará is the first for northeastern Brazil, north of the São Francisco River.

6.4 Richness Gradient of Caatinga Lizard Species

We reconstructed the distribution of each Caatinga lizard species using the species distribution modeling software MaxEnt (Phillips et al. 2006). Some species did not have enough locality records (less than five) to build reliable models and were excluded from this analysis. We also excluded one species with dubious identification (*Hemidactylus agrius*) and one exotic species (*H. mabouia*), modeling in total of 63 species. We used locality records obtained from museums, our field surveys, and the literature. For species with distributions reaching other regions, we included all known locality records to build the distribution models. As environmental predictors, we used the same variables selected in a previous study on the distributions of Cerrado lizards and snakes (Costa et al. 2007). We built models at 5 km^2 resolution and generated a richness map by overlapping all species potential distributions in ArcGIS/ArcMap 9.3©. This map consists of a total richness distributed in each cell grid (Fig. 6.1).

The map highlights the region of paleoquaternary sandy dunes across the São Francisco River as having high potential richness (Fig. 6.1). In addition, other high richness areas were identified in northeastern Caatinga, reaching Rio Grande do Norte and Paraíba. This area harbors part of the ‘Depressões Sertanejas’, but mainly the ‘Depressão Setentrional’ and the ‘Borborema Plateau’. Smaller areas are also evident in Bahia, in ‘Depressão Sertaneja Meridional’ between ‘Chapada Diamantina’ and the ‘Raso da Catarina’, as well as east of Ceará, in the Baturité range, and in the central portion of Pernambuco, between the ‘Depressão Sertaneja Meridional’ and the ‘Raso da Catarina’. In addition, there are two main contiguous belts east and west of the Caatinga, connected to each other in the extreme west of Pernambuco and Paraíba. This connection occurs near Chapada do Araripe region, in the ecoregion of ‘Ibiapaba-Araripe’ and ‘Depressão Sertaneja Meridional’. The map also shows that the central regions of the Caatinga have lower richness than marginal areas (Fig. 6.1).

6.5 Patterns of Species Endemism

To test if lizard assemblages match the ecoregions proposed for the Caatinga (Chap. 1; Velloso et al. 2002), we conducted a parsimony analysis of endemicity (PAE) to identify and classify areas of endemism (Eldredge and Cracraft 1980; Rosen 1988, 1992; Morrone 2014). The Caatinga ecoregions is one of the most widely used divisions for research and conservation policy. Such regions were proposed based on morphopedological, climatic, geological, and phytophysionomical information, and therefore its effectiveness as a surrogate of Caatinga’s biodiversity requires further testing.

We selected 97 sites with the best sampling efforts from the literature (at least ten species recorded). To run the PAE, we used distribution information for all species found in the sampled sites, excluding *Hemidactylus agrius* and *H. mabouia*, for the reasons given in Sect. 6.4. We conducted the analysis using the software PAST (Hammer et al. 2001) performing Heuristic searches.

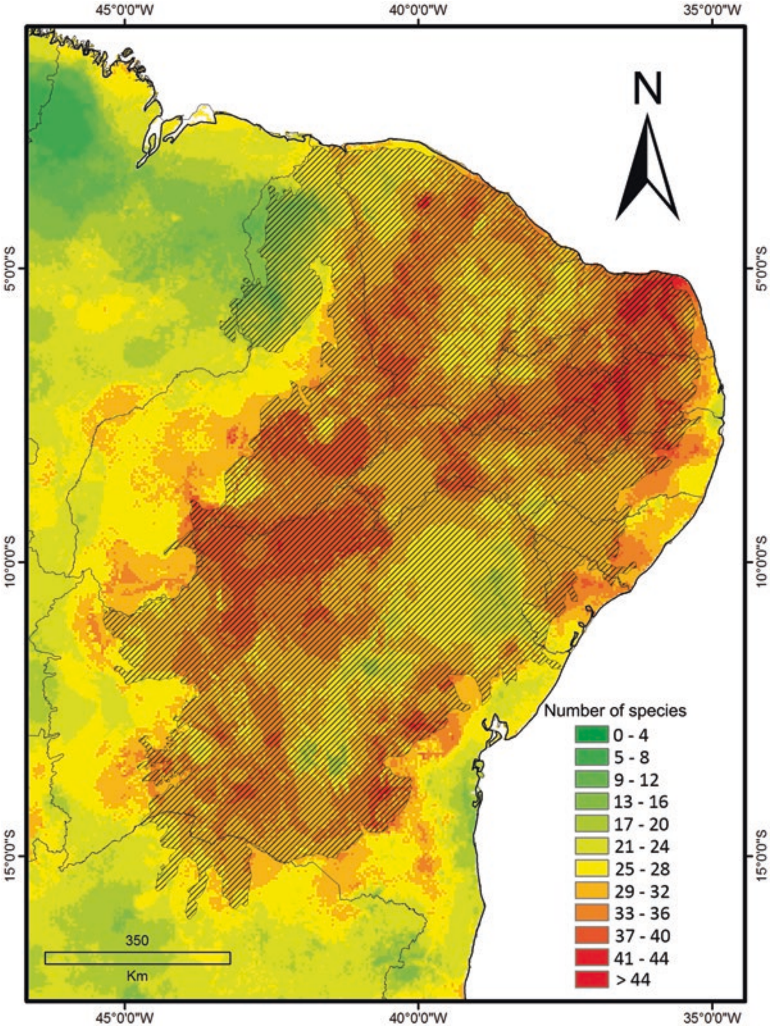

Fig. 6.1 Map of Caatinga lizard richness based on individual distribution maps modeled for 63 species typical from the Caatinga and related with adjacent regions and forested areas

We grouped the sites according to distance to the closest neighbor, resulting in 61 units. From all sites used, 11 were in ‘Depressão Sertaneja Meridional’, seven in the ‘Ibiapaba-Araripe’, six in the ‘Depressão Sertaneja Setentrional’, ten in the ‘Borborema Plateau’, five in the SF, four in the ‘Chapada Diamantina’, three in the ‘Raso da Catarina’, five in the ‘São Francisco-Gurguéia’, and only one in a humid forest enclave (Fig. 6.2). Another four sites were included due to their position in transitional areas among Atlantic Forest/Caatinga or Cerrado/Caatinga. The cladogram showed eight main groups (Fig. 6.2). Five of seven endemism areas generated by the PAE match the ecoregions (Fig. 6.3).

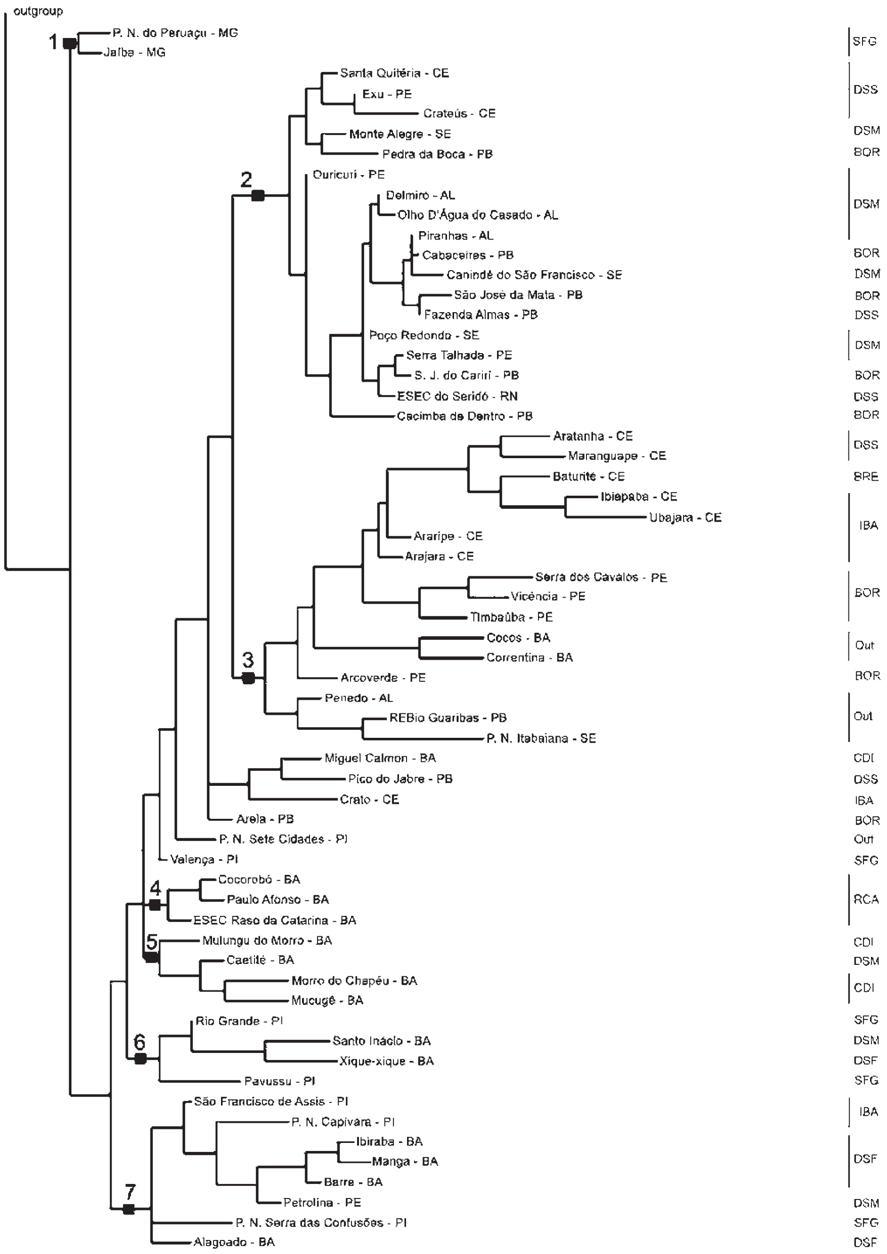

Fig. 6.2 Area relations among collecting sites in the Caatinga region. Tree length: 502; Ensemble Consistency Index*:* 0.212; Ensemble Retention Index*:* 0.575. The square represents each group indicated by the parsimony analysis of endemicity (PAE). Ecoregion for each location: *BOR* 'Borborema Plateau', *BRE* '*Brejos*', *CDI* 'Chapada Diamantina', *DSF* 'Dunas do São Francisco', *DSM* 'Depressão Sertaneja Meridional', *DSS* 'Depressão Sertaneja Setentrional', *IBA* 'Ibiapaba-Araripe', *Out* locations outside of the Caatinga, *RCA* 'Raso da Catarina', *SFG* 'São Francisco-Gurguéia'

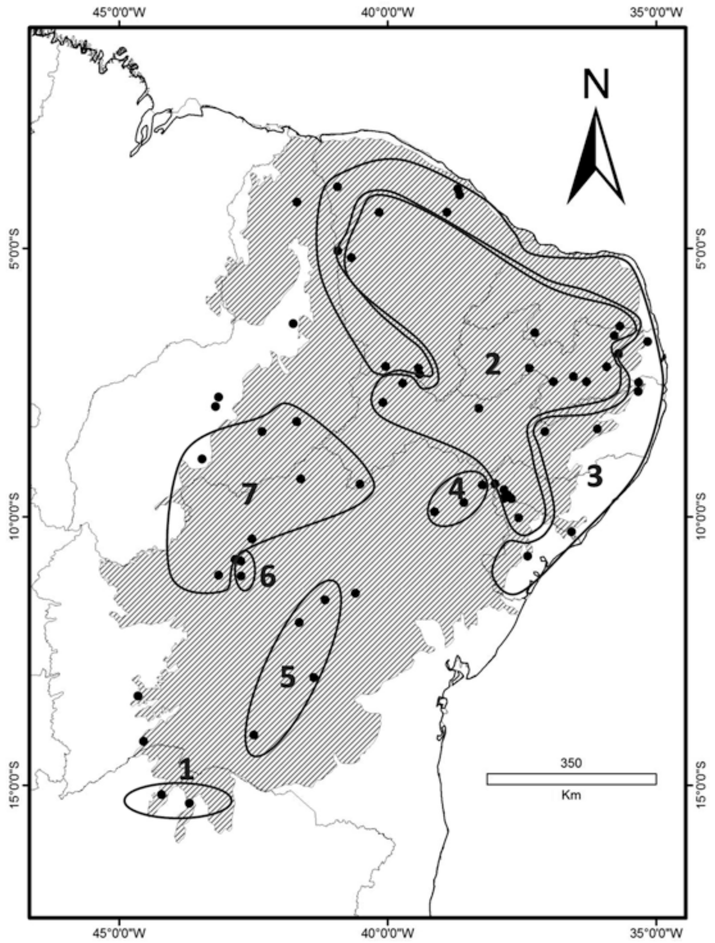

Fig. 6.3 Sites used in the parsimony analysis of endemicity (PAE) and endemism areas (groups) indicated in the analysis. Group 1—rocky outcrops from Minas Gerais with direct influence of Cerrado; Group 2—'Depressões sertanejas' + 'Borborema Plateau'; Group 3—areas with direct influence of rainforests, Amazon and Atlantic Forest (Brejos + 'Chapada do Araripe' + coastal transitional areas); Group 4—'Raso da Catarina'; Group 5—'Chapada Diamantina'; Group 6—right side of paleoquaternary sandy dunes complex from São Francisco River; Group 7—left side of paleoquaternary sandy dunes complex from São Francisco River + southern Piauí

The lizard fauna from the Caatinga is one of the best known for the region, despite only a handful of sites having been adequately sampled (Rodrigues 2005b). Using a selection of well-sampled localities, it was possible to confidently recover a pattern of distribution endemism that matched most ecoregions. Using a PAE, we show a possible pattern of lizard fauna in some ecoregions (Fig. 6.4). Only the 'São Francisco-Gurguéia' and '*Ibiapaba-Araripe*' complexes were not recovered as endemism areas matching the ecoregions. However, the first one could be biased due to lack of information, because only one well-sampled area was included in the

Fig. 6.4 Examples of distribution patterns of species in Caatinga. Widely distributed species: (**a**) *Ameiva ameiva* and (**b**) *Lygodactylus klugei*. Relictual distribution species: (**c**) *Tropidurus cocorobensis* and (**d**) *Enyalius bibronii*. Species with limited distribution: (**e**) *Glaucomastix venetacauda*. Species related with paleoquaternary sandy dunes from São Francisco River: (**f**) *Procellosaurinus erythrocercus*. Typical species from adjacent open regions: (**g**) *Stenocercus squarrosus*. Species related with remaining forest environments in altitude areas from the Caatinga: (**h**) *Strobilurus torquatus*

analysis; and the second grouped together some humid forest enclaves from Ceará with Atlantic Forest from northeast Brazil, probably due to the limited option of inclusion of altitude areas in the analysis. Each endemism area or ecoregion showed exclusive characteristics and is evaluated separately in Sects. 6.5.1, 6.5.2, 6.5.3, 6.5.4, 6.5.5, and 6.5.6.

6.5.1 *Depressão Sertaneja Meridional and Depressão Sertaneja Sententrional*

The 'Depressão Sertaneja Meridional' and 'Depressão Sertaneja Sententrional' ecoregions are distinct in climatic, geological, and phytophysiognomical parameters (Velloso et al. 2002), but their lizard fauna areas are remarkably similar (Arzabe et al. 2005; Delfim and Freire 2007; Freire et al. 2009; Caldas et al. 2016). The two 'Depressões Sertanejas' occupy most of the Caatinga and share the most typical landscapes in the region (Velloso et al. 2002). Lizard richness varies across these regions, with nuclear regions of the Caatinga having lower richness, and the richest areas being (1) south of Chapada do Araripe in Pernambuco; (2) the oriental portion of Rio Grande do Norte; (3) the southeast portion of Caatinga in Bahia (transition with Chapada Diamantina and the Atlantic Forest); and (4) the center-west of Ceará. Each of these areas have less arid climates and are influenced by coastal winds and moisture (Velloso et al. 2002). In general, the fauna of these areas is typical of the Caatinga, with widely distributed species. Relictual elements are usually related to less arid climates and occur on the borders of these ecoregions, characterizing higher richness areas.

About 50–60% of these areas have some level of disturbance, especially due to itinerant agriculture (Velloso et al. 2002). However, until recently, few herpetological surveys had been carried out in such areas. It was only after the discovery of the divergent faunas of the São Francisco River paleoquaternary sandy dunes and humid forest enclaves that more attention was directed to them (Rodrigues 1996, 2005b; Borges-Nojosa and Caramaschi 2005). This resulted in a higher number of inventories, but most of them were in atypical environments within the Caatinga (Rodrigues 1993; Borges-Nojosa and Caramaschi 2005; Borges-Nojosa and Cascon 2005; Garda et al. 2013; Pedrosa et al. 2013; Cavalcanti et al. 2014; Magalhães et al. 2015). Hence, the current knowledge of the Caatinga lizard fauna is still superficial for typical nuclear areas, a region under strong environmental pressure.

6.5.2 *Borborema Plateau*

The 'Borborema Plateau' ecoregion shares its lizard fauna with the two 'Depressões Sertanejas' and is one of the richest areas in the Caatinga. Like the marginal areas from the 'Depressões Sertanejas', the 'Borborema Plateau' is influenced by coastal winds and moisture (Velloso et al. 2002). The area is under the influence of three ecoregions: the 'Borborema Plateau', 'Raso da Catarina', and the 'Depressão Sertaneja Meridional'. This ecoregion is the most disturbed in the Caatinga. Only a few native fragments persist, covering less than 10% of its original area (Velloso et al. 2002). The region's high richness and disturbance point to the need for more studies and conservation efforts (Velloso et al. 2002; Delfim and Freire 2007; Freire et al. 2009).

6.5.3 Ibiapaba-Araripe

The sites from the 'Ibiapaba-Araripe' ecoregion were grouped with humid forest enclaves and Atlantic Forest areas (Fig. 6.4). The use of data from 'Chapadas' and plateaus occupied by '*carrasco*' vegetation could explain the observed pattern. With the increase of surveys, another endemism center may be found with PAE because these high areas are occupied by many species from Cerrado and Atlantic Forest (Borges-Nojosa and Caramaschi 2005; Borges-Nojosa and Cascon 2005; Ribeiro et al. 2012).

The portion from the center of this ecoregion to its meridional limit shows high richness, probably due to the occurrence of some species from the SF (Delfim et al. 2006, 2011; Freitas and Silva 2007). In the past, during periods of expansion of dunes, Serra da Capivara and Serra das Confusões National Parks were connected to this region (Tricart 1985); the presence of typical species from the dunes corroborates this historical connection (Rodrigues et al. 2001; Delfim et al. 2006, 2011). Around 50–70% of the area is disturbed, but this is the ecoregion with the most protected areas (Velloso et al. 2002).

6.5.4 Paleoquaternary Sandy Dunes from São Francisco River

The SF region has a distinct fauna, with plenty of endemics, several with psamophilous habits. They probably result from climatic changes that promoted the expansion and retractions of sandy soils, as well as the changing of the river course (Tricart 1985; Rodrigues 1996; Delfim et al. 2006). The differences in faunas of each margin justified the separation of groups indicated in the PAE (Fig. 6.3), despite these groups not being monophyletic (Fig. 6.3) as expected due to the presence of congeners on both margins (Rodrigues 1984a, b, 1986, 1991c, 1996).

The region harbors the most Caatinga endemics, with 13 species (Rodrigues 1996), and it also has high richness (Figs. 6.3 and 6.4). This ecoregion was also recovered by the PAE (Fig. 6.4). Because this region holds many microendemics, it has generated an increase in research interest in recent years (Rodrigues 2005b). This ecoregion still holds around 80% of its original area in well-preserved conditions, although there is no conservation protection area assigned to this ecoregion (Rodrigues 2005b).

6.5.5 Chapada Diamantina

The 'Chapada Diamantina' ecoregion also has high richness and plenty of endemics. There has been recent active research identifying and describing new species from this ecoregion (Rodrigues 1987; Rodrigues et al. 2006, 2009a, 2017; Arias et al.

2011b). The landscapes in this ecoregion are very different from other areas in the Caatinga, and, like the ecoregion of paleoclimatic dunes of São Francisco River, are considered to be important speciation centers (Rodrigues et al. 2006; Magalhães et al. 2015; Werneck et al. 2015), mostly in rocky fields and influenced by the Espinhaço Range (Rodrigues et al. 2006, 2009a Cassimiro and Rodrigues 2009). Most species from ‘Chapada Diamantina’ were not used in the niche modeling (Fig. 6.1) because most species had less than five records. It is one of the most fragile ecoregions, which is threatened by agriculture, cattle breeding, mining, and tourism (Velloso et al. 2002).

6.5.6 Raso da Catarina

Several Caatinga endemics are related to sand soils, mostly in SF. The ‘Raso da Catarina’ ecoregion also has many sandy soil areas and species associated with such environments including *Tropidurus cocorobensis* and *Amphisbaena arenaria* (Rodrigues 1996, 2005b). The soil of these areas are deep and sandy but flat, in contrast to the dunes of São Francisco River (Velloso et al. 2002). Hence, the ‘Raso da Catarina’ could present many species adapted to such soils (as seen in SF), but this ecoregion is still poorly sampled, with only one detailed inventory for the Raso da Catarina Ecological Station (Garda et al. 2013). The region is indicated as potentially having low species richness in our map. Although sandy soils in general tend to present high species richness in the Caatinga, this ecoregion suffers from a small amount of surface water availability (Velloso et al. 2002), which could explain this low richness. In addition, the low water availability also results in very low human population densities in the region, which helps maintain the natural environments. Approximately 60–70% of the ecoregion is still undisturbed (Velloso et al. 2002).

6.6 Conclusions and Suggestions for Future Investigations

The endemism areas recovered by the PAE corroborate most of the proposed ecoregions for the Caatinga (Velloso et al. 2002). Three ecoregions (paleoclimatic dunes of São Francisco River, ‘Chapada Diamantina’, and ‘Raso da Catarina’) appear to have enough endemic elements exclusive to each ecoregion. The ‘Depressões Sertanejas’ and ‘Borborema Plateau’ represent the core area of the Caatinga, and even though they show some heterogeneity in climate and geomorphology, such differences do not seem to influence their lizard fauna.

Some areas within the ecoregions have specific characteristics that are reflected in their lizard fauna. Forested areas are an example of such areas, especially when we consider the humid forest enclaves from Ceará, Paraíba, and Pernambuco. Despite being inserted in different ecoregions, the PAE grouped them with other areas clearly influenced by Atlantic and Amazon Forests (Borges-Nojosa and Caramaschi 2005; Borges-Nojosa and Cascon 2005). Adjacent regions influence the faunas of these sites, but their origin and maintenance are key to achieving a thorough knowledge of the Caatinga's biogeography.

The most diverse areas in the Caatinga occur along its marginal portions, with central areas showing fewer species (Fig. 6.1), highlighting the importance of shared elements with adjacent regions. In addition, Caatinga endemismics, contrary to expectations, are numerous and concentrated in paleoclimatic dunes from São Francisco River and 'Raso da Catarina'. In addition, at least 12 additional endemics (*Tropidurus helenae*, *T. jaguaribanus*, *T. pinima*, *Phyllopezus periosus*, *Ameivula nigrigula*, *Glaucomastix cyanura*, *Acratosaura mentalis*, *Anotosaura collaris*, *A. vanzolinia*, *Colobosauroides carvalhoi*, *C. cearensis*, and *Placosoma limaverdorum*) occur in other ecoregions and are not dependent on sandy soils, rather occurring in mesic habitats or rocky outcrops. Some of these species probably drive the high richness indicated in the northeast portion of the Caatinga (Fig. 6.1), which covers part of 'Depressão Sertaneja Sententrional' in Rio Grande do Norte and the 'Borborema Plateau' and a small portion of 'Depressão Sertaneja Meridional' in Paraíba and Pernambuco.

Significant advances in our knowledge of Caatinga lizards and their distribution patterns were made in the last decade. The sampling effort is still low, but has increased a lot since the 1990s (Rodrigues 2005b; Freire et al. 2009; Garda et al. 2013; Pedrosa et al. 2013; Cavalcanti et al. 2014; Magalhães et al. 2015; Caldas et al. 2016). We now know that theories about Caatinga lizard fauna being species poor and having low endemism are not correct. It is clear that the Caatinga shares part of its fauna with Cerrado, and even with Chaco, but the number of endemics is relatively high and still rising as new data become available. These new discoveries represent an important opportunity for the understanding of the historical process that drove Caatinga diversity. With the results generated here, we can indicate some directions for future studies and conservation priorities. For example, the 'São Francisco-Gurguéia' is one of the less sampled ecoregions; the 'Ibiapaba-Araripe', where species previously believed to be endemic to paleoquaternary sandy dunes were recently collected, support a past connection among these areas; the 'Depressões Sertanejas', neglected due its apparent homogeneity, could harbor some surprises, such as the recently described *Tropidurus jaguaribanus* (Passos et al. 2011); the 'Borborema Plateau', the most threatened ecoregion, also deserves special attention, as indicated in the richness map we produced; despite harboring the most Caatinga endemics, the paleoclimatic dunes of São Francisco River need more strict protection and this ecoregion still has many areas that have never been sampled; and the 'Chapada Diamantina', despite not being indicated in our analysis as having high potential diversity, presents a great variety of environments, and consequently a great number of endemics. Such research directions will contribute directly to a better understanding of the biogeography, ecology, and species richness of Caatinga lizards.

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Chapter 7
The Avifauna of the Caatinga: Biogeography, Ecology, and Conservation

Helder Farias Pereira de Araujo and José Maria Cardoso da Silva

Abstract The Caatinga harbors 548 species 24of birds, of which 67 species or subspecies originated within the region. The regional avifauna has been assembled over time as a consequence of speciation in situ and biotic exchanges with the adjacent regions. The role played by regional mass extinction remains unknown. Local assemblages range from 90 to 259 species. The richest local assemblages are found in heterogeneous and well-protected landscapes. Both regional and local assemblages exhibit strong seasonality associated with rainfall as bird species are always tracking humid and thus more productive spots. As a consequence, they move within landscapes, between landscapes, and between regions. Although several species are able to cope with the disturbance of their habitats by humans, we predict that no more than 162 species will be able to survive in a degraded Caatinga under a more unpredictable climate regime.

Keywords Birds • Evolution • Biogeography • Ecology • Conservation • Migration

7.1 Introduction

The Caatinga is one of the most fascinating regions for new studies of birds in South America. Once thought to be populated by only a few widespread species, it harbors diverse avifauna, including several species found nowhere else (Cracraft 1985; Haffer 1985; Silva et al. 2003). The Caatinga's avifauna inhabit complex environmental gradients created by various types of seasonally dry tropical forests (SDTFs) that cover its extensive level peneplains, as well as islands of vegetation types that

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range from grasslands to tropical humid forests, which are found on the tops or slopes of isolated plateaus (Cole 1986; Prado 2003). The SDTFs represent a vegetation type that was once more broadly distributed across the Americas but is currently found only in patches scattered from northwestern Mexico to southwestern Argentina (Dirzo et al. 2011; Linares-Palomino et al. 2011). The other vegetation types found in the Caatinga are relicts of vegetation types now found in Amazonia, the Atlantic Forest, and the Cerrado, three of the major ecological regions that surround the Caatinga (Ab'Saber 1977; Silva et al. 2003).

The composition and richness of the regional and local bird assemblages vary over time and space and are the result of several biotic and abiotic factors operating on different scales. At the regional scale, biotas are assembled via three primary biogeographic processes: species production, biotic interchange, and regional extinction (Ricklefs and Schluter 1993). Species production is a consequence of speciation, a process by which two or more species are formed through fragmentation of the populations of an ancestor species due to the formation of geographic barriers (Mayr 1963). By contrast, biotic interchange is a process through which several species from a region colonize an adjacent region by using corridors created as a consequence of environmental changes (Rosen 1988; Silva and Garda 2010). Finally, regional extinction is the process by which populations of several species within a region become extinct in a relatively short evolutionary period as a result of drastic environmental changes (Silva and Garda 2010). Therefore, species accumulate in a region through both species production and biotic interchange but are lost as a result of regional extinction. Habitat selection determines what species can co-occur at the local scale. Species assemblages are ephemeral at the local scale and are a result of the interaction between competition, predation, and stochastic extinction (Ricklefs and Schluter 1993).

Without human interference, the balance between the accumulation and loss of species at the regional scale is a consequence of tectonics and climate. These two primary abiotic factors influence regional biotas in three ways. First, they can generate, alone or together, the barriers or corridors required for speciation or biotic interchange, respectively. Second, the interplay between these two factors creates large-scale environmental gradients, thereby enabling maintenance of the species pool that has been assembled over time. Third, changes in tectonics or climate can lead to the large-scale disruption of environmental conditions and consequently trigger massive regional extinctions. However, no region can be considered free of human intervention, and most of the evolutionary and ecological processes that have assembled and maintained regional biotas worldwide have been disturbed. In fact, changes in land use, the introduction of invasive species, and resource extraction, among other human actions, have disrupted key ecological processes. In addition, the pollution of the atmosphere has led to irreversible changes in the Earth's climate regime (Chap. 14). Fully understanding the consequences of these global changes for regional biotas is a major research agenda in the tropics. This is especially true for the drylands because these areas are much more vulnerable to irreversible degradation than other tropical regions. In this chapter, we discuss how the avifauna of the Caatinga was assembled over time at both the regional and local scales. We then make some predictions about the future of the Caatinga's avifauna given human interventions in the region.

7.2 Regional Species Composition and Richness

We recorded 548 bird species from 74 families (Table 7.1), which represents 28.6% of the total number of species recorded in Brazil (Piacentini et al. 2015). Our list has 47 more species than were recorded by Silva et al. (2003). Most of the new records come from surveys conducted at the periphery of the region, but there are also several records produced by bird watchers and photographers (www.wikiaves.org.br), which demonstrates the importance of citizen-science in improving our knowledge of regional avian assemblages in tropical regions (Lees 2016).

The bird species recorded in the Caatinga may breed in the region or use the region only during their non-breading seasons. The first group are the resident species, while the second are the visitor species. A total of 509 species are residents because they are known or assumed to breed in the region. These are distributed over 73 families. There are 32 visitor species, and these represent 12 families. These visitor species in the Caatinga come from both the northern hemisphere and from the southern hemisphere. There are 22 visitors from the northern hemisphere, and these belong to the Anatidae, Pandionidae, Accipitridae, Charadriidae, Scolopacidae, Sternidae, Cuculidae, Caprimulgidae, Falconidae, Tyrannidae, Hirundinidae, and Turdidae families. There are ten visitors from the southern hemisphere, and these are restricted to three families (Anatidae, Tyrannidae, and Turdidae). In general, visitor species stay in the Caatinga for just a few days, using the region as a stopover during their movements between their breeding and non-breeding ranges. However, a few species, such as *Elaenia chilensis* and *Turdus amaurochalinus*, are found in the region during most of the austral winter (Araujo 2009; Ruiz-Esparza et al. 2011; Araujo et al. 2012; Pereira and Azevedo-Junior 2013), indicating that the Caatinga is perhaps a critical part of their non-breeding ranges.

7.3 Biogeographical Dynamics

At the regional level, biogeographical dynamics are a product of species production, biotic interchange, and regional extinctions. There is no doubt that several bird species originated within the Caatinga (Muller 1973; Cracraft 1985; Haffer 1985). What remain to be determined are the evolutionary lineages (species or subspecies) that have originated in the region, as well as their phylogenetic relationships. To support this research program, we present a list of 67 species and subspecies that are assumed to have originated within the Caatinga for further scrutiny (Table 7.2). These 67 species and subspecies can be classified into three major groups. The first group is composed of species with small ranges whose boundaries are entirely

Table 7.1 List of bird species recorded in the Caatinga with their status, habitat use, adaptive capacity, and source

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Rheidae				
Rhea Americana	RE	1	M	1
Tinamidae				
Crypturellus undulatus	RE	3	L	1
Crypturellus noctivagus	RE	3	L	1
Crypturellus parvirostris	RE	1	H	1
Crypturellus tataupa	RE	3	L	1
Rhynchotus rufescens	RE	1	H	1
Nothura boraquira	RE	2	H	1
Nothura maculosa	RE	1	H	1
Taoniscus nanus	RE	1	L	9
Anhimidae				
Anhima cornuta	RE	1	M	1
Anatidae				
Dendrocygna bicolor	RE	1	M	1
Dendrocygna viduata	RE	1	M	1
Dendrocygna autumnalis	RE	1	M	1
Cairina moschata	RE	1	M	1
Sarkidiornis sylvicola	RE	1	M	1
Anas georgica	SV	1	M	1
Amazonetta brasiliensis	RE	1	M	1
Anas bahamensis	RE	1	M	1
Anas discors	NV	1	M	1
Netta erythrophthalma	RE	1	M	1
Nomonyx dominicus	RE	1	M	1
Cracidae				
Penelope superciliaris	RE	3	L	1
Penelope jacucaca	RE	3	L	1
Ortalis araucuan	RE	2	M	1
Odontophoridae				
Odontophorus capueira	RE	3	L	1
Podicipedidae				
Tachybaptus dominicus	RE	1	M	1
Podilymbus podiceps	RE	1	M	1
Ciconiidae				
Ciconia maguari	RE	1	M	1
Jabiru mycteria	RE	1	M	1
Mycteria americana	RE	1	M	1
Phalacrocoracidae				
Nannopterum brasilianus	RE	1	M	1
Anhingidae				
Anhinga anhinga	RE	1	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Ardeidae				
Tigrisoma lineatum	RE	1	M	1
Cochlearius cochlearius	RE	1	M	1
Botaurus pinnatus	RE	1	M	5
Ixobrychus exilis	RE	1	M	9
Ixobrychus involucris	RE	1	M	1
Nycticorax nycticorax	RE	1	M	1
Nyctanassa violacea	RE	2	M	1
Butorides striata	RE	1	H	1
Bubulcus ibis	RE	1	H	1
Ardea cocoi	RE	1	M	1
Ardea alba	RE	1	H	1
Syrigma sibilatrix	RE	1	M	1
Pilherodius pileatus	RE	1	M	1
Egretta tricolor	RE	2	M	1
Egretta thula	RE	1	H	1
Egretta caerulea	RE	1	M	1
Threskiornithidae				
Mesembrinibis cayennensis	RE	2	M	1
Phimosus infuscatus	RE	1	M	1
Theristicus caerulescens	RE	1	H	1
Theristicus caudatus	RE	1	H	1
Platalea ajaja	RE	1	M	1
Cathartidae				
Cathartes aura	RE	1	H	1
Cathartes burrovianus	RE	1	H	1
Coragyps atratus	RE	1	H	1
Sarcoramphus papa	RE	2	L	1
Pandionidae				
Pandion haliaetus	NV	1	M	1
Accipitridae				
Leptodon cayanensis	RE	3	L	1
Chondrohierax uncinatus	RE	2	H	1
Elanoides forficatus	RE	1	M	1
Gampsonyx swainsonii	RE	1	H	1
Elanus leucurus	RE	1	H	1
Harpagus diodon	RE	3	L	9
Circus buffoni	RE	1	M	1
Accipiter superciliosus	RE	3	L	5
Accipiter striatus	RE	2	M	1
Accipiter bicolor	RE	3	L	1
Ictinia plumbea	RE	2	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Busarellus nigricollis	RE	1	M	1
Rostrhamus sociabilis	RE	1	M	1
Geranospiza caerulescens	RE	2	M	1
Buteogallus aequinoctialis	RE	3	L	1
Heterospizias meridionalis	RE	1	H	1
Urubitinga urubitinga	RE	2	M	1
Urubitinga coronata	RE	2	M	1
Rupornis magnirostris	RE	1	H	1
Parabuteo unicinctus	RE	1	H	1
Geranoaetus albicaudatus	RE	1	H	1
Geranoaetus melanoleucus	RE	1	M	1
Buteo nitidus	RE	2	M	1
Buteo brachyurus	RE	2	M	1
Buteo swainsoni	NV	1	M	1
Buteo albonotatus	RE	1	M	1
Spizaetus tyrannus	RE	3	L	1
Aramidae				
Aramus guarauna	RE	1	M	1
Rallidae				
Rallus longirostris	RE	3	L	1
Aramides ypecaha	RE	2	M	1
Aramides mangle	RE	3	L	1
Aramides cajaneus	RE	2	M	1
Laterallus viridis	RE	2	M	1
Laterallus melanophaius	RE	2	M	1
Laterallus exilis	RE	1	M	1
Porzana flaviventer	RE	1	M	9
Mustelirallus albicollis	RE	1	M	1
Neocrex erythrops	RE	2	M	1
Pardirallus maculatus	RE	3	L	1
Pardirallus nigricans	RE	2	M	1
Gallinula galeata	RE	1	M	1
Porphyriops melanops	RE	1	M	1
Porphyrio martinicus	RE	1	M	1
Charadriidae				
Vanellus cayanus	RE	1	H	1
Vanellus chilensis	RE	1	H	1
Pluvialis dominica	NV	1	M	3
Charadrius semipalmatus	NV	1	M	1
Charadrius collaris	RE	1	M	1
Recurvirostridae				
Himantopus mexicanus	RE	1	H	1
Himantopus melanurus	RE	1	H	4

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Scolopacidae				
Gallinago paraguaiae	RE	1	H	1
Bartramia longicauda	NV	1	M	1
Actitis macularius	NV	1	M	1
Tringa solitaria	NV	1	M	1
Tringa melanoleuca	NV	1	M	1
Tringa flavipes	NV	1	M	1
Calidris alba	NV	1	M	9
Calidris minutilla	NV	1	M	1
Calidris fuscicollis	NV	1	M	1
Calidris melanotos	NV	1	M	9
Jacanidae				
Jacana jacana	RE	1	H	1
Laridae				
Chroicocephalus cirrocephalus	RE	1	M	9
Sternidae				
Sternula superciliaris	RE	1	M	9
Phaetusa simplex	RE	1	M	1
Sterna hirundo	NV	2	M	1
Sterna paradisaea	RE	1	M	1
Rynchopidae				
Rynchops niger	RE	1	M	1
Columbidae				
Columbina passerina	RE	1	H	1
Columbina minuta	RE	1	H	1
Columbina talpacoti	RE	1	H	1
Columbina squammata	RE	1	H	1
Columbina picui	RE	1	H	1
Claravis pretiosa	RE	2	M	1
Patagioenas picazuro	RE	2	M	1
Patagioenas cayennensis	RE	3	L	1
Patagioenas plumbea	RE	3	L	1
Zenaida auriculata	RE	1	H	1
Leptotila verreauxi	RE	2	M	1
Leptotila rufaxilla	RE	3	L	1
Geotrygon montana	RE	3	L	1
Cuculidae				
Micrococcyx cinereus	RE	2	M	1
Piaya cayana	RE	2	M	1
Coccyzus melacoryphus	RE	2	H	1
Coccyzus americanus	NV	2	M	1
Coccyzus euleri	RE	2	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Coccyzus minor	RE	2	M	9
Crotophaga major	RE	2	M	1
Crotophaga ani	RE	1	H	1
Guira guira	RE	1	H	1
Tapera naevia	RE	1	H	1
Dromococcyx phasianellus	RE	3	L	1
Dromococcyx pavoninus	RE	3	L	9
Neomorphus geoffroyi	RE	3	L	8
Tytonidae				
Tyto furcata	RE	1	H	1
Strigidae				
Megascops choliba	RE	2	H	1
Pulsatrix perspicillata	RE	3	L	6
Pulsatrix koeniswaldiana	RE	3	L	5
Bubo virginianus	RE	1	H	1
Strix virgata	RE	3	L	1
Glaucidium brasilianum	RE	2	M	1
Athene cunicularia	RE	1	H	1
Aegolius harrisii	RE	2	L	1
Asio clamator	RE	1	H	1
Asio stygius	RE	2	M	1
Asio flammeus	RE	1	H	9
Nyctibiidae				
Nyctibius griseus	RE	2	M	1
Caprimulgidae				
Antrostomus rufus	RE	2	M	1
Lurocalis semitorquatus	RE	3	L	1
Nyctiprogne vielliardi	RE	3	L	1
Nyctidromus albicollis	RE	2	M	1
Nyctidromus hirundinaceus	RE	1	M	1
Hydropsalis parvula	RE	1	H	1
Hydropsalis longirostris	RE	1	H	1
Hydropsalis torquata	RE	1	H	1
Nannochordeiles pusillus	RE	1	H	1
Podager nacunda	RE	1	H	1
Chordeiles minor	NV	1	H	1
Chordeiles acutipennis	RE	1	H	1
Apodidae				
Cypseloides fumigatus	RE	2	M	9
Cypseloides senex	UN	1	M	1
Streptoprocne zonaris	UN	1	M	1
Streptoprocne biscutata	RE	1	M	1
Chaetura cinereiventris	RE	1	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Chaetura meridionalis	UN	2	M	1
Tachornis squamata	RE	1	H	1
Trochilidae				
Glaucis hirsutus	RE	3	L	9
Anopetia gounellei	RE	3	L	1
Phaethornis maranhaoensis	RE	2	M	1
Phaethornis ruber	RE	3	L	1
Phaethornis pretrei	RE	2	M	1
Campylopterus diamantinesis	RE	3	L	10
Campylopterus calcirupicola	RE	3	L	10
Eupetomena macroura	RE	1	H	1
Aphantochroa cirrochloris	RE	3	L	1
Florisuga fusca	RE	3	L	1
Colibri delphinae	RE	1	M	1
Colibri serrirostris	RE	2	H	1
Anthracothorax nigricollis	RE	2	M	1
Chrysolampis mosquitus	RE	2	H	1
Lophornis magnificus	RE	2	H	1
Chlorestes notata	RE	3	L	1
Chlorostilbon lucidus	RE	2	M	1
Thalurania furcata	RE	2	M	1
Thalurania glaucopis	RE	3	L	1
Hylocharis sapphirina	RE	3	L	1
Hylocharis cyanus	RE	2	M	1
Polytmus guainumbi	RE	2	M	1
Amazilia leucogaster	RE	2	M	1
Amazilia versicolor	RE	3	L	1
Amazilia fimbriata	RE	2	M	1
Amazilia lacteal	RE	2	M	9
Augastes scutatus	RE	1	M	7
Augastes lumachella	RE	1	M	1
Heliactin bilophus	RE	1	M	1
Heliomaster longirostris	RE	3	L	1
Heliomaster squamosus	RE	3	L	1
Calliphlox amethystina	RE	2	M	1
Trogonidae				
Trogon surrucura	RE	3	L	1
Trogon curucui	RE	3	L	1
Alcedinidae				
Megaceryle torquata	RE	1	M	1
Chloroceryle amazona	RE	2	M	1
Chloroceryle americana	RE	2	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Momotidae				
Momotus momota	RE	3	L	9
Galbulidae				
Galbula ruficauda	RE	2	M	1
Bucconidae				
Nystalus chacuru	RE	1	H	1
Nystalus maculatus	RE	2	M	1
Nonnula rubecula	RE	3	L	1
Chelidoptera tenebrosa	RE	2	M	1
Ramphastidae				
Ramphastos toco	RE	2	M	4
Ramphastos dicolorus	RE	3	L	9
Selenidera gouldii	RE	3	L	1
Picidae				
Picumnus pygmaeus	RE	3	L	1
Picumnus cirratus	RE	2	M	5
Picumnus albosquamatus	RE	2	M	1
Picumnus fulvescens	RE	2	M	1
Picumnus limae	RE	2	M	1
Melanerpes candidus	RE	2	H	1
Veniliornis passerinus	RE	2	H	1
Piculus chrysochloros	RE	3	L	1
Colaptes melanochloros	RE	2	H	1
Colaptes campestris	RE	1	H	1
Celeus ochraceus	RE	3	L	1
Dryocopus lineatus	RE	2	M	1
Campephilus melanoleucos	RE	3	L	1
Cariamidae				
Cariama cristata	RE	1	H	1
Falconidae				
Caracara plancus	RE	1	H	1
Milvago chimachima	RE	1	H	1
Herpetotheres cachinnans	RE	2	H	1
Micrastur ruficollis	RE	3	L	1
Micrastur semitorquatus	RE	2	M	1
Falco sparverius	RE	1	H	1
Falco rufigularis	RE	3	L	1
Falco deiroleucus	RE	2	M	1
Falco femoralis	RE	1	H	1
Falco peregrines	NV	1	M	1
Psittacidae				
Anodorhynchus leari	RE	3	L	1
Cyanopsitta spixii	EX	3	L	1
Ara ararauna	RE	2	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Ara chloropterus	RE	3	L	1
Primolius maracana	RE	2	M	1
Diopsittaca nobilis	RE	2	M	9
Thectocercus acuticaudatus	RE	2	M	1
Psittacara leucophthalmus	RE	2	M	1
Aratinga auricapillus	RE	3	L	1
Aratinga jandaya	RE	2	M	1
Eupsittula aurea	RE	1	H	1
Eupsittula cactorum	RE	2	H	1
Pyrrhura cruentata	RE	3	L	1
Pyrrhura frontalis	RE	3	L	1
Pyrrhura griseipectus	RE	3	L	1
Forpus xanthopterygius	RE	1	H	1
Brotogeris tirica	RE	3	L	1
Brotogeris chiriri	RE	2	M	1
Pionus maximiliani	RE	2	M	1
Amazona vinacea	RE	3	L	1
Amazona amazonica	RE	3	L	1
Amazona aestiva	RE	3	L	1
Thamnophilidae				
Myrmorchilus strigilatus	RE	2	M	1
Formicivora iheringi	RE	2	L	1
Formicivora grisea	RE	2	M	1
Formicivora melanogaster	RE	2	M	1
Formicivora rufa	RE	1	H	1
Formicivora grantsaui	RE	1	M	2
Dysithamnus mentalis	RE	3	L	1
Herpsilochmus sellowi	RE	2	M	1
Herpsilochmus atricapillus	RE	3	L	1
Herpsilochmus pectoralis	RE	2	M	1
Herpsilochmus longirostris	RE	3	L	1
Herpsilochmus rufimarginatus	RE	3	L	1
Sakesphorus cristatus	RE	2	M	1
Thamnophilus capistratus	RE	2	H	1
Thamnophilus torquatus	RE	1	M	1
Thamnophilus pelzelni	RE	3	L	1
Thamnophilus caerulescens	RE	3	L	1
Taraba major	RE	2	H	1
Myrmoderus loricatus	RE	3	L	1
Pyriglena leucoptera	RE	3	L	1
Rhopornis ardesiacus	RE	2	L	1
Drymophila ochropyga	RE	3	L	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Melanopareiidae				
Melanopareia torquata	RE	1	M	1
Conopophagidae				
Conopophaga cearae	RE	3	L	1
Conopophaga lineata	RE	3	L	1
Conopophaga roberti	RE	3	L	1
Grallariidae				
Hylopezus ochroleucus	RE	3	L	1
Rhinocryptidae				
Scytalopus diamantinensis	RE	3	L	1
Formicariidae				
Formicarius colma	RE	3	L	1
Chamaeza campanisona	RE	3	L	1
Scleruridae				
Sclerurus cearensis	RE	3	L	1
Dendrocolaptidae				
Sittasomus griseicapillus	RE	3	L	1
Xiphorhynchus atlanticus	RE	3	L	9
Xiphorhynchus fuscus	RE	3	L	1
Xiphorhynchus guttatoides	RE	3	L	1
Campylorhamphus falcularius	RE	3	L	1
Campylorhamphus trochilirostris	RE	3	L	1
Dendroplex picus	RE	3	L	1
Lepidocolaptes angustirostris	RE	2	H	1
Lepidocolaptes wagleri	RE	3	L	1
Lepidocolaptes squamatus	RE	3	L	1
Dendrocolaptes platyrostris	RE	3	L	1
Xiphocolaptes falcirostris	RE	3	L	1
Xiphocolaptes albicollis	RE	3	L	1
Xenopidae				
Xenops rutilans	RE	3	L	1
Furnariidae				
Furnarius figulus	RE	1	H	1
Furnarius leucopus	RE	2	H	1
Furnarius rufus	RE	1	H	1
Lochmias nematura	RE	3	L	1
Clibanornis rectirostris	RE	3	L	1
Megaxenops parnaguae	RE	3	L	1
Syndactyla dimidiata	RE	3	L	7
Pseudoseisura cristata	RE	2	H	1
Phacellodomus rufifrons	RE	2	H	1
Phacellodomus ruber	RE	2	H	1
Schoeniophylax phryganophilus	RE	1	H	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Certhiaxis cinnamomeus	RE	1	H	1
Synallaxis hellmayri	RE	1	H	1
Synallaxis cinerea	RE	3	L	1
Synallaxis frontalis	RE	2	H	1
Synallaxis albescens	RE	1	H	1
Synallaxis spixi	RE	3	L	1
Synallaxis hypospodia	RE	1	M	7
Synallaxis scutata	RE	2	M	1
Cranioleuca vulpina	RE	1	M	1
Cranioleuca semicinerea	RE	2	M	1
Pipridae				
Neopelma pallescens	RE	3	L	1
Pipra fasciicauda	RE	3	L	1
Manacus manacus	RE	3	L	1
Chiroxiphia pareola	RE	3	L	1
Antilophia bokermanni	RE	3	L	1
Antilophia galeata	RE	3	L	9
Onychorhynchidae				
Myiobius barbatus	RE	3	L	1
Myiobius atricaudus	RE	3	L	1
Tityridae				
Schiffornis virescens	RE	3	L	1
Tityra inquisitor	RE	3	L	1
Tityra cayana	RE	3	L	1
Pachyramphus viridis	RE	2	M	1
Pachyramphus castaneus	RE	3	L	1
Pachyramphus polychopterus	RE	2	M	1
Pachyramphus validus	RE	3	L	1
Xenopsaris albinucha	RE	1	M	1
Cotingidae				
Phibalura flavirostris	RE	2	M	1
Pyroderus scutatus	RE	3	L	1
Procnias averano	RE	3	L	1
Procnias nudicollis	RE	3	L	1
Platyrinchidae				
Platyrinchus mystaceus	RE	3	L	1
Rhynchocyclidae				
Leptopogon amaurocephalus	RE	3	L	1
Corythopis delalandi	RE	3	L	6
Phylloscartes beckeri	RE	3	L	1
Phylloscartes roquettei	RE	3	L	1
Tolmomyias sulphurescens	RE	3	L	1
Tolmomyias flaviventris	RE	3	L	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Todirostrum cinereum	RE	2	H	1
Poecilotriccus plumbeiceps	RE	3	L	1
Poecilotriccus fumifrons	RE	2	H	1
Myiornis auricularis	RE	3	L	1
Hemitriccus diops	RE	3	L	1
Hemitriccus striaticollis	RE	2	M	1
Hemitriccus nidipendulus	RE	2	M	1
Hemitriccus margaritaceiventer	RE	2	H	1
Hemitriccus mirandae	RE	3	L	1
Tyrannidae				
Hirundinea ferruginea	RE	2	H	1
Zimmerius acer	RE	3	L	1
Stigmatura napensis	RE	1	M	1
Stigmatura budytoides	RE	1	M	1
Euscarthmus meloryphus	RE	2	H	1
Euscarthmus rufomarginatus	RE	1	L	1
Camptostoma obsoletum	RE	1	H	1
Elaenia flavogaster	RE	2	M	1
Elaenia spectabilis	UN	3	L	1
Elaenia chilensis	SV	2	M	1
Elaenia parvirostris	SV	2	M	1
Elaenia mesoleuca	SV	3	L	1
Elaenia cristata	RE	1	H	1
Elaenia chiriquensis	RE	1	H	1
Elaenia obscura	SV	3	L	1
Suiriri suiriri	RE	1	H	1
Myiopagis caniceps	RE	3	L	1
Myiopagis viridicata	RE	3	L	1
Capsiempis flaveola	RE	3	L	1
Phaeomyias murina	RE	1	H	1
Phyllomyias reiseri	RE	3	L	1
Phyllomyias fasciatus	RE	2	M	1
Culicivora caudacuta	RE	1	M	1
Polystictus superciliaris	RE	1	M	1
Serpophaga subcristata	RE	2	H	1
Legatus leucophaius	RE	2	H	1
Myiarchus tuberculifer	RE	3	L	1
Myiarchus swainsoni	RE	1	H	1
Myiarchus ferox	RE	2	M	1
Myiarchus tyrannulus	RE	2	M	1
Sirystes sibilator	RE	3	L	1
Casiornis fuscus	RE	3	L	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Pitangus sulphuratus	RE	1	H	1
Philohydor lector	RE	3	L	1
Machetornis rixosa	RE	1	H	1
Myiodynastes maculatus	RE	3	L	1
Megarynchus pitangua	RE	2	H	1
Myiozetetes cayanensis	RE	2	M	7
Myiozetetes similis	RE	2	M	1
Tyrannus albogularis	RE	1	H	4
Tyrannus melancholicus	RE	1	H	1
Tyrannus savanna	SV	1	H	1
Griseotyrannus aurantioatrocristatus	SV	2	H	1
Empidonomus varius	RE	2	H	1
Colonia colonus	RE	3	L	1
Myiophobus fasciatus	RE	1	H	1
Sublegatus modestus	RE	2	M	1
Pyrocephalus rubinus	RE	1	H	1
Fluvicola albiventer	RE	1	H	9
Fluvicola nengeta	RE	1	H	1
Arundinicola leucocephala	RE	1	H	1
Cnemotriccus fuscatus	RE	3	L	1
Lathrotriccus euleri	RE	3	L	1
Contopus cinereus	RE	3	L	1
Knipolegus franciscanus	RE	3	L	1
Knipolegus lophotes	RE	1	M	9
Knipolegus nigerrimus	RE	2	M	1
Satrapa icterophrys	UN	1	H	1
Xolmis cinereus	RE	1	H	1
Xolmis velatus	SV	1	M	1
Xolmis irupero	RE	1	H	1
Vireonidae				
Cyclarhis gujanensis	RE	2	H	1
Hylophilus amaurocephalus	RE	3	L	1
Hylophilus poicilotis	RE	3	L	5
Vireo chivi	RE	3	L	1
Corvidae				
Cyanocorax cristatellus	RE	2	M	1
Cyanocorax cyanopogon	RE	2	M	1
Hirundinidae				
Pygochelidon cyanoleuca	RE	1	H	1
Stelgidopteryx ruficollis	RE	1	H	1
Progne tapera	RE	1	H	1
Progne subis	NV	1	H	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Progne chalybea	RE	1	H	1
Tachycineta albiventer	RE	1	M	1
Tachycineta leucorrhoa	UN	1	M	1
Riparia riparia	NV	1	H	1
Hirundo rustica	NV	1	H	1
Troglodytidae				
Troglodytes musculus	RE	1	H	1
Pheugopedius genibarbis	RE	3	L	1
Cantorchilus leucotis	RE	2	H	4
Cantorchilus longirostris	RE	3	L	1
Donacobiidae				
Donacobius atricapilla	RE	1	M	1
Polioptilidae				
Ramphocaenus melanurus	RE	3	L	1
Polioptila plumbea	RE	2	H	1
Turdidae				
Catharus fuscescens	NV	2	M	9
Turdus flavipes	RE	3	L	1
Turdus leucomelas	RE	2	H	1
Turdus rufiventris	RE	1	H	1
Turdus amaurochalinus	SV	2	H	1
Turdus subalaris	SV	3	L	1
Turdus albicollis	RE	3	L	1
Mimidae				
Mimus gilvus	RE	1	H	1
Mimus saturninus	RE	1	H	1
Motacillidae				
Anthus lutescens	RE	1	H	1
Passerellidae				
Zonotrichia capensis	RE	1	H	1
Ammodramus humeralis	RE	1	H	1
Arremon taciturnus	RE	3	L	1
Arremon franciscanus	RE	3	L	1
Parulidae				
Setophaga pitiayumi	RE	3	L	1
Geothlypis aequinoctialis	RE	1	H	1
Basileuterus culicivorus	RE	3	L	1
Myiothlypis flaveola	RE	3	L	1
Myiothlypis leucophrys	RE	3	L	1
Icteridae				
Psarocolius decumanus	RE	2	M	9
Procacicus solitarius	RE	2	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Cacicus haemorrhous	RE	2	H	1
Cacicus cela	RE	2	M	9
Icterus pyrrhopterus	RE	2	M	1
Icterus jamacaii	RE	2	H	1
Gnorimopsar chopi	RE	1	H	1
Anumara forbesi	RE	3	L	1
Agelasticus cyanopus	RE	1	M	1
Chrysomus ruficapillus	RE	1	H	1
Agelaioides fringillarius	RE	1	H	1
Molothrus rufoaxillaris	RE	1	H	1
Molothrus oryzivorus	RE	1	H	1
Molothrus bonariensis	RE	1	H	1
Sturnella superciliaris	RE	1	H	1
Thraupidae				
Porphyrospiza caerulescens	RE	1	M	1
Pipraeidea melanonota	RE	1	L	9
Neothraupis fasciata	RE	1	M	1
Schistochlamys melanopis	RE	1	H	1
Schistochlamys ruficapillus	RE	1	H	1
Paroaria dominicana	RE	1	H	1
Tangara cyanocephala	RE	3	L	1
Tangara cyanoventris	RE	3	L	1
Tangara sayaca	RE	2	H	1
Tangara palmarum	RE	2	M	1
Tangara cayana	RE	1	H	1
Nemosia pileata	RE	3	L	1
Compsothraupis loricata	RE	2	M	1
Conirostrum speciosum	RE	3	L	1
Conirostrum bicolor	RE	2	M	1
Sicalis citrine	RE	1	H	1
Sicalis flaveola	RE	1	H	1
Sicalis columbiana	RE	1	M	1
Sicalis luteola	RE	1	M	1
Hemithraupis guira	RE	3	L	1
Volatinia jacarina	RE	1	H	1
Trichothraupis melanops	RE	3	L	1
Coryphospingus pileatus	RE	2	H	1
Tachyphonus rufus	RE	3	L	1
Ramphocelus bresilius	RE	3	L	1
Charitospiza eucosma	RE	1	M	9
Tersina viridis	RE	3	L	1
Dacnis cayana	RE	2	M	1

(continued)

Table 7.1 (continued)

Taxon	Status	Habitat use	Adaptive capacity	Source[a]
Coereba flaveola	RE	2	H	1
Tiaris fuliginosus	RE	2	M	9
Sporophila lineola	RE	1	H	1
Sporophila plumbea	RE	1	H	1
Sporophila nigricollis	RE	1	H	1
Sporophila ardesiaca	RE	1	H	9
Sporophila caerulescens	RE	1	H	7
Sporophila albogularis	RE	1	H	1
Sporophila leucoptera	RE	1	M	1
Sporophila bouvreuil	RE	1	H	1
Sporophila angolensis	RE	1	M	1
Embernagra longicauda	RE	1	H	1
Emberizoides herbicola	RE	1	H	1
Saltatricula atricollis	RE	1	M	1
Saltator coerulescens	RE	2	M	1
Saltator similis	RE	2	M	1
Thlypopsis sordida	RE	2	H	1
Cypsnagra hirundinacea	RE	1	M	1
Cardinalidae				
Piranga flava	RE	1	M	1
Amaurospiza moesta	RE	3	L	7
Cyanoloxia brissonii	RE	2	M	1
Fringillidae				
Spinus yarrellii	RE	2	M	1
Spinus magellanicus	RE	1	M	1
Euphonia chlorotica	RE	2	H	1
Euphonia violacea	RE	3	L	1
Euphonia cyanocephala	RE	1	L	9

[a] Source: 1 = Silva et al. (2003); 2 = Gonzaga et al. (2007); 3 = Olmos and Albano (2012); 4 = Schunck et al. (2012); 5 = Dornelas et al. (2012); 6 = Silveira and Santos (2012); 7 = Vasconcelos et al. (2012); 8 = Roos et al. (2012); 9 = www.wikiaves.com.br; 10 = Lopes et al. (2017)

Status: *EX* extinct in wild, *NV* northern visitor, *RE* resident, *SV* southern visitor, *UN* unknown status

Habitat use: (1) open vegetation species, found only in open habitats (rivers, lakes, caatingas, grasslands and rupestrian grasslands); (2) generalist species, flexible enough to be use both open and forest ecosystems, sometimes living in the interface of these two major groups of ecosystems; (3) forest species, found in arboreal caatingas and all forests in the region (dry or humid)

Adaptive capacity: *H* high capacity—species found in anthropogenic ecosystems regardless if they are near natural ecosystems, *L* low capacity—species found only in landscapes composed of intact or almost undisturbed ecosystems, *M* medium capacity—species found in anthropogenic ecosystems only if they are near natural ecosystems or aquatic ecosystems

Table 7.2 List of bird species that possibly had their origins within the Caatinga as well as species that are currently classified as threatened by extinction

Species or subspecies	Origin	IUCN	MMA
Crypturellus noctivagus zabele	X		VU
Taoniscus nanus		VU	EN
Penelope jacucaca	X	VU	VU
Odontophorus capueira plumbeicollis			
Urubitinga coronata		EN	EN
Neomorphus geoffroyi		VU	VU
Nyctiprogne vielliardi	X		
Nyctidromus hirundinaceus	X		
Nannochordeiles pusillus novaesi	X		
Streptoprocne biscutata seridoensis	X		
Anopetia gounellei	X		
Campylopterus calcirupicola	X		
Colibri delphinae grenewalti	X		
Augastes lumachella	X		EN
Selenidera gouldii baturitensis	X		EN
Picumnus pygmaeus	X		
Picumnus fulvescens	X		
Picumnus limae	X		
Campephilus melanoleucos cearae	X		
Anodorhynchus leari	X	EN	EN
Cyanopsitta spixii	X	CR	CR
Thectocercus acuticaudatus haemorrhous	X		
Eupsittula cactorum	X		
Pyrrhura cruentata		VU	VU
Pyrrhura griseipectus	X	CR	EN
Amazona vinacea		EN	VU
Myrmorchilus strigilatus strigilatus	X		
Formicivora iheringi	X		
Formicivora melanogaster bahiae	X		
Formicivora grantsaui	X	EN	EN
Herpsilochmus sellowi	X		
Herpsilochmus pectoralis		VU	
Sakesphorus cristatus	X		
Thamnophilus capistratus	X		
Thamnophilus caerulescens cearensis	X		VU
Rhopornis ardesiacus	X	EN	EN
Conopophaga cearae	X		EN
Conopophaga lineata lineata			VU
Hylopezus ochroleucus	X		
Scytalopus diamantinensis	X	EN	EN
Sclerurus cearensis	X	VU	VU
Xiphorhynchus atlanticus			VU

(continued)

Table 7.2 (continued)

Species or subspecies	Origin	IUCN	MMA
Xiphorhynchus guttatoides gracilirostris	X		EN
Lepidocolaptes wagleri	X		EN
Xiphocolaptes falcirostris	X	VU	VU
Xiphocolaptes albicollis villanovae	X		
Megaxenops parnaguae	X		
Pseudoseisura cristata	X		
Phacellodomus rufifrons rufifrons/specularis	X		
Synallaxis hellmayri	X		
Cranioleuca vulpina reiseri	X		
Cranioleuca semicinerea	X		
Antilophia bokermanni	X	CR	CR
Procnias averano averano	X		
Procnias nudicollis		VU	
Platyrinchus mystaceus niveigularis			VU
Phylloscartes beckeri	X	EN	EN
Phylloscartes roquettei	X	EN	EN
Hemitriccus mirandae	X	VU	VU
Stigmatura napensis bahiae	X		
Stigmatura budytoides gracilis	X		
Suiriri suiriri bahiae	X		
Phyllomyias fasciatus cearae	X		
Culicivora caudacuta		VU	
Knipolegus franciscanus	X		
Knipolegus nigerrimus hoflingi	X		
Xolmis irupero niveus	X		
Cantorchilus longirostris bahiae	X		
Mimus saturninus arenaceus	X		
Arremon franciscanus	X		
Icterus pyrrhopterus tibialis	X		
Icterus jamacaii	X		
Anumara forbesi		EN	VU
Agelaioides fringillarius	X		
Paroaria dominicana	X		
Tangara cyanocephala cearenis	X		VU
Compsothraupis loricata	X		
Sporophila albogularis	X		
Saltator coerulescens superciliaris	X		
Spinus yarrellii	X	VU	VU

Origin: species and subspecies marked with an ‘X’ had their origin within the Caatinga
IUCN: species considered as threatened in the IUCN (International Union for the Conservation of Nature) Red List
MMA: species regarded as threatened in the MMA (Brazilian Ministry of Environment) Red List
Categories in both Red Lists are: *CR* critically endangered, *EN* endangered, *VU* vulnerable

within the Caatinga (e.g., *Antilophia bokermanni*). They are found in ecosystems that have a patchy distribution within the region, such as rupestrian grasslands and humid forests. The second group includes species and subspecies (e.g., *Stigmatura budytoides bahiae*) with relatively large ranges whose limits are restricted to the current boundaries of the Caatinga. Finally, the third group is composed of species and subspecies whose ranges are highly congruent with the current boundaries of the Caatinga (e.g., *Picumnus pygmaeus* and *Knipolegus franciscanus*) but who are not restricted to it. Several species and subspecies from the third group can be found in patches of SDTFs within the Cerrado or Atlantic Forest. In addition, there are some other species (e.g., *Sakesphorus cristatus*, *Icterus jamacaii*, and *Paroaria dominicana*) whose ranges are expanding rapidly toward other regions due to either the replacement of the native forests and savannas by anthropogenic ecosystems or the live bird trade in Brazil (Alves et al. 2013).

Species that have originated in the Caatinga date from a range of periods, from Early Holocene, such as *Antilophia bokkermani* (Luna et al. 2017), to Middle Miocene, such as *Cyanopsitta spixii* (Tavares et al. 2006). In general, birds have been conservative in terms of choosing their habitats during diversification, indicating that major habitat shifts are not common during speciation events. For instance, the closest relatives of the species now inhabiting tall dry forest habitats or humid forest enclaves are in the Atlantic Forest (e.g., *Lepidocolaptes wagleri*), Amazonia (*Xiphorhynchus guttatoides gracilirostris*), or the gallery forests of the Cerrado (*Antilophia bokermanni*). On the other hand, the species living in thorny shrub or open habitats have their sister species in regions dominated by open ecosystems, such as the Cerrado (*Suiriri s. bahiae*) and Chaco (e.g., *Myrmochilus s. strigilatus*). As an area of endemism, the Caatinga should be considered as a composite because the phylogenetic relationships between its endemic species and their closest relatives indicate multiple historical linkages with other South American areas of endemism.

Several species that originated in adjacent regions (Amazonia, the Atlantic Forest, and the Cerrado) have small populations within the Caatinga. These species are thought to have been added to the regional biota as a consequence of biotic interchange. The relative contribution of biotic interchange to the Caatinga's regional species richness remains to be estimated. In the adjacent Cerrado, Silva (1996) found that at least 36.3% of the regional avifauna were added through biotic interchange. Generally, the species received through biotic interchange tend to be more numerous along the boundaries between regions, with only a few species reaching the core of the region that has been colonized (Silva 1996). Furthermore, such species have narrow and continuous ranges that follow the corridors that allowed them to expand their ranges into a new region, as was described by Silva (1996) regarding the gallery forests of the Cerrado. However, several species that colonized the Caatinga have isolated and patchy ranges, rather than narrow and continuous ranges. We argue that this distribution pattern suggests that the ecological conditions that enabled these species to expand their ranges into the Caatinga no longer exist.

Evidence for the mass extinction of birds in the Caatinga is non-existent because bird fossils have not yet been found in any of the numerous limestone caves in the region (Castro et al. 2014). However, studies of mammals suggest that several species went extinct as a consequence of the climate change across the region during Quaternary (Vivo and Carmignotto 2004; Lima-Ribeiro and Diniz-Filho 2013). Until fossil data become available for birds, ornithologists interested in the evolution of the Caatinga's avifauna should focus their research agenda on determining the roles played by species production and biotic interchange in assembling the current regional avifauna. Silva and Santos (2005) compared the avifaunas of the major Brazilian ecological regions and suggested that in the Caatinga, Cerrado, and Pantanal, biotic interchange, rather than species production, is the most important biogeographical factor in terms of shaping the current regional avifauna. This is a workable hypothesis for future research.

7.4 Local Species Composition and Richness

Species richness at the regional level is connected to species richness at the local level through habitat selection. Species can have overlapping ranges on a large scale, but if they do not inhabit the same habitat, they will not co-occur at the local level. In other words, they can be sympatric but not syntopic. Processes such as competition, predation, and stochastic local extinction can filter the regional species pool still more, making local assemblages only a subset of the regional avifauna.

To evaluate habitat selection by birds in the Caatinga, we classified bird species into three groups: (a) forest species, found in arboreal caatingas and all forests in the region (dry or humid); (b) open vegetation species, found only in open habitats, such as lakes, rivers, open caatingas, grasslands, and rupestrian grasslands; and (c) generalist species, flexible enough to use both open and forest ecosystems, sometimes living in the interface between these two habitat groups. We found that among the 509 resident bird species in the region, 166 were forest species, 200 were open vegetation species, and 143 used both habitat types. This simple analysis demonstrates that even though forests cover less than 15% of the Caatinga (IBGE 1993), they support at least 60% of the bird species (i.e., forest + generalist species). This percentage is similar to that reported by Silva (1995) for birds in the Cerrado, where gallery and dry forests maintain most of the regional avifauna.

Oliveira and Diniz-Filho (2010) overlaid the ranges of 477 avian species within the Caatinga using 0.5° × 0.5° (around 3000 km^2) grid cells. They found out that 29–63 species could co-occur in the same grid cell and that species diversity declined from the center to the periphery, with the areas having the highest species number being in the middle southern region. However, moving to the next spatial level (sites and landscapes up to 100 km^2), the number of species recorded in various field surveys across the Caatinga ranged from 56 (Farias 2007) to 259 (Vasconcelos et al. 2012), indicating that up to 48.7% of regional avifauna can co-occur in a relatively small area. These levels of local species richness are higher than those expected based on the species density maps produced by Oliveira and Diniz-Filho (2010). Of course, comparisons among field surveys are always limited due to differences in the sampling techniques, areas covered, and methods. However, a general pattern that involves habitat heterogeneity, geographical location, and conservation state seems to emerge from the available information. The sites with the highest species richness (210–259) are located along the boundaries of the Caatinga, in the states of Piauí, Bahia, and Minas Gerais (Olmos and Albano 2012; Schunck et al. 2012; Silveira and Santos 2012; Vasconcelos et al. 2012). These sites have heterogeneous landscapes composed of several different types of vegetation, including those that are more generally found in the Cerrado and Atlantic Forest, as well as being in an excellent conservation state. The sites with 154–204 species are found in the core of the Caatinga (e.g., Nascimento et al. 2000; Farias et al. 2005; Barnett et al. 2014; Pichorim et al. 2016). These sites are usually covered by tall dry forests or riverine forests, along with open caatingas and aquatic ecosystems, and are relatively well-protected. The sites with 121–145 species are covered by open caatingas associated with rivers and other bodies of water; they are in a good or moderate conservation state (e.g., Telino-Junior et al. 2005; Pereira and Azevedo-Júnior 2011; Las-Casas et al. 2012). Finally, the sites with the lowest number of species (56–120) contain open caatingas and aquatic ecosystems surrounded by agricultural fields or pastures; therefore, they are under continuous human pressure (e.g., Olmos et al. 2005; Araujo and Rodrigues 2011; Pereira and Azevedo-Júnior 2011).

7.5 Ecological Dynamics

Local bird assemblages in the Caatinga are distinctly seasonal, with the number of species and individuals declining sharply from the rainy season to the dry season (Araujo 2009). These assemblages are composed of core species, which persist in a habitat over time, and transient species, which occur intermittently in a habitat as a result of their dispersal from surrounding habitats or regions (Coyle et al. 2013). There are, of course, species that are intermediate between these two groups (Boss and Silva 2014). In the only study in the Caatinga in which a bird assemblage was sampled monthly over 48 months, Araujo (2009) found 18 core species (present in >18 months), 29 transient species (present in <8 months), and 27 intermediaries (present from 9 to 17 months). The pattern found for the Caatinga is similar to that described for the avifauna of a seasonal Amazonian savanna by Boss and Silva (2014). In local assemblages, core and transient species arise via different mechanisms. Core species are influenced mostly by local-scale factors that allow the persistence of these species in a habitat, whereas transient species are influenced mostly by regional factors that govern the number of species that can potentially move into a habitat from the surrounding landscape (Coyle et al. 2013). Boss and Silva (2014) made three predictions regarding seasonal savanna bird assemblages that are also valid for local bird assemblages in the Caatinga: (a) local bird assemblages will be composed of a small number of species that occupy the site almost year-round, combined with a high number of less abundant transient species that are habitat generalists and use the site only during some periods of their annual lifecycles; (b) because local diversity is a consequence of regional diversity and habitat selection, the number of core species in a given site will increase with the structural complexity of the vegetation (MacArthur and MacArthur 1961; Karr and Roth 1971); and (c) because the number of transient species in a site is dependent on the pool of species in the landscape (Belmaker 2009) and because the landscape's species richness is correlated with landscape heterogeneity (Coyle et al. 2013), the richness of transient species in a local assemblage should increase with the heterogeneity of the landscape in which the site is located (Coyle et al. 2013).

As in any semiarid region, local bird assemblages in the Caatinga exhibit large seasonal variations that are associated with variations in rainfall. Rains increase arthropod populations, as well as the production of leaves, flowers, and fruits by plants. Given this seasonal environment, most species in the region use both animal and vegetal foods in their diets as a survival strategy. One good example is the 32 species of hummingbirds found in the region. They consume small spiders and the floral resources provided by at least 60 plant species across the region to guarantee the energy required for their very demanding lives (Araujo 2009; Las-Casas 2009; Machado 2009; Chap. 9). Fleshy fruits are an important resource for birds across the region. They are available to birds mostly during the rainy season and more rarely during the dry season (Araujo 2009; Gomes et al. 2014). Large frugivorous birds, such as *Penelope jacucaca*, feed on the fruits of at least 30 plant species and play a key role as seed dispersers (Bezerra 2015; Castro 2016). During the rainy season, grasses produce seeds that are consumed by several bird species, such as doves, tanagers, and seedeaters. Some of these species are able to feed on fallen seeds on the ground, whereas others are stem-gleaner specialists; i.e., they feed mainly on seeds still borne on plants' stalks (Remsen and Hunt 1979). The first group may stay in the same area most of the year, whereas the latter group may search for food elsewhere. Eating other vertebrates, such as other birds, small mammals, bats, snakes, and lizards, is usually restricted to birds of prey. However, small arboreal lizards have also been found in the stomachs and feces samples of woodcreepers and jays (Araujo 2009).

Most of the bird species in the Caatinga breed only during the 3–4 months of the rainy season, with very few species breeding outside of this period (Araujo 2009; Vilas-Boas 2013; Cavalcanti 2016; Cavalcanti et al. 2016). The breeding season in the Caatinga is shorter than in the adjacent mesic regions, such as the Cerrado (Piratelli et al. 2000; Marini and Durães 2001), Atlantic Forest (Mallet-Rodrigues 2005), and Amazonia (Stouffer et al. 2013), but it is similar to the breeding season in other dry regions, such as northeastern Venezuela (Poulin et al. 1992). Caatinga birds will begin their breeding activities only when the trees and shrubs are fully covered with leaves because leaves help to mitigate the impact of the strong solar radiation on their eggs and nestlings. Caatinga birds build different types of nests, ranging from open to closed. Some species nest directly on the ground or in cavities, but open basket nests are the most common nest type among Caatinga birds (Vilas-

Boas 2013). Many species lay two eggs, but usually only one will hatch (Vilas-Boas 2013). The nesting success rate is much higher in closed nests than in open nests and decreases towards the second half of the breeding season (França et al. 2016). As in any neotropical environment, nest predation is the main cause of decreased reproductive success (Vilas-Boas 2013; França et al. 2016). Woodpeckers, which nest in cavities, have a distinct seasonal breeding pattern. They usually begin to breed during the first months of the dry season, just shortly after the end of the rainy season (Araujo 2009; Cavalcanti 2016). Another species that has an unusual breeding period is *Antilophia bokermanni*, which inhabits evergreen forests along perennial streams in the escarpment of the Chapada do Araripe. They breed only from the second half of the dry period (September) to the early rainy season (January) (Girão and Souto 2005). It is possible that birds living in the patches of humid forests within the Caatinga have a different breeding season than birds living in the various types of caatingas, but this hypothesis is yet to be tested. In birds, breeding and molting do not usually overlap because these lifecycle stages require additional energy (Wingfield 2008). In the Caatinga, birds change their body, tail, and flying feathers during the second half of the rainy season and the beginning of the dry season (Araujo et al. 2017). However, there is evidence that some bird species in the region exhibit molting–breeding overlap, suggesting that in regions in which food resources are concentrated within a short season, the overlapping of these two lifecycle stages is much more common than expected (Araujo et al. 2017).

After the breeding season, birds in the Caatinga ecosystems may stay at the same site at which they bred or go elsewhere. Although more studies are required, the available information suggests that moving, rather than staying, is the norm among the region's birds (Araujo 2009; Ruiz-Esparza et al. 2011; Araujo et al. 2012; Pereira and Azevedo-Junior 2013). Such movements can occur within a landscape, between landscapes, within a region, or between regions. The Caatinga's birds exhibit all of these types of movement. Movements between habitats within a landscape are relatively short, with the birds typically moving from the site at which they breed to the closest spot where key resources will be available during the dry season. These birds typically move towards areas along rivers, creeks, lakes, or gorges. Even within a continuous area covered by tropical dry forest, small topographic changes create spots that are much more humid than their surroundings. These spots are local micro-refuges. During the dry season, bird abundance in these places is extraordinarily high, only decreasing when the rains return and the entire landscape becomes green again. Movements between landscapes are typically medium-distance movements between sub-regions of the Caatinga. These include altitudinal migrations along the slopes of the plateaus, movements along the rivers, and movements following the availability of specific resources. The movement of *Zenaida auriculata* to follow the availability of seeds (mainly species of *Croton* sp.) across the Caatinga is an example of movement between landscapes (Azevedo-Júnior and Antas 1990). Finally, in inter-regional migrations, a species that breeds in the Caatinga migrates to another region afterward. The textbook example of this type of movement is *Sporophila lineola*, which breeds in the Caatinga between January and May–June and then migrates to the north-central region of Venezuela through northeastern

Pará and Suriname (Silva 1995). More recently, Lees (2016) demonstrated that at least some populations of Ash-throated Casiornis (*Casiornis fusca*) breed in the Caatinga and then migrate to Amazonia.

7.6 Caatinga Birds in a Changing Climate

The Caatinga will pass through a large-scale process of transformation during the next decades. Currently, at least 63.3% of the region is occupied by anthropogenic ecosystems, which are less diverse and resilient than native ones (Chap. 13). Furthermore, climatic models predict that the Caatinga will experience rainfall reductions, temperature increases, and a higher frequency of extreme events, such as droughts, in the future (Chap. 14). Together, land use changes and climatic changes can lead to desertification. Sá and Angelotti (2009) estimated at least 75% of the region has a high potential for desertification.

In a region dominated by degraded lands and experiencing a more severe climate, it is expected that few bird species will be able to maintain viable populations. To estimate how species can cope with land use transformations and climate change, we used our field experience and a literature survey to classify each species into one of three adaptive capacity categories: (a) high capacity—species that can be found in anthropogenic ecosystems far from any natural or aquatic ecosystems; (b) medium capacity—species that can be found in anthropogenic ecosystems if and only if these ecosystems are near natural or aquatic ecosystems; and (c) low capacity—species found only in landscapes composed of intact or almost undisturbed ecosystems. We found that 162 species had a high adaptive capacity, 207 had a medium adaptive capacity, and 179 had a low adaptive capacity (Table 7.1). Thirty-five species are classified as threatened by either the IUCN (International Union for the Conservation of Nature) or the Brazilian Government. Most of these species (83%) have low adaptive capacity, with 17% exhibiting medium adaptive capacity. In general, our analysis demonstrates that most (70.4%) of the birds inhabiting the Caatinga, including the most threatened ones, have low to medium adaptive capacity and require natural or aquatic ecosystems to survive. The long-term conservation of this regional avifauna is dependent on the outright protection of environmental heterogeneity across the region. The protection and restoration of the natural ecosystems on the tops and slopes of isolated plateaus, as well as the river valleys, is the backbone of a conservation plan for the regional avifauna. If the Brazilian society fails to implement this conservation network and the current land-use and climate change trends continue as usual, then a massive bird extinction can be expected across the region.

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Chapter 8
Mammals of the Caatinga: Diversity, Ecology, Biogeography, and Conservation

Ana Paula Carmignotto and Diego Astúa

Abstract In this chapter we provide an updated checklist of Caatinga mammals, with a critical review of previous lists, and an overview of our current knowledge on the distribution and endemism patterns, ecology, behavior, evolution, and biogeography of these mammals. The Caatinga mammal fauna is composed of 183 species (including 11 endemics) that occur within its boundaries, mostly represented by rodents and bats. This list includes taxa with broad distributional ranges within the Caatinga only, those distributed in the Caatinga and in other regions, as well as taxa with very restricted distributions in the region, whether at its borders, in enclaves of specific vegetation types, or endemic to a particular region within the Caatinga. Ecology and behavior studies are still scarce for most species, and although there has been progress in assessing the relationship between precipitation and reproductive biology in small mammals and the physiological adaptations in selected taxa, there is a pressing need for more information on ecology, physiology, and behavior for most species. Caatinga mammals include taxa descending from forest ancestors as well as open area endemics that have been shown to be temporally heterogeneous, with divergence estimates ranging from Late Miocene to Early Pleistocene, leading to a complex evolutionary history for the Caatinga mammals. These mammals also show distinctive distributional patterns, posing challenges for conservation efforts, as these need to address the diversity of Caatinga vegetation physiognomies, such as transitional areas along its borders, humid forest enclaves, and dry formations in nearby '*Serras*' and '*Chapadas*', in order to preserve most of its richness.

Keywords Caatinga mammals • Composition • Distribution • Dry forest • Ecology • Richness • Seasonal • Semiarid • South America

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8.1 Introduction

Of all of the major Brazilian ecological regions, the Caatinga likely holds the least studied mammal fauna. The current level of knowledge of Caatinga mammals is directly related to the history of previous important fieldwork efforts in that region, and few large collecting efforts have occurred so far in the Caatinga. One of the largest surveys of the whole region was made possible through the contributions of Dr. João Moojen, then Curator of Mammals at the Museu Nacional (MN), and of the National Plague Service (Serviço Nacional da Peste [SNP]) around 1950. By adjusting the SNP's original collecting protocol, including careful annotation of accompanying data and training field technicians in proper skin preparation techniques, the SNP obtained over 55,000 specimens in a few years. The taxonomic scope, however, was restricted, as the project focused on potential plague vectors, and as such mainly small mammals—marsupials and small rodents—were collected (see detailed information in Oliveira and Franco 2005). These data were first published by Freitas (1957) and reanalyzed by Oliveira et al. (2003b), yet only part of that huge collection has subsequently been adequately studied in terms of current taxonomy, morphology, morphometrics, or reproductive or ecological data (Oliveira et al. 1992, 1998; Lorini et al. 1994; Camardella et al. 1998; Sobral and Oliveira 2014; Caccavo and Oliveira 2016). The material, however, is still available for study at the MN in Rio de Janeiro, Brazil.

Later, fieldwork led by researchers from the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA) and supported by the Academia Brasileira de Ciências in the Chapada do Araripe region (in western Pernambuco and southern Ceará) resulted in over 6000 specimens, currently housed in the Carnegie Museum and the Museu de Zoologia de São Paulo (MZUSP) (Willig and Mares 1989; Oliveira et al. 2003b). This work led to a series of papers on the ecology, natural history, distribution, and systematics of Caatinga mammals (Lacher 1981; Mares et al. 1981, 1985; Streilein 1982a, b, c, d, e, f; Willig 1983, 1985, 1986; Lacher and Mares 1986; Mares and Lacher 1987; Willig and Mares 1989), and to what can be considered the first checklist of Caatinga mammals, which was published as one of their first results (Mares et al. 1981) and updated a few years later (Willig and Mares 1989) based on their own collected samples and on specimens examined from the MN. This checklist recorded 84 mammals in the Caatinga, the taxonomic status of which was later updated, resulting in 81 species after exclusion of the exotic ones (Willig and Mares 1989).

The 1980s also witnessed the birth of the mammal collections of the Universidade Federal da Paraíba (UFPB) and Universidade Federal de Pernambuco (UFPE), which were coordinated, respectively, by Dr. Alfredo Langguth and Mr. Deoclécio Guerra. Upon their creation, local surveys were initiated and since then have resulted in around 13,000 specimens between the two collections. This material later led to checklists of mammals recorded in northeastern Brazilian states (considering all vegetation physiognomies represented) and, as such, in the Caatinga and northeastern

Atlantic Forest (Oliveira and Langguth 2004; Astúa and Guerra 2008; Feijó and Langguth 2011, 2013; Gurgel-Filho et al. 2015).

It took almost 20 years for an updated list of mammals from the whole Caatinga to be compiled by Oliveira et al. (2003b), who recorded 143 species in the region. Finally, this list was updated a decade later to include 153 species in what was until now the most recent checklist of Caatinga mammals (Carmignotto et al. 2012). Other noteworthy checklists of Caatinga mammals were actually part of the checklist of Brazilian mammals first published by Fonseca et al. (1996) and updated by Paglia et al. (2012), which classified the mammals by their occurrence in the distinct regions in Brazil; 101 species were reported for the Caatinga in the first edition and 153 species in the most recent checklist.

Analyzing these checklists over the past 30 years (1981–2012), we observe an increasing number of mammal species recorded in the Caatinga. Such an increase results from new fieldwork in areas not yet or poorly surveyed, surveys applying new techniques (e.g., pitfall and harp traps), taxonomic revision of material housed in scientific collections, and new analytical methods (e.g., molecular phylogeny or geometric morphometrics) (Mares et al. 1981; Willig and Mares 1989; Oliveira et al. 2003b; Carmignotto et al. 2012; Paglia et al. 2012).

Mares et al. (1981) provided one of the first maps of the mammal records in the Caatinga, represented by the localities of the voucher specimens they examined. This map clearly shows a few regions with a greater concentration of records, such as the region of the Chapada do Araripe, in southern Ceará and western Pernambuco; the humid enclaves (*brejos de altitude*) in northern Ceará; areas in the interior and eastern Pernambuco; northern Alagoas; and eastern and central Bahia. In contrast, most parts of the Rio Grande do Norte, Paraíba, and Piauí states completely lacked specimen records (see Fig. 15, page 181 in Mares et al. 1981).

After more than two decades, this picture remained largely unchanged, as Oliveira et al. (2003b) have shown, pointing out that the most complete mammal surveys were concentrated in the humid forest enclaves in northern Ceará and eastern Pernambuco and Alagoas, in addition to the region of the Chapada do Araripe: one locality in northwestern Minas Gerais; three localities in the western limits of Caatinga, in Piauí; two localities in the interior of Pernambuco; and two in northern Bahia (see Fig. 1, page 285 in Oliveira et al. 2003b). These authors have also elected nine priority areas for mammal surveys: (1) northern Maranhão, which represents the northwestern limit of the Caatinga; (2) northwestern Piauí, represented by *babaçual* vegetation; (3) central Ceará; (4) the Caatinga in Rio Grande do Norte; (5) northern Paraíba; (6) central Pernambuco; (7) central-eastern Bahia; (8) southwestern Bahia; and (9) northeastern Minas Gerais (see Fig. 1, page 285 in Oliveira et al. 2003a).

Similar results were found by Oliveira and Langguth (2004), Astúa and Guerra (2008), Feijó and Langguth (2013), and Gurgel-Filho et al. (2015), who emphasized that the drier and more central areas in the Caatinga are yet poorly sampled, with the central region of Ceará, central and southwestern Pernambuco, and the whole area of Caatinga in Alagoas being identified as priority regions for inventories, making a total, in addition to the ones proposed by Oliveira et al. (2003b), of 11 priority areas for mammal surveys. Few inventories have so far been conducted in these poorly known areas, but they have already led to important records for the Caatinga (Cruz et al. 2005; Miranda et al. 2005, 2009; Ferreira et al. 2009; Geise et al. 2010).

The conclusions of the first studies of the Caatinga mammals (e.g., Mares et al. 1981; Willig 1983; Willig and Mares 1989) on richness, endemism, distributional, and ecological patterns of this fauna can be summarized as follows: (1) the Caatinga has low species richness and endemism compared with other adjacent regions; (2) most mammal species are shared with the Cerrado, and the Caatinga fauna can be considered a subset of the fauna of that region; and (3) Caatinga mammal species are not physiologically adapted to the semiarid conditions but, instead, present behavioral traits to cope with the harsh environments of the Caatinga.

What the studies of the Caatinga mammals from the 1990s until now (e.g., Fonseca et al. 1996; Oliveira et al. 2003b; Carmignotto et al. 2012; Paglia et al. 2012; Gutiérrez and Marinho-Filho 2017) have shown, however, is that species richness and endemism are increasing. Although the Caatinga still shows lower levels of endemism than the Cerrado, Amazonia, and Atlantic forests, it certainly cannot be considered as a species-poor region (e.g., Albuquerque et al. 2012; Carmignotto et al. 2012). The patterns of shared mammals are much more complex than previously thought, with species shared not only with the Cerrado but with the Amazon, Atlantic Forest, and Chaco as well, and species are not homogeneously distributed along the Caatinga, leading to distinct richness and biogeographic patterns that are only beginning to be unveiled. The same can be said for the endemics, which have distinct phylogenetic relationships and habitat associations, leading to a complex evolutionary history for the Caatinga mammals (e.g., Lara and Patton 2000; Gonçalves et al. 2005; Carmignotto et al. 2012; Faria et al. 2013; Nascimento et al. 2013b; Gutiérrez and Marinho-Filho 2017).

As for the hypothesized lack of physiological adaptations in Caatinga mammals, this has been partially supported, as physiological adaptations do exist but they are not nearly as extreme as those found in desert rodents (Mendes et al. 2004; Ribeiro et al. 2004; Carvalhaes et al. 2015). Moreover, behavioral traits related to the climatic variations of the Caatinga do seem to be an additional strategy to help them survive in this semiarid environment, as reproduction is somehow related to the onset of rainfall for most small non-volant species studied so far, whether as a proximal or ultimate factor (e.g., Cerqueira 2005; Sobral and Oliveira 2014). Likewise, some species from more open habitats are nocturnal and dig holes to escape the higher diurnal temperature and predators (e.g., Rocha 1995; Santos and Lacey 2011), while others adjust their activity budgets to cope with the variation in heat and drought throughout the year (e.g., Abreu et al. 2016). However, there is still much to understand about the ecology and behavior of the majority of the mammal species that inhabit the Caatinga.

Our goals here were to update the most recent list of Caatinga mammals (Carmignotto et al. 2012) and to evaluate the current knowledge on patterns of richness, endemism, phylogenetic relationships, and species distribution within the region, as well as on ecology and behavior of Caatinga mammals.

8.2 Region Limits, Taxa Included, and Data Sources

In order to update the checklist of mammals from the Caatinga we considered all records within its area (i.e., 912,529 km^2; see Chap. 1). Thus, we considered as part of the Caatinga mammal fauna not only those species present in Caatinga vegetation physiognomies, but also those often found in enclaves of other vegetation formations within the Caatinga core area, such as humid forest enclaves in Alagoas, Ceará, Paraíba, and Pernambuco, and Cerrado pockets in western Ceará (see the vegetation classifications of Velloso et al. 2002; WWF 2014). In addition, we highlighted the records restricted to its borders to better understand the composition and distribution of the mammals present in this region. Therefore, species that are often found in areas near its limits, such as Serra das Confusões and Serra da Capivara National Parks in southern Piauí, as well as those species found in transitional areas, such as the Chapada Diamantina complex in the southern portion of the region, were all included in the checklist. Another group of mammals that we thought also deserved a distinction in the checklist is the large species that once were found in a wider range in the region, and currently are restricted to more preserved areas, most of them situated in its borders, such as the Serra das Confusões and Serra da Capivara National Parks in southern Piauí state which also harbor a great richness of mammals from the Caatinga and nearby regions.

The checklist presented here is based on records already published, as well as those from voucher specimens housed in scientific collections that have not yet published. We refer to the most recent lists for the Caatinga (i.e., Oliveira et al. 2003b; Carmignotto et al. 2012) and Brazil (Paglia et al. 2012) for comparisons. We also updated those lists using records from Gardner (2008c), Tavares et al. (2008), Nogueira et al. (2014), Patton et al. (2015), and Carvalho-Neto et al. (2016), as well as those from state checklists and taxonomic revisions based on specimens housed in mammal collections, such as Astúa and Guerra (2008), Percequillo et al. (2008), Tavares et al. (2010), Feijó and Langguth (2011, 2013), Bornholdt et al. (2013), and Gurgel-Filho et al. (2015), faunal surveys from specific localities (e.g. Pereira and Geise 2009; Silva and Marinho-Filho 2010; Silva et al. 2011; Leal et al. 2013; Nascimento et al. 2013a; Sá-Neto and Marinho-Filho 2013; Bezerra et al. 2014; Novaes and Laurindo 2014a; Fernandes-Ferreira et al. 2015; Lapenta and Bueno 2015; Nogueira et al. 2015; Novaes et al. 2015; Silva et al. 2015; Delciellos 2016; Dias and Bocchiglieri 2016a), new records of geographical expansions (e.g., Miranda et al. 2005, 2009; Fernandes-Ferreira et al. 2011; Rocha et al. 2012, 2014a, b, 2015; Nascimento et al. 2016), and the description of new species (Taddei and Lim 2010; Moratelli et al. 2011; Moratelli and Dias 2015). Taxonomic nomenclature and classification follows Gardner (2008c) and Voss and Jansa (2009) for the marsupials, Gardner (2008c) for Cingulata, Pilosa, and Chiroptera, Patton et al. (2015) for the rodents, and Wilson and Reeder (2005) for the other mammal orders, unless specified in the taxonomic notes of Table 8.1.

8.3 Current Composition of Caatinga Mammal Fauna

We obtained a list of 183 species of mammals with documented occurrences within the boundaries of the Caatinga (listed in Table 8.1). Some of these taxa (34) have only been recorded in the Caatinga in border localities, such as Jaíba and Cavernas do Peruaçu National Park (northern Minas Gerais); in areas of the Chapada Diamantina Complex or near the São Francisco River, at the Cerrado-Caatinga transition in Bahia; in the Serra das Confusões and Serra da Capivara National Parks (southern Piauí); or in wet forest enclaves in eastern Alagoas, Pernambuco, and Paraíba (indicated with an asterisk in Table 8.1). We have also included four large mammal taxa (*Hydrochoerus hydrochaeris*, *Panthera onca*, *Tapirus terrestris*, and *Tayassu pecari*) that are presently restricted to well-preserved areas located at the borders of the Caatinga (such as Serra da Capivara and Serra das Confusões National Parks) but that formerly had ranges that extended well within the Caatinga (see Feijó and Langguth 2013; Alves et al. 2016; Barboza et al. 2016).

As already shown in previous Caatinga mammal checklists (Mares et al. 1981; Oliveira et al. 2003b; Carmignotto et al. 2012; Paglia et al. 2012), the most representative orders are the Chiroptera (90 species) and Rodentia (41 species), totaling 72% of the mammals recorded for the region (see Fig. 8.1). These two orders also include ten of the 11 Caatinga endemic species. The Caatinga mammal fauna for these two groups represent half of all Brazilian bat species, based on the list of Nogueira et al. (2014), but less than 20% of rodent species, based on Paglia et al. (2012). The remaining eight orders account for around 28% of all the region's fauna, but some groups are far more representative than others. While Caatinga Didelphimorphia, Pilosa, and primates represent only 25%, 22%, and 7%, respectively, of all species occurring in Brazil, the Caatinga mammal fauna harbors 40% of all Brazilian Artiodactyla, 48% of all Brazilian Carnivora, and 64% of all Brazilian Cingulata species. For Didelphimorphia, Pilosa, and primates, the low representativeness is probably due to the higher diversity of these groups being associated with wet forests, with the majority of species being arboreal to some degree; while the more elevated representation of Artiodactyla, Carnivora, and Cingulata is more likely related to the fact that they are all wide-ranging species, with geographic distribution that spans multiple regions. The same is true for the presence of tapirs (Perissodactyla) and tapetis (Lagomorpha), both single representatives of their orders with occurrence throughout all the Brazilian territory, at least historically (but see Ruedas et al. 2017 for updates on the systematics of the South American tapeti).

The Caatinga rodents constitute a relatively poor subsample of the Brazilian rodent fauna, both as a whole and for the most speciose groups (Ca. 12% of Brazilian echimyids, 17% of Brazilian cricetids, and 9% of Brazilian sciurids, for example), even though four (45%) of the nine Brazilian caviid species occur in the Caatinga. Rodents are, however, particularly interesting for endemism, as nearly two-thirds (64%) of all endemic Caatinga mammal species are rodents. Of the seven endemic rodents, only *Kerodon rupestris* has long been considered a Caatinga endemic, and

Table 8.1 List of the 183 species of mammals with documented occurrence within the boundaries of the Caatinga (as defined in this volume)

	Adjacent biomes				Previous checklists		
Taxon	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
DIDELPHIMORPHIA							
DIDELPHIDAE							
Caluromyinae							
Caluromys philander (Linnaeus 1758)	X		X	X		X	
Didelphinae							
Cryptonanus agricolai (Moojen 1943)	X			X	X[1]	X[1]	X
Didelphis albiventris Lund, 1840[2]	X	X			X	X	X
Didelphis marsupialis Linnaeus, 1758[3]			X				
Gracilinanus agilis (Burmeister, 1854)	X	X				X	X
Gracilinanus microtarsus (Wagner, 1842)*				X			
Marmosa demerarae (Thomas, 1905)	X		X	X	X[4]	X	X
Marmosa murina (Linnaeus, 1758)	X		X	X		X	X
Marmosops incanus (Lund, 1840)*	X			X		X	
Metachirus nudicaudatus (É. Geoffroy St.-Hilaire, 1803)*			X	X			
Monodelphis americana (Müller, 1776)	X		X	X		X	X
Monodelphis domestica (Wagner, 1842)	X	X			X	X	X
Thylamys karimii (Petter, 1968)	X				X	X	X
CINGULATA							
DASYPODIDAE							
Dasypodinae							
Dasypus novemcinctus Linnaeus, 1758	X	X	X	X	X	X	X
Dasypus septemcinctus Linnaeus, 1758	X	X		X		X	X
Euphractinae							
Euphractus sexcinctus (Linnaeus, 1758)	X	X	X	X	X	X	X

(continued)

Table 8.1 (continued)

	Adjacent biomes				Previous checklists		
Taxon	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Tolypeutinae							
Cabassous tatouay (Desmarest, 1804)[5]	X			X			
Cabassous unicinctus (Linnaeus, 1758)*	X		X			X	X
Priodontes maximus (Kerr, 1792)*	X	X	X	X			
Tolypeutes tricinctus (Linnaeus, 1758)	X					X	X
PILOSA							
MYRMECOPHAGIDAE							
Myrmecophaga tridactyla Linnaeus, 1758	X	X	X	X		X	X
Tamandua tetradactyla (Linnaeus, 1758)	X	X	X	X	X	X	X
PRIMATES							
ATELIDAE							
Alouattinae							
Alouatta caraya (Humboldt, 1812)*	X	X				X	
Alouatta ululata Elliot, 1912[6]	X					X	X
CEBIDAE							
Callitrichinae							
Callithrix jacchus (Linnaeus, 1758)				X	X	X	X
Callithrix penicillata (É. Geoffroy, 1812)*	X					X	
Cebinae							
Cebus libidinosus (Spix, 1823)[7]	X				X[7]	X[7]	X
Cebus xanthosternos (Wied-Neuwied, 1826)*[7]				X			X
PITHECIIDAE							
Callicebinae							
Callicebus barbarabrownae Hershkovitz, 1990 (E)						X	X
Callicebus melanochir Wied-Neuwied, 1820*[8]				X			X
RODENTIA							
CAVIIDAE							

(continued)

Table 8.1 (continued)

Taxon	Adjacent biomes				Previous checklists		
	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Caviinae							
Cavia aperea Erxleben, 1777*	X	X					X
Galea spixii (Wagler, 1831)	X		X	X	X	X	X
Hydrochoerinae							
Hydrochoerus hydrochaeris (Linnaeus, 1766)**	X	X	X	X			X
Kerodon rupestris (Wied-Neuwied, 1820) (E)					X	X	X
CRICETIDAE							
Sigmodontinae							
Akodon cursor (Winge, 1887)				X	X[9]	X	X
Calomys expulsus (Lund, 1840)	X				X[10]	X	X
Cerradomys langguthi (Percequillo et al. 2008)[11]				X	X	X	X
Cerradomys vivoi Percequillo et al. 2008[11]	X			X	X	X	X
Euryoryzomys russatus (Wagner, 1848)	X			X		X	
Holochilus sciureus Wagner, 1842[12]	X		X	X	X	X	X
Hylaeamys megacephalus (Fischer, 1814)	X		X				
Necromys lasiurus (Lund, 1840)	X	X	X	X	X	X	X
Nectomys rattus Pelzeln, 1883	X	X	X			X	X
Oecomys catherinae Thomas, 1909*				X			
Oligoryzomys mattogrossae (Allen, 1916)[13]	X	X				X	X
Oligoryzomys nigripes (Olfers, 1818)	X	X		X	X	X	X
Oligoryzomys rupestris Weksler and Bonvicino, 2005*	X						X
Oligoryzomys stramineus Bonvicino and Weksler, 1998	X					X	X
Oxymycterus dasytrichus (Schinz 1821)[*,14]	X			X	X	X	X
Oxymycterus delator Thomas, 1903[14]	X	X			X	X	X
Pseudoryzomys simplex (Winge, 1887)*	X	X	X	X			X

(continued)

Table 8.1 (continued)

Taxon	Adjacent biomes				Previous checklists		
	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Rhipidomys cariri Tribe, 2005 (E)[15]					X	X	X
Rhipidomys cearanus Thomas, 1910 (E)[15]						X	
Rhipidomys macrurus (Gervais, 1855)*[15]	X						
Rhipidomys mastacalis (Lund 1840)*[15]	X			X		X	X
Wiedomys cerradensis Gonçalves et al. 2005	X						
Wiedomys pyrrhorhinos (Wied-Neuwied, 1821) (E)					X	X	X
CUNICULIDAE							
Cuniculus paca (Linnaeus, 1766)	X	X	X	X		X	X
DASYPROCTIDAE							
Dasyprocta azarae Lichtenstein, 1823*	X		X	X			
Dasyprocta prymnolopha Wagler, 1831			X	X	X	X	X
ECHIMYIDAE							
Echimyinae							
Makalata didelphoides (Desmarest, 1817)	X		X				
Phyllomys blainvilii (Jourdan, 1837) (E)						X[16]	X
Phyllomys lamarum (Thomas, 1916)*				X			X
Eumysopinae							
Thrichomys apereoides (Lund, 1839)*[17]	X						
Thrichomys inermis (Pictet, 1843)[17]	X				X	X	X
Thrichomys laurentius Thomas, 1904[17]					X	X	X
Trinomys albispinus albispinus (I. Geoffroy St.-Hilaire, 1838)[18]	X			X		X	X
Trinomys albispinus minor (Reis and Pessôa, 1995) (E)[18]						X	X

(continued)

Table 8.1 (continued)

	Adjacent biomes				Previous checklists		
Taxon	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Trinomys yonenagae (Rocha, 1996) (E)						X	X
ERETHIZONTIDAE							
Erethizontinae							
Coendou baturitensis Feijó and Langguth 2013 (E)[19]						X	
Coendou prehensilis (Linnaeus 1758)*	X	X	X	X		X	X
SCIURIDAE							
Sciurinae							
Guerlinguetus brasiliensis (Gmelin 1788)[20]			X	X		X	X
LAGOMORPHA							
LEPORIDAE							
Sylvilagus minensis (Thomas 1901)[21]	X	X	X	X	X	X	X
CHIROPTERA							
EMBALLONURIDAE							
Emballonurinae							
Peropteryx kappleri Peters, 1867*			X	X		X	
Peropteryx macrotis (Wagner, 1843)	X	X	X	X	X	X	X
Peropteryx trinitatis Miller, 1899			X				X
Rhynchonycteris naso (Wied-Neuwied, 1820)	X		X	X		X	X
Saccopteryx bilineata (Temminck, 1838)			X	X	X	X	X
Saccopteryx leptura (Schreber, 1774)			X	X	X	X	X
FURIPTERIDAE							
Furipterus horrens (Cuvier, 1828)	X		X	X	X	X	X
MOLOSSIDAE							
Molossinae							
Cynomops abrasus (Temminck, 1826)	X	X	X	X	X	X	X
Cynomops greenhalli Goodwin, 1958			X				X

(continued)

Table 8.1 (continued)

Taxon	Adjacent biomes				Previous checklists		
	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Cynomops planirostris (Peters, 1866)	X	X	X	X	X[22]	X	X
Eumops auripendulus (Shaw, 1800)	X	X	X	X	X	X	X
Eumops glaucinus (Wagner, 1843)	X	X	X	X			
Eumops perotis (Schinz, 1821)		X	X	X		X	X
Molossops temminckii (Burmeister, 1854)	X	X	X		X	X	X
Molossus molossus (Pallas, 1766)	X	X	X	X	X	X	X
Molossus pretiosus Miller, 1902*	X		X				
Molossus rufus É. Geoffroy St.-Hilaire, 1805[23]	X	X	X	X	X	X	X
Neoplatymops mattogrossensis (Vieira, 1942)	X		X	X	X	X	X
Nyctinomops aurispinosus (Peale, 1848)	X	X	X				X
Nyctinomops laticaudatus (É. Geoffroy St.-Hilaire, 1805)	X	X	X	X	X	X	X
Nyctinomops macrotis (Gray, 1839)	X		X	X			
Promops nasutus (Spix, 1823)	X	X	X	X	X[24]	X[24]	X
Tadarida brasiliensis (I. Geoffroy St.-Hilaire, 1824)*	X	X	X	X			X
MORMOOPIDAE							
Pteronotus gymnonotus (Wagner, 1843)	X		X		X[25]	X[25]	X
Pteronotus parnellii (Gray, 1843)	X		X		X	X	X
Pteronotus personatus (Wagner, 1843)			X		X	X	X
NATALIDAE							
Natalus macrourus Gervais, 1856[26]	X		X	X	X	X	X
NOCTILIONIDAE							
Noctilio albiventris Desmarest, 1818	X	X	X			X	X

(continued)

Table 8.1 (continued)

	Adjacent biomes				Previous checklists		
Taxon	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Noctilio leporinus (Linnaeus, 1758)	X	X	X	X	X	X	X
PHYLLOSTOMIDAE							
Carolliinae							
Carollia brevicauda (Schinz, 1821)	X		X	X	X	X	X
Carollia perspicillata (Linnaeus, 1758)	X	X	X	X	X	X	X
Desmodontinae							
Desmodus rotundus (É. Geoffroy St.-Hilaire, 1810)	X	X	X	X	X	X	X
Diaemus youngii (Jentink, 1893)	X	X	X	X	X		
Diphylla ecaudata Spix, 1823	X		X	X	X	X	X
Glossophaginae							
Anoura caudifer (É. Geoffroy St.-Hilaire, 1818)*	X	X	X	X			
Anoura geoffroyi Gray, 1838	X		X	X	X	X	X
Dryadonycteris capixaba Nogueira, Lima, Peracchi, and Simmons, 2012*				X			
Glossophaga soricina (Pallas, 1766)	X	X	X	X	X	X	X
Lionycteris spurrelli Thomas, 1913*	X	X	X	X			X
Lonchophylla dekeyseri Taddei, Vizotto, and Sazima, 1983	X						
Lonchophylla inexpectata Moratelli and Dias, 2015 (E)							
Lonchophylla mordax Thomas, 1903	X		X	X	X	X	X
Xeronycteris vieirai Gregorin and Ditchfield, 2005 (E)							X
Phyllostominae							
Chrotopterus auritus (Peters, 1856)	X	X	X	X		X	X
Lonchorhina aurita Tomes, 1863	X		X	X	X	X	X
Lophostoma brasiliense Peters, 1867	X	X	X	X	X	X	X
Lophostoma carrikeri (Allen, 1910)			X				X

(continued)

Table 8.1 (continued)

	Adjacent biomes				Previous checklists		
Taxon	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Lophostoma silvicolum d'Orbigny, 1836		X	X	X	X	X	X
Macrophyllum macrophyllum (Schinz, 1821)*	X	X	X	X			
Micronycteris megalotis (Gray, 1842)	X		X	X	X	X	X
Micronycteris minuta (Gervais, 1856)	X		X	X	X	X	X
Micronycteris sanborni Simmons, 1996	X					X	X
Micronycteris schmidtorum (Sanborn, 1935)	X		X	X		X	X
Mimon bennettii (Gray, 1838)	X		X	X		X	X
Mimon crenulatum (É. Geoffroy St.-Hilaire, 1803)	X		X	X	X	X	X
Phylloderma stenops Peters, 1865*	X		X	X			X
Phyllostomus discolor (Wagner, 1843)	X	X	X	X	X	X	X
Phyllostomus elongatus (É. Geoffroy St.-Hilaire, 1810)*			X	X		X	
Phyllostomus hastatus (Pallas, 1767)	X		X	X	X	X	X
Tonatia bidens (Spix, 1823)	X	X		X		X	X
Tonatia saurophila Koopman and Williams, 1951			X				X
Trachops cirrhosus (Spix, 1823)	X		X	X	X	X	X
Vampyrum spectrum (Linnaeus, 1758)*			X				X
Stenodermatinae							
Artibeus cinereus (Gervais, 1856)	X		X	X	X	X	X
Artibeus concolor Peters, 1865	X		X		X	X	X
Artibeus fimbriatus Gray, 1838			X	X			
Artibeus lituratus (Olfers, 1818)	X	X	X	X	X	X	X
Artibeus obscurus (Schinz, 1821)			X	X	X[27]	X	X
Artibeus planirostris (Spix, 1823)	X	X	X	X	X[28]	X	X

(continued)

Table 8.1 (continued)

	Adjacent biomes				Previous checklists		
Taxon	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
Chiroderma villosum Peters, 1860	X		X	X		X	X
Chiroderma vizottoi Taddei and Lim, 2010 (E)							
Platyrrhinus lineatus (É. Geoffroy St.-Hilaire, 1810)	X	X		X	X	X	X
Platyrrhinus recifinus (Thomas, 1901)				X			X
Pygoderma bilabiatum (Wagner, 1843)			X	X			
Sturnira lilium (É. Geoffroy St.-Hilaire, 1810)	X	X	X	X	X	X	X
Sturnira tildae de la Torre, 1959	X		X	X			
Uroderma bilobatum Peters, 1866	X		X	X	X[29]		X
Uroderma magnirostrum Davis, 1968	X		X	X	X	X	X
VESPERTILIONIDAE							
Myotinae							
Myotis albescens (É. Geoffroy St.-Hilaire, 1806)*	X	X	X	X			X
Myotis lavali Moratelli et al. 2011		X		X			
Myotis nigricans (Schinz, 1821)	X	X	X	X	X[30]	X	X
Myotis riparius Handley 1960	X	X	X	X		X	X
Myotis ruber (É. Geoffroy St.-Hilaire, 1806)				X			
Vespertilioninae							
Eptesicus brasiliensis (Desmarest, 1819)	X	X	X	X		X	X
Eptesicus furinalis (d'Orbigny and Gervais, 1847)	X	X	X	X	X	X	X
Histiotus velatus (I. Geoffroy St.-Hilaire, 1824)	X		X	X		X	X
Lasiurus blossevillii [Lesson, 1826]	X	X	X	X	X[31]	X[31]	X
Lasiurus ega (Gervais, 1856)	X	X	X	X	X	X	X
Lasiurus egregius (Peters, 1870)	X		X	X			X
Rhogeessa hussoni Genoways and Baker, 1996	X		X		X[32]	X[32]	

(continued)

Table 8.1 (continued)

Taxon	Adjacent biomes				Previous checklists		
	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
CARNIVORA							
CANIDAE							
Cerdocyon thous (Linnaeus, 1766)	X	X		X	X	X	X
Lycalopex vetulus Lund, 1842	X						X
Speothos venaticus (Lund, 1842)	X	X	X	X			
FELIDAE							
Felinae							
Leopardus braccatus (Cope, 1889)*	X	X					
Leopardus pardalis (Linnaeus, 1758)	X	X	X	X		X	X
Leopardus tigrinus (Schreber, 1775)	X	X	X	X		X	X
Leopardus wiedii (Schinz, 1821)	X	X	X	X		X	X
Puma concolor (Linnaeus, 1771)	X	X	X	X	X	X	X
Puma yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	X	X	X	X	X	X	X
Pantherinae							
Panthera onca (Linnaeus, 1758)**	X	X	X	X	X	X	X
MEPHITIDAE							
Conepatus amazonicus (Lichtenstein, 1838)[33]	X				X	X	X
MUSTELIDAE							
Lutrinae							
Lontra longicaudis (Olfers, 1818)*	X	X	X	X			
Mustelinae							
Eira barbara (Linnaeus, 1758)	X	X	X	X		X	X
Galictis cuja (Molina, 1782)[34]	X	X		X	X	X	
PROCYONIDAE							
Nasua nasua (Linnaeus 1766)	X	X	X	X		X	X
Procyon cancrivorus (G. Cuvier 1798)	X	X	X	X	X	X	X
PERISSODACTYLA							
TAPIRIDAE							
Tapirus terrestris (Linnaeus 1758)**	X	X	X	X		X	X

(continued)

Table 8.1 (continued)

	Adjacent biomes				Previous checklists		
Taxon	CE	CH	AM	AF	Mares et al. (1981), Willig and Mares (1989)	Oliveira et al. (2003b)	Carmignotto et al. (2012)
ARTIODACTYLA							
CERVIDAE							
Capreolinae							
Mazama americana (Erxleben 1777)*	X	X	X	X		X	
Mazama gouazoubira (Fischer 1814)	X	X		X	X	X	X
TAYASSUIDAE							
Pecari tajacu (Linnaeus 1758)	X	X	X	X		X	X
Tayassu pecari (Link 1795)**	X	X	X	X		X	X

For each taxon, its occurrence in adjacent biomes is also indicated. Taxa are listed in the same order as in Carmignotto et al. (2012) for comparisons. The presence of each species in any of the main three previous checklists of Caatinga mammals is also shown

AF Atlantic Forest, *AM* Amazon Forest, *CE* Cerrado, *CH* Chaco

* Indicates species is only recorded in this area

** Indicates large mammals currently limited to bordering localities, and extinct in the core of Caatinga (E) Indicates the species is endemic for the Caatinga

[1] Some specimens cited as *Marmosa karimii* by Mares et al. (1981) are, in fact, *Cryptonanus agricolai* (see Carmignotto and Monfort 2006). Cited as *Gracilinanus emiliae* in Oliveira et al. (2003b), we follow Voss et al. (Voss et al. 2005), which treated specimens from the Caatinga as *C. agricolai*

[2] Gurgel-Filho et al. (2015) proposed the use of the name *D. marsupialis* Linnaeus, 1758 for this species. Here we follow the established usage as *D. albiventris* Lund, 1840 for this taxon in order to avoid taxonomic misunderstands (see ICZN 1999 under "Conservation of prevailing usage")

[3] Gurgel-Filho et al. (2015) proposed the use of the name *D. kankrivora* Zimmermann, 1780 for this species. Here we follow the established usage as *D. marsupialis* Linnaeus, 1758 for this taxon in order to avoid taxonomic misunderstands (see ICZN 1999 under "Conservation of prevailing usage")

[4] Cited as *Marmosa cinerea* by these authors, and treated as *Micoureus demerarae* by Gardner and Creighton (2008). We follow Voss and Jansa (2009) and Voss et al. (2014), which currently treat this taxon as a subgenus of *Marmosa*

[5] Feijó and Langguth (2013) treated the taxon widely distributed in northeastern Brazil as *Cabassous tatouay*, not *C. unicinctus*. We follow these authors here. Some specimens treated as *Cabassous* sp. by Oliveira et al. (2003b) probably refer to this taxon

[6] We follow the classification of *Alouatta ululata* as a full species, and not as a subspecies of *Alouatta belzebul,* as proposed by Gregorin (2006)

[7] We treat the name *Sapajus* as a subgenus rank level for *C. libidinosus* and *C. xanthosternos* following the opinion of other authors (Feijó and Langguth 2013; Garbino 2015; Gutiérrez and Marinho-Filho 2017). Cited as *Cebus apella* by these authors and treated here as *Cebus libidinosus* based on the geographic distribution of the records; see also Rylands and Kierulff (2015)

[8] The record of *Callicebus personatus* by Pereira and Geise (2009) probably refers to *C. melanochir* based on the geographic distribution of these species; see Veiga et al. (2008a)

[9] Cited as *Akodon arviculoides* by these authors; they refer to *A. cursor*, see Oliveira et al. (2003b)

[10] Cited as *Calomys callosus* by these authors; they refer to *C. expulsus*, see Oliveira et al. (2003b)

(continued)

Table 8.1 (continued)

[11]These two species had been recognized as two new and distinct species from *Cerradomys subflavus* by Percequillo et al. (2008). Thus, records cited as *Oryzomys subflavus* by Mares et al. (1981) and as *Oryzomys* aff. *subflavus* by Oliveira et al. (2003b) refer to these species

[12]Brandão and Nascimento (2015) treated the records from Caatinga as *Holochilus sciureus*. Thus, records cited as *H. brasiliensis* by Mares et al. (1981) and Oliveira et al. (2003b) were treated as *H. sciureus*

[13]Weksler and Bonvicino (2015) restricted the occurrence of *Oligoryzomys fornesi* (Massoia, 1973) to Argentina and treated the Brazilian specimens as *Oligoryzomys mattogrossae* (Allen, 1916). Thus, records referring to *O. fornesi* were treated as *O. mattogrossae*

[14]Oliveira and Goncalves (2015) treated *Oxymycterus angularis* as a synonym of *O. dasytrichus*. The records cited by Mares et al. (1981) as *O. angularis*, however, refer to *O. dasytrichus* (specimens from Alagoas and Pernambuco) and, as well, to *O. delator* (specimens from Ceará); see Oliveira and Goncalves (2015). Specimens from Ceará were cited as *Oxymycterus* sp. n. by Oliveira et al. (2003b)

[15]Gurgel-Filho et al. (2015) treated *Rhipidomys cearanus* Thomas, 1910 as a valid species based on a molecular analysis that segregated specimens from São Benedito, Ceará from those of Crato, Ceará, known as *Rhipidomys cariri* Tribe 2005. Thus, records from São Benedito, Guaraciaba do Norte, and Ibiapaba, Ceará were treated as *R. cearanus* and those from Crato, Pacoti, and Baturité, Ceará as *R. cariri* following those authors. The specimens cited by Mares et al. (1981) were treated as *R. cariri* (see also Tribe 2015). Oliveira et al. (2003b) treated specimens from Crato as *Rhipidomys* sp. n. ssp. 1 and specimens from Pacoti as *Rhipidomys* sp. n. ssp. 2. Also, we restricted the occurrence in the Caatinga of *R. macrurus* to southern Piauí and western Bahia, following Tribe (2015), and *R. mastacalis* to Chapada Diamantina, Bahia following Tribe (2015) and Gurgel-Filho et al. (2015)

[16]Leite and Loss (2015) treated the species widely distributed in the Caatinga as *P. blainvilii*, and *P. lamarum* was restricted to its border; we follow these authors. Oliveira et al. (2003b) cited as *P. lamarum* records that we consider here as *P. blainvilii*

[17]Specimens occurring in the core area of Caatinga treated as *Thrichomys apereoides* by Mares et al. (1981) and Oliveira et al. (2003b) are currently treated as *T. inermis* and *T. laurentius*. *T. apereoides* is restricted to areas of Caatinga in the northern Minas Gerais (see Pessôa et al. 2015a)

[18]These two taxa were treated as two subspecies by Pessôa et al. (2015b). We follow these authors. Oliveira et al. (2003b) cited *Trinomys albispinus sertonius* for the Caatinga, treated as a synonym of *T. albispinus albispinus* by Pessôa et al. (2015b)

[19]Feijó and Langguth (2013) treated specimens of *Coendou* from Ceará as *C. baturitensis*. We follow these authors. Thus, records from Ceará in Oliveira et al. (2003b) were treated as *C. baturitensis*

[20]Cited as *Sciurus aestuans* and *S. alphonsei* by Oliveira et al. (2003b) and as *Guerlinguetus alphonsei* and *G. ingrami* by Carmignotto et al. (2012), and treated as synonyms of *G. brasiliensis* by de Vivo and Carmignotto (2015). We follow these latter authors

[21]Ruedas et al. (2017) restricted the name *S. brasiliensis* (formerly used to designate all tapetis occurring in Brazil) to the taxon occurring exclusively in the northeastern coastal Atlantic Forest, and suggested that the most senior name applicable to *Sylvilagus* in the Caatinga region should be *Sylvilagus minensis* Thomas 1901, with the caveat that future work in this genus may illuminate additional taxonomic variations sufficient for species–level recognition

[22]Cited as *Molossops greenhalli* by Mares et al. (1981); we follow Eger (2008) who treated those records as *Cynomops planirostris*

[23]*Molossus ater* was treated as a synonym of *M. rufus* by Eger (2008). Thus, records referred to *M. ater* for the Caatinga were treated as *M. rufus*

[24]Cited as *Promops* sp. by these authors; we follow Eger (2008) who treated those records as *Promops nasutus*

(continued)

Table 8.1 (continued)

[25] Cited as *Pteronotus davyi* by these authors, but treated as *P. gymnonotus* by Patton and Gardner (2008). We follow these latter authors

[26] *Natalus macrourus* was treated as a subspecies of *N. stramineus* by Gardner (2008a), and as a full species by Garbino and Tejedor (2012). So, records previously reported as *N. stramineus* were treated here as *N. macrourus*

[27] Cited as *A. fuliginosus* by Mares et al. (1981). These records are referred to here as *A. obscurus* following Marques-Aguiar (2008)

[28] Cited as *A. jamaicensis* by Mares et al. (1981). These records are referred to here as *A. planirostris* following Marques-Aguiar (2008)

[29] Gardner (2008b) treated the records of *Uroderma bilobatum* provided by Mares et al. (1981) as this taxon, and not as *U. magnirostrum* as suggested by Willig and Mares (1989). We follow Gardner (2008b)

[30] Wilson (2008) treated the records of *Myotis nigricans* provided by Mares et al. (1981) as this taxon, and not as *M. riparius* as suggested by Willig and Mares (1989). We follow Wilson (2008)

[31] Cited as *Lasiurus borealis* by these authors; we follow Gardner and Handley (2008) who treated those records as *Lasiurus blossevillii*

[32] Cited as *Rhogeessa tumida* by these authors. Bickham and Ruedas (2008) treated *R. tumida* as a synonym of *R. hussoni*, and considered the records of Caatinga part of this taxon. We follow these authors

[33] Feijó and Langguth (2013) treated the specimens from eastern Brazil as *Conepatus amazonicus* (Lichtenstein, 1838) and not *C. semistriatus* (Boddaert, 1785); we follow these authors

[34] Feijó and Langguth (2013) and Bornholdt et al. (2013) treated the specimens from eastern Brazil as *Galictis cuja* (Molina, 1782) and not *G. vittata* (Schreber, 1776); we follow these authors

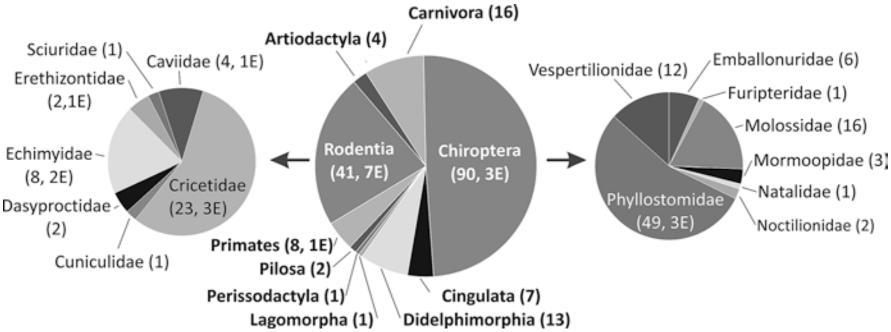

Fig. 8.1 Distribution of the 183 Caatinga mammal species, listed in Table 8.1, by order (main chart, center), and by family, within Rodentia (left chart) and Chiroptera (right chart). Numbers in parentheses indicate the overall number of species for each group (order or family), and, when appropriate, the number of Caatinga endemic species ('E')

it is the only species recognized as such in the first checklist by Willig and Mares (1989). The new endemic status of the other species currently treated as Caatinga endemic was the direct result of new field surveys, new karyological and molecular data, systematic analyses, and taxonomic reviews of taxa that were considered otherwise widespread across two or more regions, or were simply unrecognized. *Wiedomys pyrrhorhinos* is a long-known member of Caatinga small mammal communities (Willig and Mares 1989; Oliveira and Franco 2005), but its recognition as a Caatinga endemic was only possible when some errors related to the type locality and geographical distribution were solved, as Hershkovitz (1959), when describing the genus, considered specimens from Rio Grande do Sul as part of *Wiedomys* (see Bonvicino 2015), an opinion later followed by several authors, including Mares et al. (1981) and Willig and Mares 1989. It is only when the taxonomic limits of *Wiedomys pyrrhorhinos* (Wied-Neuwied, 1821), *Wilfredomys oenax* (Thomas, 1928), and *Juliomys pictipes* (Osgood, 1933), three morphologically similar species, were defined, that their geographic ranges were also delimited (see González 2000; Musser and Carleton 2005; Brandão and Nascimento 2015). Taxonomic confusion also occurred with *Phyllomys blainvilii*, which had often been treated as *P. lamarum* by several authors, based on the reverse characterization of both species by Moojen (1952) (see Leite and Loss 2015). Additionally, specimens identified as *P. blainvilii* from coastal areas in northeastern Brazil may represent an undescribed *Phyllomys* species, thus restricting *P. blainvilii* to inland wet enclaves in Caatinga (Leite and Loss 2015). These latter species are endemics widespread in the Caatinga (see also Oliveira et al. 2003b).

On the other hand, all other endemic species present restricted distributions in the region: *Trinomys yonenagae* was described in 1995 based on specimens collected in the late 1980s from sandy dunes along the shores of the São Francisco river (Rocha 1995); *Rhipidomys cariri* was only described in 2005 based on material collected by the SNP in the 1950s from wet enclaves in Ceará (Tribe 2005); and *Coendou baturitensis* was described a few years ago (Feijó and Langguth 2013) in a study of northeastern medium and large mammals based on the analyses of material housed in scientific collections, and is restricted to the Baturité slopes in Ceará state. Although Voss (2015) had considered *C. baturitensis* to be a synonym of *C. prehensilis*, we regard this later taxon as a full species until these populations are included in molecular and morphometric analyses and can be further compared with other populations treated as *C. prehensilis* from Brazil. *Rhipidomys cearanus*, although considered a synonym of *R. mastacalis* by Tribe (2015), was treated as a distinct taxon by Gurgel-Filho et al. (2015) based on the molecular distinction of specimens from southern Ceará from those currently treated as *R. cariri* and *R. mastacalis*. Therefore, it is treated as a Caatinga endemic restricted to southern Ceará. An additional taxon merits note in this report. *Trinomys minor* was treated as a full species in Carmignotto et al. (2012), following Iack-Ximenes (2005), and as such was considered an additional Caatinga endemic species. However, here it has been considered as a subspecies of *Trinomys albispinus* based on the current taxonomic status proposed by Pessôa et al. (2015b). This treatment leads to a wider geographic range for this species, with *T. a. albispinus* also occurring in Atlantic Forest and Cerrado regions (Pessôa et al. 2015b).

The Caatinga bat fauna, in turn, shows an inverse pattern: it is richer and more representative of the overall Brazilian bat fauna, yet the number of endemics (three) is proportionally low. For those families with low overall species numbers, such as Furipteridae and Noctilionidae, or few species occurring in Brazil, such as Mormoopidae and Natalidae, all species that occur in Brazil also occur in the Caatinga. For the other more diverse families, Caatinga bat species represent from

35% of all Brazilian bat species (in Emballonuridae) to approximately 50% (in Phyllostomidae and Molossidae) and up to 57% (in Vespertilionidae) of all Brazilian bat species. The three endemic species, *Lonchophylla inexpectata*, *Xeronycteris vieirai*, and *Chiroderma vizottoi*, are all phyllostomids, two nectarivorous and one fruit-/seed-eating, respectively, having in common that they were all described in the last 12 years (Gregorin and Ditchfield 2005; Taddei and Lim 2010; Moratelli and Dias 2015). While their recognition as distinct taxa is recent, all three species include in their type series specimens that had been collected in the 1970s (*X. vieirai* and *C. vizottoi*) and as far back as 1908 (*L. inexpectata*), but had gone unnoticed until new specimens were collected and all other specimens available were properly reexamined. With recent increases in field surveys in some Caatinga localities, coupled with adequate training of mammal taxonomists, it is not unlikely that the number of Caatinga endemic bats will increase in the future.

The Caatinga primate fauna is particularly poor when compared with other regions and with the overall Brazilian primates, with less than 7% of all species. However, it also includes the only endemic mammal outside of rodents and bats, the highly endangered *Callicebus barbarabrownae.* As for all other mammal orders that occur in the Caatinga, species either are wide-ranging ones or are shared with one or more regions (see below and Table 8.1).

Differences between the checklist presented here and previous ones (see Table 8.1) come from a variety of sources. Some are more obvious, such as the endemic bats *Lonchophylla inexpectata* and *Chiroderma vizottoi*, both recently described. Likewise, in the last few years a number of new Caatinga records have resulted from range expansions or first Caatinga occurrences after new field surveys, such as for *Caluromys philander* (Nascimento et al. 2013a), *Dryadonycteris capixaba* (Rocha et al. 2014a), *Sturnira tildae* (Novaes and Laurindo 2014a), *Myotis lavali* (Novaes and Laurindo 2014a; Silva et al. 2015), *Nyctinomops macrotis* (Rocha et al. 2015), *Oecomys catherinae* (Rocha et al. 2014b), *Speothos venaticus* (Fernandes-Ferreira et al. 2011), *Lontra longicaudis* (Dias and Bocchiglieri 2016a), or incidental findings, as for *Leopardus braccatus* (Nascimento et al. 2016). There have also been a number of revisionary works of specimens housed in several mammal collections (e.g., Bornholdt et al. 2013), and in particular in institutions located in northeastern Brazil, such as the works of Feijó and Langguth (2013) and Gurgel-Filho et al. (2015), which better delimited some species, resulting in the validation of taxa such as *Rhipidomys cearanus*, in the description of new species, such as *Coendou baturitensis*, and in changes on nomenclature for some taxa previously known for the Caatinga, such as *Conepatus amazonicus*, *Galictis cuja*, and *Cabassous tatouay*, for example (see taxonomic comments in Table 8.1). Additionally, the majority of species considered here as restricted to Caatinga limits were not considered by Carmignotto et al. (2012), such as *Marmosops incanus*, *Alouatta caraya*, and *Peropteryx kappleri*, due to methodological distinctiveness.

Species that were formerly considered as present in the Caatinga and were not considered as part of this fauna in this study also deserve attention. Most of these species were found only in areas that are part of other regions, such as Atlantic Forest areas near Caatinga limits for *Cyclopes didactylus*, *Bradypus variegatus*, *Coendou insidiosus*, and *Diclidurus albus*, for example (see Feijó and Langguth 2013; Ferreira et al. 2013; Voss 2015), and also related to taxonomic revisionary work that has better delimited the species present in the Caatinga, resulting exclusion of some taxa from the region, such as *Calomys tener*, *Holochilus brasiliensis*, *Rhogeessa hussoni*, and *Lonchophylla bokermanni* (Nogueira et al. 2014; Brandão and Nascimento 2015; Salazar-Bravo 2015). Ferreira et al. (2009) published a record of *Cebus flavius* for the Caatinga of Rio Grande do Norte. However, as this record may represent a non-native population due to its location, which is well within the Caatinga, and all other populations of *C. flavius* are restricted to Atlantic Forest (Oliveira and Langguth 2006; Oliveira et al. 2015), we do not consider this record here.

The checklists also differ for the endemic species, mainly due to the limits used for the region and to new taxonomic and geographic limits considered for those taxa. For example, *Kerodon rupestris* and *Wiedomys pyrrhorhinos* were treated as occurring in the Cerrado by Carmignotto et al. (2012) due to records in transitional areas in the Caatinga-Cerrado limits (northern Minas Gerais, western Bahia and southern Piauí—material housed in the MZUSP). These same areas were treated as part of the Caatinga limits here and by other authors (e.g., Bonvicino 2015; Dunnum 2015). As for *Cryptonanus agricolai* and *Thrichomys laurentius*, treated as Caatinga endemics by Carmignotto et al. (2012), they were found to also occur in areas well within adjacent regions, such as Atlantic Forest regions in northeastern Brazil for *T. laurentius* (Pessôa et al. 2015a), and Cerrado in eastern Tocantins and western Piauí for *C. agricolai* (material housed in the MZUSP) (Carmignotto and Aires 2011).

8.4 Distribution Patterns

8.4.1 Non-volant Small Mammals

In this section we consider mammal species from the orders Didelphimorphia and Rodentia, excluding the larger rodents such as the capybaras, agoutis, paca, and porcupines, a total of 48 mammal species in this group (see Table 8.1).

For the 13 marsupial species registered in the region, three species, *Gracilinanus microtarsus*, *Marmosops incanus*, and *Metachirus nudicaudatus*, presented records restricted to areas near the region’s limits or in transitional areas. *G. microtarsus* is known from only one locality, Chapada Diamantina Complex, Bahia (Oliveira and Pessôa 2005; Pereira and Geise 2009), and although *M. incanus* shows a greater number of records, i.e., in northern Minas Gerais, Chapada Diamantina region, and western Sergipe (Mustrangi 1994; Oliveira and Pessôa 2005; Pereira and Geise 2009; Rocha et al. 2012; Nogueira et al. 2015), we consider its presence in the Caatinga to be restricted to the southern and eastern limits of the region, on the right bank of the São Francisco River (see Fig. 8.1 in Rocha et al. 2012). Both species are associated with transitional areas with the Atlantic Forest, the region of typical occurrence of these taxa. *Metachirus nudicaudatus* was recorded in a region of '*babaçual*' near the limits with the Cerrado in western Piauí (Miranda et al. 2009). As this species is typically found in Amazon and Atlantic forest regions (see Gardner and Dagosto 2008), this record consists of a great range extension, which may be related to humid forest enclaves present in the Caatinga. For *Caluromys philander*, we found records for the Caatinga in the '*brejos de altitude*' of Serra de Ibiapaba and Ipu, northwestern Ceará (Oliveira et al. 2003b; Gurgel-Filho et al. 2015), in the Parque Nacional Serra das Confusões, southern Piauí (material housed in MZUSP), and in eastern Pernambuco (Nascimento et al. 2013a); and for *Didelphis marsupialis*, records were found only in the '*brejos de altitude*' in northeastern Ceará (Fernandes-Ferreira et al. 2015; Gurgel-Filho et al. 2015). Thus, these two species also present a restricted distribution in Caatinga, being associated with forest enclaves and transitional areas in this latter region, while they are widely distributed in Atlantic and/or Amazonian forests (see Paglia et al. 2012). The eight remaining species are widely distributed in Caatinga, with *Didelphis albiventris*, *Gracilinanus agilis*, and *Monodelphis domestica* representing the most common marsupial species found in previous and recent surveys throughout the region (Streilein 1982b; Freitas et al. 2005; Bezerra et al. 2014; Rocha et al. 2014b; Delciellos 2016).

Among the 35 Caatinga rodents, eight are species with restricted distributions in the Caatinga, and which are confined to its limits, represented by one member of the family Caviidae (*Cavia aperea*), five Cricetidae (*Oecomys catherinae*, *Oligoryzomys rupestris*, *Pseudoryzomys simplex*, *Rhipidomys macrurus*, and *R. mastacalis*), and two Echimyidae (*Phyllomys lamarum* and *Thrichomys apereoides*) (see Table 8.1). As mentioned for marsupials, some of these species (*C. aperea*, *O. catherinae*, *R. mastacalis*, and *P. lamarum*) are associated with forested habitats, and are widely distributed in neighboring forested regions (Atlantic and/or Amazonian forests). *Oligoryzomys rupestris*, *P. simplex*, *R. macrurus*, and *T. apereoides*, however, are associated with open habitats, and are widely found in the Cerrado (see Carmignotto et al. 2012). Other species also present a restricted distribution in the Caatinga, mainly associated with humid forest enclaves, such as the Cricetidae *Euryoryzomys russatus* and *Hylaeamys megacephalus*, the Echimyidae *Makalata didelphoides*, and the Sciuridae *Guerlinguetus brasiliensis*, recorded only in the '*brejos de altitude*' in Ceará (Oliveira et al. 2003b; Emmons and Patton 2015; Fernandes-Ferreira et al. 2015; Percequillo 2015a, b; Vivo and Carmignotto 2015), and also in eastern Paraíba for *E. russatus* (Oliveira and Langguth 2004). Two rodents typical of the Cerrado mammal fauna, *Oxymycterus delator* and *Wiedomys cerradensis*, were also recorded in enclaves of this vegetation within the Caatinga as well as in western Ceará (Bonvicino 2015; Oliveira and Goncalves 2015).

The remaining 21 species include typical Caatinga species, with six endemic rodents. One member of the family Caviidae, *Kerodon rupestris*, two from the family Cricetidae, *Rhipidomys cariri* and *Wiedomys pyrrhorhinus*, and one from the family Echimyidae, *Phyllomys blainvilii*, present wide geographic ranges in the Caatinga (Bonvicino 2015; Dunnum 2015; Leite and Loss 2015; Tribe 2015). In contrast, one Cricetidae and one Echimyidae present restricted distributions in the region, namely *Rhipidomys cearanus*—restricted to Serra de Ibiapada in northwestern Ceará—and *Trinomys yonenagae*—restricted to sandy dunes on the left margin of São Francisco River, in northwestern Bahia (Gurgel-Filho et al. 2015; Pessôa et al. 2015b). Although Pessôa et al. (2015b) considered *Trinomys minor* to be a subspecies of *T. albispinus* (see taxonomic comments in Table 8.1), and it is thus not counted here as an endemic species, this taxon (*Trinomys albispinus minor*) presents a restricted distribution in the Caatinga, being endemic to inland Bahia. The remaining 15 species present a wide distribution in the Caatinga, occurring also in neighboring regions (see Table 8.1).

Of the 48 small non-volant mammal species, six are Caatinga endemics (12.5%), eight are shared exclusively with the Cerrado (17%), seven are exclusively shared with the Cerrado and Chaco, characterizing species common to the Dry Arid Diagonal (15%), six are exclusively shared with the Atlantic Forest (12.5%), and just one, *Didelphis marsupialis*, is shared exclusively with the Amazon (2%); only two, *Metachirus nudicaudatus* and *Guerlinguetus brasiliensis*, are shared with both forested regions, the Atlantic and Amazon forests (4%) (see Table 8.1). The remaining 18 species are widely distributed, occurring on both forested and open regions (37%) (see Table 8.1). These data show the greater importance of the open area inhabitants in the Caatinga fauna, representing 44.5% of its species, while 18.5% are forest dwellers. They also indicate the stronger influence of Atlantic Forest, when compared with the Amazon Forest, for these forest mammals.

8.4.2 Bats

We treated 11 of the 90 bat species recorded for the Caatinga as restricted to its borders (see Table 8.1). *Tadarida brasiliensis* was recorded only in the locality of Barra, western Bahia (Eger 2008) and *Myotis albescens* was recorded in the region of the middle São Francisco River plain as well as in western Bahia (Sá-Neto and Marinho-Filho 2013); *Vampyrum spectrum* is only known to occur in the Serra das Confusões National Park, southern Piauí (Gregorin et al. 2008); *Peropteryx kappleri* and *Molossus pretiosus* were recorded only in northern Minas Gerais (Nogueira et al. 2008; Tavares et al. 2010; Nogueira et al. 2015); *Macrophyllum macrophyllum* is restricted to the Chapada Diamantina region, Bahia (Oliveira and Pessôa 2005; Sbragia and Cardoso 2008); *Dryadonycteris capixaba* and *Phyllostomus elongatus* were recorded only in eastern Alagoas and Pernambuco (Oliveira et al. 2003b; Sousa et al. 2004; Rocha et al. 2014a); *Anoura caudifer* is restricted to northern Minas Gerais (Pinto et al. 2010) and the region of Chapada Diamantina (Oliveira and Pessôa 2005); *Lionycteris spurrelli* was also found in those two latter regions and in the mid São Francisco River, western Bahia (Gregorin and Mendes 1999; Oliveira and Pessôa 2005; Pinto et al. 2010; Tavares et al. 2010; Sá-Neto and Marinho-Filho 2013); and *Phylloderma stenops*, is known to occur in eastern Pernambuco (Sousa et al. 2004) and western Bahia (Sá-Neto and Marinho-Filho

2013). As only four species are exclusively shared with forested regions (*Dryadonycteris capixaba*—Atlantic Forest; *Vampyrum spectrum*—Amazon Forest; *Peropteryx kappleri* and *Phyllostomus elongatus*—Atlantic Forest and Amazon Forest; see Table 8.1), it is expected that the remaining seven species present new records of occurrence within the core areas of Caatinga, at least in mesic or Cerrado enclaves within this region.

Five other species also present a restricted distribution in the region, but occur in regions well within the Caatinga limits. *Peropteryx trinitatis* is known to occur in Queimadas, northeastern Bahia (Hood and Gardner 2008); *Cynomops greenhalli* is restricted to the region of Exu, Pernambuco (Eger 2008); *Nyctinomops aurispinosus* is only known to occur in Paulistana, eastern Piauí (Eger 2008); *Nyctinomops macrotis* was recorded only in one locality in northern Bahia (Rocha et al. 2015); and *Sturnira tildae* is restricted to the Chapada do Araripe region, Ceará (Novaes and Laurindo 2014b). Since these species occur in other adjacent regions as well, we also expect to obtain more records within the Caatinga, especially for *N. aurispinosus* and *S. tildae* which are widely distributed in Brazil.

Additionally, three species are endemic to the Caatinga: *Lonchophylla inexpectata* was recently described, and is known to occur in three localities—two in the interior of Pernambuco and one in western Bahia (Moratelli and Dias 2015); *Xeronycteris vieirai* was recorded in four localities—two in the interior of Pernambuco, one in northern Bahia, and one in northern Minas Gerais, presenting a wide distribution in the region (Gregorin and Ditchfield 2005; Nogueira et al. 2015); and *Chiroderma vizottoi* is the most restricted endemic, occurring only in Piauí and western Ceará (Gregorin et al. 2008; Taddei and Lim 2010; Silva et al. 2015).

The Caatinga bat fauna is composed of three endemic species (3%); two species—*Lonchophylla dekeyseri* and *Micronycteris sanborni*—exclusively shared with the Cerrado (2%); no species restricted to the Arid Diagonal, i.e., the Caatinga, Cerrado, and Chaco; three species—*Dryadonycteris capixaba*, *Platyrrhinus recifinus*, and *Myotis ruber*—exclusively shared with the Atlantic Forest (3%); six species exclusively shared with the Amazon (7%); seven species shared with the two forested regions, the Atlantic and Amazon forests (8%); and the remaining 69 species (77%) shared with both forested and open area regions (see Table 8.1). This pattern contrasts with that found for the small non-volant mammals, where most species present more restricted distributions (63%) associated with the type of habitat physiognomy: forest and open. Most bats present wider distributions, encompassing a variety of habitat physiognomies (77%). However, for species with more restricted distributions, there is a greater influence of species limited to the forest regions (18%) versus the open habitat dwellers (5%) in the Caatinga, with the Amazonian species being more representative than the Atlantic Forest ones (see Table 8.1). This is also the opposite pattern to the one found for the non-volant small mammals.

8.4.3 Medium and Large Mammals

Of the 45 species of medium and large terrestrial mammals, 11 were restricted to the Caatinga limits: *Callithrix penicillata*, a species typical of the Cerrado (see Gutiérrez and Marinho-Filho 2017), is also present within Caatinga limits in the northern Minas Gerais (Oliveira et al. 2003b) and at the Chapada Diamantina Complex, Bahia (Pereira and Geise 2009); *Leopardus braccatus*, a species occurring in Chaco, Pantanal, and Cerrado, was recently found in areas of Caatinga in northern Minas Gerais and southern Piauí (Nascimento et al. 2016); *Alouatta caraya*, another species typical of the Cerrado, Chaco and Pantanal, was recorded in areas of Caatinga in northern Minas Gerais, southern Piauí, western Bahia (Oliveira et al. 2003b), and in Chapada Diamantina, Bahia (Pereira and Geise 2009); and *Cebus xanthosternos* and *Callicebus melanochir*, two species typical of the Atlantic Forest, were recorded in areas of southern Bahia (Kierulff et al. 2015) and the Chapada Diamantina (Pereira and Geise 2009; see taxonomic comments in Table 8.1). The remaining six species present wider distributions in adjacent regions, and occur in restricted Caatinga regions: *Cabassous unicinctus* in northern Minas Gerais (Oliveira et al. 2003b; see taxonomic comments in Table 8.1); *Priodontes maximus* in southern Piauí (material housed at MZUSP); *Mazama americana* in northern Minas Gerais and southern Piauí (Oliveira et al. 2003b); *Lontra longicaudis* in eastern Sergipe (Dias and Bocchiglieri 2016a); *Dasyprocta azarae* in northern Minas Gerais and Chapada Diamantina, Bahia (Pereira and Geise 2009; Nogueira et al. 2015); and *Coendou prehensilis* in western Bahia (see taxonomic comments in Table 8.1).

Four species of large mammals deserve attention, since they historically had a wider range in the Caatinga, but recently are restricted to marginal areas of the region and are practically extinct in the Caatinga (see further comments in Feijó and Langguth 2013). These are the pecari *Tayassu pecari*, currently recorded only in Serra da Capivara National Park, southern Piauí (Oliveira et al. 2003b); the tapir *Tapirus terrestris*, with records restricted to northern Minas Gerais (Oliveira et al. 2003b); the jaguar *Panthera onca*, recorded in Serra da Capivara National Park, southern Piauí (Brandão et al. 2009; Silveira et al. 2010) and Chapada Diamantina, Bahia (Pereira and Geise 2009); and the capybara *Hydrochoerus hydrochaeris*, with a record for Aquiraz, northeastern Ceará (Feijó and Langguth 2013) and Chapada Diamantina, Bahia (Pereira and Geise 2009).

Other species, on the other hand, had never been recorded before for the Caatinga. Examples are the bush dog *Speothos venaticus*, recently recorded in a humid forest enclave in northeastern Ceará (Fernandes-Ferreira et al. 2011), and the hoary fox *Lycalopex vetulus*, once considered a species endemic to the Cerrado (Marinho-Filho et al. 2002), yet records of this species were found in areas of the Caatinga in northern and southern Piauí (material housed at MZUSP; Costa and Courtenay 2003), Ceará (Olifiers and Delciellos 2014), and Chapada Diamantina, Bahia (Pereira and Geise 2009). Other species, such as the red-handed howler monkey *Alouatta ululata*, have a restricted distribution in the Caatinga, limited to areas in the northern Piauí and Ceará states (Oliveira and Kierulff 2008). Additionally, there are two endemic medium terrestrial mammals that also present a limited distributional range in the Caatinga: the blond titi monkey, *Callicebus barbarabrownae*, restricted to central Bahia and Sergipe states (Veiga et al. 2008b); and the porcupine *Coendou baturitensis*, recently described and known only from the region of the Baturité Ridge in northeastern Ceará (Feijó and Langguth 2013). The remaining 25 species present wide distributions in the Caatinga.

The medium and large terrestrial Caatinga mammal fauna presents two endemic species (4.5%) and share six species exclusively with the Cerrado (13%)—two carnivores, one armadillo, and three primates—and two species with the Cerrado and Chaco as well (4.5%)—*Leopardus braccatus* and *Alouatta caraya.* Three primates are exclusively shared with the Atlantic Forest (7%); no species are exclusively shared with the Amazon; and only *Dasyprocta prymnolopha* is exclusively shared with both forested regions (2%). The remaining 31 species (69%) are widespread in both open and forested adjacent regions (see Table 8.1). Although the general pattern appears to be more similar to the one found for Caatinga bat species, with most species widely distributed in the Caatinga and shared with adjacent regions, the pattern that emerges for species with more restricted distributions is more similar to the one observed for the non-volant small mammals, with greater numbers of open area inhabitants (22%) versus forest dwellers (9%), and species of the Atlantic Forest, in the case of the forest inhabitants, being more representative (7%).

As a whole, the Caatinga mammal fauna is constituted by species with distinct distributional patterns throughout the region, and although there is yet much to survey, these distributional patterns lead to dissimilar richness and mammal composition along the Caatinga, as has already been pointed out by other authors for mammals (e.g., Oliveira et al. 2003b) and other vertebrate groups (e.g., Guedes et al. 2014), and that have recently been uncovered through phylogenetic and phylogeographic molecular studies (see Sect. 8.7 for further discussion).

8.5 Areas of Interest for Surveys and Conservation Based on Richness and/or Endemism

As shown earlier, there are some areas near the limits of the Caatinga, such as areas in southern Piauí and northern Minas Gerais, transitional regions with adjacent biomes or vegetal formations, such as the Chapada Diamantina Complex in central Bahia, and humid forest enclaves, such as areas in northern Ceará and eastern Pernambuco and Paraíba, that harbor a high number of mammal species. It is important to highlight that these areas also present large remnants of Caatinga vegetation preserved as protected areas, such as the Serra da Capivara and Serra das Confusões National Parks in southern Piauí, the Cavernas do Peruaçu National Park in northern Minas Gerais, and the Chapada Diamantina National Park in central Bahia, that most certainly have contributed to the elevated richness found in these regions. These areas are also the only ones to harbor populations of the four largest mammal species (*T. pecari*, *P. onca*, *T. terrestris*, and *H. hydrochaeris*) in the Caatinga nowadays. For the humid enclaves, however, there are few protected areas, such as the Ubajara National Park and the Serra de Ibiapaba Environmental Protection Area in the extreme west of Ceará and northern Piauí. For example, the areas around Baturité Ridge, which harbors a high richness and also endemic mammal species, are not preserved as a protected area, and neither are the enclaves in eastern Pernambuco and Paraíba (ICMBio 2016). These areas are a high priority for Caatinga mammal conservation, as shown by Oliveira et al. (2003a) who have elected 18 priority areas for mammal conservation based on species richness, endemism, and also on the vulnerability of these areas due to anthropogenic pressures, such as habitat fragmentation and alteration. Among these 18 areas, the humid enclaves in northern Ceará and eastern Pernambuco, and areas in southern Piauí, northern Minas Gerais, and the base of Chapada Diamantina Complex were considered to be of extreme priority for conservation based on their biological importance (see Fig. 1, page 285 in Oliveira et al. 2003a).

The priority areas for surveys are concentrated in the core areas of the Caatinga, representing drier vegetation formations, and are thus widespread along the whole region, such as regions in the interior of Rio Grande do Norte and Alagoas, in central Ceará, northern Paraíba, central and southwestern Pernambuco, and central-eastern Bahia. Additionally, some areas at the limits of the region are still poorly known, such as regions in northern Maranhão and western Piauí represented by a unique type of vegetation formation, '*babaçual*', and transitional areas in northeastern Minas Gerais and western Bahia (Oliveira et al. 2003a; Oliveira and Langguth 2004; Astúa and Guerra 2008; Feijó and Langguth 2013; Gurgel-Filho et al. 2015; Carvalho-Neto et al. 2016). Unfortunately, several of these regions had only been poorly surveyed until recently (Cruz et al. 2005; Miranda et al. 2005, 2009; Ferreira et al. 2009; Geise et al. 2010; Sá-Neto and Marinho-Filho 2013) and none of the areas are preserved as protected areas. Thus, if these regions still maintain preserved Caatinga vegetation, they are in a high priority for mammal surveys, such as the Catimbau National Park in the inland Pernambuco (see Geise et al. 2010), and especially the Raso da Catarina Ecological Station in northern Bahia.

As already pointed out by Oliveira et al. (2003b), most of the Caatinga mammal inventories done so far did not properly cover the heterogeneity of habitat types present in the surveyed areas, they were held for short periods of time, usually focused in one of the groups of mammals—small non-volants, bats, or large mammals—and did not involve complementary field survey techniques. Thus, although some protected areas present in the Caatinga have already been studied, due to their extreme importance in conservation, they must be continually surveyed for the whole group of mammals, and long-term studies must be established in order to increase our knowledge in relation not only to species richness, distribution, and composition, but also in relation to ecological data such as home range areas, population densities, diets, reproductive cycles, and physiological and behavioral adaptations, among many other factors that are still lacking for the majority of mammal species (see Sect. 8.6). One recent and promising improvement in this direction is the recent establishment of an LTER (Long Term Ecological Research) site in the Catimbau National Park in Pernambuco (https://www.peldcatimbau.org/).

8.6 Ecology and Behavior of Caatinga Mammals: What Do We Know?

Current knowledge on the ecology and behavior of Caatinga mammals is still in its infancy, especially when compared to other much better studied regions such as the Atlantic Forest or the Amazon. For decades, all that was known (or even inferred) for the ecology of Caatinga mammals relied on the results from now classical works from a few Caatinga localities studied in depth in the 1980s and early 1990s (Lacher 1981; Mares et al. 1981; Streilein 1982b, c, d, e, f; Willig 1983, 1985; Willig and Mares 1989; Olmos 1993b; Rocha 1995), and from analyses of material collected by the SNP in the 1960s (Cerqueira et al. 1989; Cerqueira and Lara 1991; Oliveira et al. 2003b; Cerqueira 2005; Oliveira and Franco 2005; Sobral and Oliveira 2014). It is only recently that new data is being collected and analyzed for Caatinga mammals (Pereira and Geise 2009; Silva and Marinho-Filho 2010; Silva et al. 2011; Leal et al. 2013; Nascimento et al. 2013a; Sá-Neto and Marinho-Filho 2013; Bezerra et al. 2014; Novaes and Laurindo 2014a; Fernandes-Ferreira et al. 2015; Lapenta and Bueno 2015; Nogueira et al. 2015; Novaes et al. 2015; Silva et al. 2015; Abreu et al. 2016; Alves et al. 2016; Delciellos 2016; Dias and Bocchiglieri 2016a). Basic parameters of species ecology such as diet, use of space, and bionomic and foraging strategies, to name a few, are virtually non-existent for almost all species, or at least for the populations living in the Caatinga. While these and other additional aspects of species ecology are always needed in order to understand how each one interacts with and evolves in its habitat(s), a few are particularly interesting given the unique precipitation pattern of the Caatinga, such as population dynamics (and breeding strategies), ecological physiology (as related to adaptations to resource scarcity and hydric stress), as well as behavioral adaptations to cope with high heat and low water availability throughout several months per year.

8.6.1 Population Ecology

Given the unpredictable and unique precipitation regime of the Caatinga, which in turn has direct influence on plant phenology and thus resource availability, it could be expected that reproductive biology and population cycles would follow precipitation patterns closely, but it seems that some mammal groups respond differently to precipitation variation or seasonal cues. Early studies on the reproductive biology of marsupials have shown that their breeding season in a specific year is not directly related to the amount of precipitation of that year, but rather to the mean rainfall variation, and is actually triggered by the photoperiod (Cerqueira 2005). Studies on the reproductive biology of *Didelphis albiventris* have found that the breeding season is strictly related to rainfall: pregnant females were only found during the wet season. Even though some of the localities studied by Cerqueira (1984) are located along the border of the Caatinga, most of his results are based on localities inland

and well within the Caatinga domain. Later, Bergallo and Cerqueira (1994) and Cerqueira and Bergallo (1993) found different patterns for the smaller gray short-tailed opossum (*Monodelphis domestica*): there was no correlation between the presence of pregnant females and the actual precipitation at the time of capture, but a significant correlation was found with the normal mean rainfall, which was interpreted as this species having a breeding season triggered by changes in the photoperiod. For this species, most pregnancies were recorded during the rainy season, and the breeding season was estimated to run from December to July (Bergallo and Cerqueira 1994). Streilein (1982d), however, recorded breeding in *M. domestica* almost all year long in a population ecology study in Exu, Pernambuco.

Analyses of the data from rodents collected by the SNP also highlighted rainfall as the proximal factor triggering the breeding season in sigmodontine rodents in the Caatinga: the presence of pregnant females was highly correlated with precipitation, but within a 1-month lag (females start breeding 1 month after the onset of rainfall [Cerqueira et al. 1989; Cerqueira 2005]). Only a few rodent species have had their reproductive patterns studied closely. For the Caatinga endemic sigmodontine rodent *Rhipidomys cearanus*, the onset of the breeding season seems to be directly related to the onset of the rains, usually within a 1-month lag (Sobral and Oliveira 2014). In another endemic sigmodontine rodent, *Wiedomys pyrrhorhinos*, not only was the breeding season found to coincide with the wet season (within a similar 1- to 2-month lag between the rainfall peak and the highest occurrence of pregnant females), but in specific cases females born early in a breeding season were able to breed in the same season (Sobral and Oliveira 2014). This increases the ability of a population to respond quickly to favorable conditions, such as longer or occasional wet seasons, when unexpected rains occur, thus leading to population outbreaks or '*ratadas*', which were defined by Jaksic and Lima (2003) as "explosive increases in population abundance or density of rodents during a relatively short period". Such outbreaks have been documented in over 50 cases, being common in several localities throughout South America and affecting several rodent species (Jaksic and Lima 2003). Increases in rainfall usually lead to increased primary production, and such augmented food availability allows for more fat accumulation, which ultimately not only triggers reproduction but also allows larger litters, thus acting synergistically and resulting in the outbreaks. Such rodent population outbreaks also generally occur in years with unexpectedly high precipitation levels and/or increased primary production in other localities (Jaksic and Lima 2003). Although no similar population increases have been reported in other groups, it is noteworthy that females of the white-eared opossum, *Didelphis albiventris*, which occur in the Caatinga as well as other areas, also have the potential to breed in the same breeding season in which they were born (Astúa and Geise 2006).

The information in this section represents the most up-to-date information available on the population ecology of Caatinga small mammals. While the work of Streilein in Exu (1982b, c, d, e, f) provides some information and there are some other more recent data (Freitas et al. 2005), knowledge is still incipient for most of the small mammal species that are part of communities in the Caatinga. In addition, unpublished data on population fluctuations of different species from a single community have shown very different responses to precipitation (Nascimento 2010), thus indicating that much effort is needed in order to properly grasp the dynamics of small mammal populations in the Caatinga. Nonetheless, while scarce, data for small mammals is still better than for bats or medium and large mammals, for which basic ecological information is even scarcer. While some work has been carried out for a few carnivore species (Olmos 1993b; Silveira et al. 2010; Dias and Bocchiglieri 2016a, b; Penido et al. 2016) as well as for peccaries (Olmos 1993a), this is limited to one or a few aspects of their ecology.

8.6.2 Ecophysiology

The individual needs of Caatinga mammals are also likely linked to the unpredictable availability of water. Streilein (1982c) suggested that, unlike species from other semiarid South American formations, Caatinga mammals lacked physiological adaptations directly related to water economy. This hypothesis seems to be supported partially by subsequent more detailed and laboratory-based studies. While physiological adaptations do exist, they are not nearly as extreme as those found in desert rodents. Preliminary data on *Wiedomys pyrrhorhinos* suggest it has some minor ability for urine concentration (Ribeiro et al. 2004). Physiological parameters for *Thrichomys inermis* vary geographically, with smaller specimens from a more arid locality showing less water intake and better tolerance for short-term water restriction than those from a more mesic locality (Mendes et al. 2004). Other species of *Thrichomys*, from the Caatinga (*T. laurentius*), Cerrado (*T.* sp.), and Pantanal (*T. pachyurus*), showed lower urine concentration values (Carvalhaes et al. 2015), suggesting that the water balance abilities of these species are still only beginning to be understood. This indicates that local populations may vary in their abilities to cope with hydric stress, and that a proper appraisal of physiologic adaptations in Caatinga mammals should be addressed by assessing these parameters throughout the species range and relating these data to local water regimes. As such, Streilein's (1982c) initial hypothesis that behavioral strategies are key for these species to survive seem to be valid, with individuals shifting microhabitat preferences due to water stress. However, subsequent results dealing with a wider variety of Caatinga habitats than those originally sampled by Streilein (1982c) have shown that habitat use by small mammals is more complex, with the relative importance of shelters, substratum, and local Caatinga physiognomies varying from species to species (Freitas et al. 2005).

8.6.3 Behavior

While the exact extent to which Caatinga mammals are physiologically adapted or not to the unpredictable precipitation regime and consequent water scarcity is not known, it is clear that many have behavioral adaptations to cope with the excessive heat and water loss in summer, as well as the resource shortage that ensue. For example, white-eared opossums (*Didelphis albiventris*) shift their habitat preference to more mesic ones when resources are scarcer in the Caatinga (Streilein 1982a), while marmosets (*Callithrix jacchus*) adjust their behavior and diet according to season (decreasing play time and increasing rest time in the hot and dry season) (Abreu et al. 2016) and also consume alternative resources in the Caatinga (Amora et al. 2013). It has also been suggested that the particular environmental features of the Caatinga might have driven populations of capuchins monkeys (*Cebus libidinosus*) to use tools to obtain and process food items such as cacti, which are not used elsewhere in their range (Moraes et al. 2014).

8.7 Evolution and Biogeography of Caatinga Mammals

The age of the Caatinga has long been debated. Most authors consider its origins in the Quaternary (e.g., Queiroz 2006; Prado 2008) while others suggest an ancient beginning for this region (e.g., Pennington et al. 2000, 2004, 2006; Collevatti et al. 2013). Regardless of its age, this seasonally dry tropical forest (SDTF) formation has also changed its limits over time, as the Caatinga has been invaded recurrently by wet forest formations (de Oliveira et al. 1999; Auler et al. 2004). These events (origin and diversification through space and time) are responsible for the current diversification patterns found in Caatinga mammals that are now beginning to be unveiled.

Carmignotto et al. (2012) pointed out two main evolutionary patterns for the mammals from tropical open formations of South America: one represented by taxa descended from well-diversified forest lineages that have colonized the open formations; and the other by lineages endemic to the open formations. Based on available phylogenetic data at the time (Lara and Patton 2000; Costa 2003; Leite 2003), these authors have suggested a Late Tertiary origin for these diversification events. However, new data provide evidence for recent events of differentiation as well, such as in the marsupial genus *Monodelphis*, for which the open-formation vicariant lineages represented by the species *M. domestica* have diversified from its Amazonian forest ancestor during Early Pleistocene (around 2.0 million years ago [mya]), thus suggesting that Caatinga mammals are composed of temporally heterogeneous lineages (Pavan et al. 2016). Indeed, there is new evidence that corroborate this hypothesis, as for both evolutionary patterns—that is, the ones descended from forest ancestors and the open area endemics—divergence estimation dates vary from Late Miocene to Early Pleistocene: for the marsupial *Thylamys karimii* and the sigmodontine rodent *Calomys expulsus*, both open area endemics, a diversification date is estimated at around 2.0 mya (Nascimento et al. 2011; Giarla and Jansa 2014); for the marsupials *Gracilinanus agilis* and *Monodelphis kunsi*, open formation vicars from forest sister taxa, the date of divergence is supposed to be during Late Pliocene, around 3.5–3.0 mya (Faria et al. 2013; Pavan et al. 2016); for the open area endemic echimyid rodent genus *Thrichomys*, the speciation occurred in Late

Miocene, around 8.5 mya (Nascimento et al. 2013b). Patterns of differentiation within the open formations probably had been continuous through Late Tertiary and Early Quaternary, triggered by climate changes and shifts in habitat type, such as dry vegetation and moist forests, as well as physical barriers such as rivers and mountains (e.g., Webb 1978; Pennington et al. 2006; Werneck et al. 2012).

For instance, events of speciation date well into the Pleistocene within lineages already diversified and currently occurring in the Caatinga, such as within the species *C. expulsus*, *G. agilis*, and *M. domestica* (Caramaschi et al. 2011; Nascimento et al. 2011; Faria et al. 2013). Whether these lineages represent morphologically cryptic valid species or just populations that are under differentiation processes, these data show diversification events along the open formations of South America and increase the current biodiversity known for regions such as the Caatinga. For terrestrial small mammals, the Rio São Francisco and the frequent changes along its course and water flow during the Tertiary and Quaternary have been identified as an important barrier to gene flow leading to allopatric divergence among populations (Faria et al. 2013; Nascimento et al. 2013b); vegetation formation may also have played a leading role in lineage diversification (Almeida et al. 2007; Caramaschi et al. 2011). In general, these biogeographic patterns resulted in distinct populations along an east–west transect, represented by the Caatinga in the eastern and Cerrado in the western range of taxa distribution, as well as a north–south distribution pattern along the Caatinga, with populations from northern Caatinga on the left margin of Rio São Francisco being divergent from those from southern Caatinga on the right bank of the Rio São Francisco (Caramaschi et al. 2011; Faria et al. 2013).

8.8 Conclusions

The list of Caatinga mammals has increased steadily from the 81 taxa listed by Willig and Mares (1989) to the 143 and 153 species listed by Oliveira et al. (2003b) and Carmignotto et al. (2012), respectively, to the current list of 183 species. Known Caatinga endemics have also increased from the original *Kerodon rupestris* to the 11 species listed here. This growing knowledge is directly related to the increase in fieldwork and revisionary and systematic studies, highlighting the importance of properly surveying a region in an homogeneous way, and the importance of adequately assessing the taxonomy and phylogenetic relationships of the taxa present in the Caatinga in order to gain proper understanding of its fauna, with all evolutionary, ecological, and conservation implications raised.

These data show that the Caatinga mammal fauna can be considered a heterogeneous fauna, both in terms of composition and evolutionary history. Its components include (1) taxa with broad distributions within the Caatinga and other regions, which can be shared with one or more adjacent biomes, whether forested or within open vegetation formations; (2) taxa with very restricted distributions at the Caatinga borders, or associated with enclaves of other vegetation types or transitional areas; and (3) endemics that can either present a wide range or occur in a limited area in the Caatinga. The number of taxa in each category varies among taxonomic groups, and is a consequence of the evolutionary history, vagility, and ecology of each group.

Our understanding of the reproductive ecology of Caatinga mammals has increased, yet it is mostly still derived from series collected in the 1950s, with some based on recent fieldwork, and is essentially restricted to small mammals. While there is scattered information on selected ecological parameters for medium and large mammals, this is still highly preliminary, and the scenario is even worse for bats. Gaining an adequate understanding of the ecology of species living in a highly unpredictable region is key to adequately assessing its evolutionary history and projecting adequate conservation policies for this unique yet highly affected Brazilian region. The same rationale goes to understanding how these species answer to climatic fluctuations in terms of physiology and behavior: while there is interesting and promising results, they are all too preliminary now.

The systematics and biogeography of Caatinga mammals are also in their infancy, but the data at hand already show the complex evolutionary history of this fauna, which have descended from both forest as well as open area endemic lineages and have diversified since Late Miocene, with populations currently inhabiting the Caatinga departing from their sister lineages as recently as Late Pleistocene. Climatic and vegetation changes may have played a major role in the diversification of this fauna, but changes in water flow and in the course of one of the most representative rivers in the Caatinga, the São Francisco, may explain the north–south biogeographical pattern found for some small mammals.

As future directions, we recommend the pursuit of additional revisionary work, field surveys in areas still poorly known, and long-term studies in preserved areas to continue this trend in increasing the knowledge on Caatinga mammals.

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Chapter 9
Plant–Animal Interactions in the Caatinga: Overview and Perspectives

Inara R. Leal, Ariadna V. Lopes, Isabel C. Machado, and Marcelo Tabarelli

Abstract Interactions between plants and animals are extremely diverse and operate as both evolutionary and ecological forces for angiosperms, insects, and many groups of vertebrates. In this chapter we present a brief overview of plant–animal interactions in the Caatinga, describe some interaction responses to human disturbances, and address future scientific agenda. Despite climatic restrictions, plant pollination in Caatinga is very specialized, involving 13 different systems and a high percentage of pollination by vertebrates. Abiotic seed dispersal prevails, but the Caatinga is a global hotspot for myrmecochory, with more than 100 woody species depending on ants for seed dispersal; saurochory is also a distinctive dispersal mode in the Caatinga. Extrafloral nectary-bearing plants also represent a conspicuous feature of the Caatinga flora (15% of woody species and 40% of individuals at the local scale), with protection against herbivores provided by a diverse ant community. Finally, leaf-cutting ants (LCAs) and exotic goats represent the most voracious herbivores (the LCA herbivory rate is 20% of leaves in their foraging areas). It has already been demonstrated that human disturbances can reduce the diversity of pollination systems and high-quality ant dispersal services in the Caatinga. On the other hand, LCA colony density usually increases along roads and other human-disturbed habitats, with increments in the herbivory rate due to the proliferation of palatable plants (e.g., native Euphorbiaceae and weeds). As climate and land use changes proceed, a substantial proportion of the Caatinga plant–animal interactions are likely to be disrupted or even become extinct, with unanticipated impacts on biodiversity persistence and sustainability in this biologically unique region.

Keywords Chronic anthropogenic disturbance • Ecosystem services • Mutualistic and antagonistic interactions • Winner–loser replacement

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9.1 Introduction

Interactions between plants and animals are extremely diverse and complex. These interactions play important roles in pollination, seed dispersal, and plant consumption as well as in animal feeding, growth, and nesting places. From the plant side, animals act as the main dispersive agents in two phases of the plant life cycle: pollination and propagule dispersal (Jordano 1987; Ollerton et al. 2011). On the other hand, plants are vital for animals in the various aspects listed. The benefits of these interactions have been essential in the evolution of angiosperms (Tiffney 1984), insects (Strong et al. 1984), and many groups of vertebrates (Pellmyr 1992), and they act as driving forces in terms of biodiversity organization from an individual to an ecosystem level (Bascompte et al. 2006; Bascompte and Jordano 2007).

Tropical rain forests have been considered a hotspot in terms of plant–animal interactions because of high levels of plant dependence from animals on mutualistic interaction for successful reproduction (e.g., pollination and seed dispersal) (e.g., Bronstein 2015). However, studies have also demonstrated that seasonally dry tropical forests (SDTFs) exhibit (1) high levels of animal dependence; (2) the full spectrum of strategies or life-history plant traits observed in humid forests; (3) the occurrence of species-specific and highly complex/specialized interactions; and (4) food production mediated by pollination services (e.g., Machado and Lopes 2004; Quesada et al. 2011; Sobrinho et al. 2016 and other references cited in this chapter).

Both the evolutionary and ecological relevance of plant–animal interactions is far more evident when considering the catastrophic consequences of anthropogenic disturbances, including species extinction (Thompson 2002; Koh et al. 2004; Tabarelli et al. 2010) or the proliferation of disturbance-adapted species such as some herbivores (Wirth et al. 2008; Leal et al. 2014a). However, many other consequences occur from human disturbances, such as the loss, depletion, or alteration of sensitive interactions (e.g., Sechrest et al. 2002; Girão et al. 2007; Silva et al. 2007; Lopes et al. 2009; Tabarelli et al. 2010; Leal et al. 2014b, 2015a, b, 2017; Sobrinho et al. 2016), with cascading effects on the functional and taxonomic diversity of plant and animal communities and ecosystem functioning (Lopes et al. 2009; Tabarelli et al. 2010; Leal et al. 2014b, 2015b, 2017; Sobrinho et al. 2016). It has been proposed and already documented, for example, that local extinctions of some animals may cause the disappearance of plants that rely on them as pollinators or seed dispersers, and vice versa (e.g., Dirzo and Miranda 1990; Silva and Tabarelli 2000; Girão et al. 2007; Lopes et al. 2009; Tabarelli et al. 2010; Leal et al. 2014b, 2015b, 2017; Sobrinho et al. 2016), while the proliferation of leaf-cutting ants (LCAs) following the abandonment of former agricultural patches or across forest edges can interfere with forest regeneration (Corrêa et al. 2010; Meyer et al. 2011, 2013; Leal et al. 2014a). Because of marked seasonality, plant–animal interactions in SDTFs are probably much more sensitive to phenological patterns and their variations, such as those resulting from climate change, such as, trait/behavior mismatch causing the collapse of interactions (Forrest 2015). Finally, we consider the spatial coexistence of livestock animals (e.g., goats and cattle), invasive plant/animal species (e.g., honey bees), and native assemblages as key features of several driving forces in SDTFs regarding plant–animal interactions and their cascade effects (Ribeiro et al. 2015).

Despite the interaction diversity and its importance for biodiversity persistence, provision of multiple ecological services, and sustainability, basic syntheses on plant–animal interactions in the Caatinga are scarce compared with other ecosystems (but see Machado and Lopes 2004; Quirino and Machado 2014; Sobrinho et al. 2016 for pollination; Griz and Machado 2001; Leal et al. 2007, 2014b, c, 2015a for seed dispersal; Leal et al. 2015b for plant protection against herbivores; and Leal et al. 2003, 2017; Siqueira et al. 2017; Tabarelli et al. 2017 for herbivory) and many potential novelties are still to be documented, such as the regional-level and seasonal migration/outbreak of Pieridae butterflies, which as yet lacks investigation. As the Caatinga's natural landscapes continue to be drastically altered, via a combination of habitat loss and chronic disturbances (e.g., firewood collection and livestock production based on native vegetation), and as it is now expected to experience high levels of aridity due to climate change (Magrin et al. 2014), much more research is required.

In this chapter, we present a brief overview of plant–animal interactions in the Caatinga dry forest, based on published reviews and case studies and unpublished data, including (1) mutualistic interactions, such as pollination, seed dispersal, and ant–plant protective mutualism; (2) antagonistic interactions, such as herbivory; and (3) the effects of human disturbance on these interactions, as well as future research directions. In addition to presenting major patterns, we highlight what Caatinga vegetation shares with other neotropical SDTFs and what so far appears to represent Caatinga singularities.

9.2 Mutualistic Interactions

9.2.1 Pollination

The available information on plant–pollinator interactions in the Caatinga already permits a general overview of the pollination process in the Caatinga biota. Diverse pollination vectors, assembled in approximately 13 pollination systems have been already documented in the Caatinga (pollination by ants, bats, bees, beetles, butterflies, 'diverse small insects', hummingbirds, lizards, moths, non-flying mammals, sphingids, wasps, and wind) (cf. Machado and Lopes 2004 for a review, but see also Gomes et al. 2014a, b; Queiroz et al. 2016; Domingos-Melo et al. 2017 for new additions) (see Fig. 9.1 for some examples).

Pollination by animals is estimated to occur in about 98% of the flowering plant species in the Caatinga (Machado and Lopes 2004). This prevalence of biotic pollination in the Caatinga is similar to other SDTFs globally. Pollination by insects (ca. 62%), mainly bees (43%; Fig. 9.1a), is the most frequent system (see Machado

Fig. 9.1 Plant–pollinator interactions in the Caatinga. (**a**) *Xylocopa grisesc*ens visiting a flower of *Cenostigma pyramidale* (Fabaceae); (**b**) a Sphingidae visiting a flower of *Pilosocereus catingicola* (Cactaceae); (**c**–**d**) hummingbirds visiting flowers of Cactaceae species—(**c**) *Anoupetia gounellei* visiting *Tacinga inamoena* and (**d**) a female of *Chlorostilbon aureoventris* visiting

and Lopes 2004; Quirino and Machado 2014; Table 9.1). Nectar and pollen represent the most common floral resources, but other resources such as oil and resin are also observed (Machado and Lopes 2004). Since both the quantity and quality of available resources for pollinators are crucial to understand the temporal dynamics of plant–pollinator communities, Quirino and Machado (2014) analyzed the pollination syndromes of 46 species over 2 years in a Caatinga area in one of its driest portions, the 'Cariris Paraibanos'. The focal community exhibited a temporal distribution of distinct pollination syndromes and floral resources among the diverse growth habits (trees, shrubs, herbs, and vines).

Although Caatinga refers to a seasonally dry forest, wind pollination, as far as we know, seems not to be frequent in this biota (2%; Machado and Lopes 2004), and this strategy appears to be restricted to few taxa within the Euphorbiaceae and Cyperaceae (Machado and Lopes 2004). While this figure may represent an underestimation due to few studies, it is similar to some SDTFs in which wind pollination is infrequent, but contrasts with some other SDTFs where wind pollination can reach 13% of the species, as documented in shrublands of Venezuela (Ramirez 1989, 2004).

Pollination by vertebrates is very frequent in the Caatinga (ca. 28%; Fig. 9.1c–h). The frequency of pollination by hummingbirds documented in the Caatinga (ca. 15%) is similar to that observed in tropical rain forests (Machado and Lopes 2004; Table 9.1). In fact, hummingbirds play an important role in the pollination of around 15% of the Angiosperms in general (Feinsinger 1983) and approximately 7000 flowering plant species that are adapted for pollination by hummingbirds depend on them for their pollination (Abrahamczyk and Kessler 2014). One of the potential singularities of the Caatinga vegetation in the context of SDTFs refers to the presence of hummingbird-pollinated plants flowering on every month of the year, which probably represents the occurrence of diverse and complex plant–hummingbird interactions on multiple spatial scales (Leal et al. 2006). Pollination by bats is impressively numerous in this vegetation domain (ca. 13%; Machado and Lopes 2004), even in the driest patches of the Caatinga such as the 'Cariris Paraibanos' (Quirino and Machado 2014). Surprisingly, nectar-feeding bats are not as diverse in the Caatinga biota (ca. eight to ten species; Machado and Lopes, unpublished data). Bat pollination is particularly frequent in the Cactaceae, especially across *Pilosocereus* species (e.g., Locatelli et al. 1997; Rocha et al. 2007; Fig. 9.1e). Hummingbird-pollinated

FIg. 9.1 (continued) *Melocactus zehntneri*; (**e**–**f**) the bat *Lonchophylla mordax* visiting flowers of (**e**) *Pilosocereus tuberculatus* (Cactaceae) and (**f**) *Mimosa lewisii* (Fabaceae); (**g**-**h**) the opossum *Didelphis albiventris* visiting inflorescences of *Encholirium spectabile* (Bromeliaceae) for drinking nectar; (**i**) the ant *Cephalothes inaequalis* visiting a flower of *Ditassa capillaris* (Apocynaceae-Asclepiadoideae) (Credits for images: (**a**) published in Leite and Machado (2009) Braz J Bot. 32:79–88, and reproduced from Scientific Electronic Library Online [SciELO] based on the Creative Commons Attribution License; (**b**) published in Locatelli et al. (1997) Bradleya 15:28–34, and reproduced with kind permission from BioOne; (**c**–**d**) I.C. Machado; (**e**) published in Rocha et al. (2007) Bradleya 25:125–128, and reproduced with kind permission from BioOne; (**f**) published in Vogel et al. (2005) Taxon 54:693–700, and reproduced with kind permission from the International Association for Plant Taxonomy [IAPT]; (**g**–**h**) kindly provided by Joel Queiroz; and (**i**) kindly provided by Arthur Domingos de Melo)

Table 9.1 Percentage of pollination systems in the Caatinga and compared with some other tropical dry or rain forest communities

Pollination systems	Dry forest 'Caatinga' (Machado and Lopes 2004)	Dry forest 'Cerrado' (Silberbauer-Gottsberger and Gottsberger 1988)	Dry forest 'Cerrado' (Oliveira and Gibbs 2000)	Coastal vegetation 'Restinga' (Ormond et al. 1993)[a]	'Shrubland' (Ramirez 1989)	Savanna (Ramirez 2004)	Rain forest (Bawa et al. 1985)	Rain forest (Kress and Beach 1994)	Dipterocarp forest (Kato 1996)
Wind	2.0	13.6	0.0	–	8.2	10.4	2.5	2.5	0.0
Beetles	0.7	2.8	2.0	–	2.7	2.3	7.3	12.7	2.4
Wasps	1.3	–	–	–	–	10.8	4.3	2.5	2.4
Moths	1.3	2.2	12.0	29.8	10.9	6.2	7.9	8.0	2.4
Butterflies	3.9		0.0			13.9	4.9	4.3	2.4
Sphingids	7.2	2.2	–	4.5	–	–	8.0	–	–
Hummingbirds	15.0	1.8	2.0	5.4	12.3	3.1	4.3	14.9	–
Sunbird	0.0	–	–	–	–	–	–	–	9.8
Diverse small insects	12.4	–	49.0	–	–	–	15.8	11.2	2.4
Bats	13.1	1.8	3.0	2.1	–	1.9	3.0	3.6	0.0
Medium–large bees	30.5	65.2	32.0	40.8	56.2	38.6	27.5	24.3	26.7
Small bees	12.6		–				14.0	14.1	44.0
Flies	0.0	10.4	–	17.8	9.6	12.7	–	1.8	7.3
Thrips	0.0	–	–	–	–	–	0.6	–	–

Modified from Machado and Lopes (2004)

[a] Data for nectariferous species only

species are also frequent in this family (e.g., Locatelli and Machado 1999; Leal et al. 2006; Gomes et al. 2014a, b; Fig. 9.1c–d). It is worth mentioning that the Cactaceae are one the most diverse families in the Caatinga biota with several endemic and threatened species (IUCN 2016; Brazilian Flora 2020 in construction).

Some case studies have revealed novelties in terms of the occurrence of bat pollination among Angiosperms as documented for *Harpochilus neesianus*, an Acanthaceae, (Vogel et al. 2004) and for *Mimosa lewisii* (Fig. 9.1f), a Leguminosae-Mimosoideae (Vogel et al. 2005). Novelties were also registered in terms of pollination by non-flying mammals (Queiroz et al. 2016), with the documentation, for the first time, of pollination by opossum in a bromeliad (Fig. 9.1g–h), which was also the first record of opossums visiting a flower in the Caatinga. Another interesting case was observed in two co-flowering *Ipomoea* taxa (*I. marcellia* and *I.* aff. *marcellia*) pollinated by bats and hummingbirds (in the 'Cariris Paraibanos'), in which some factors favoring reproductive isolation and pollinator sharing by these plants reveals a possible example of sympatric speciation (Queiroz et al. 2015). This vertebrate mixed pollination system seems to be advantageous in the Caatinga, where the availability of pollinators and floral resources changes considerably throughout the year, mainly as a result of rainfall seasonality (Queiroz et al. 2016).

In fact, specialized pollination mechanisms, usually sensitive to human disturbances, are not rare in the Caatinga as one could empirically expect for open, dry vegetation exposed to a semiarid climate with low and irregularly distributed rainfall (Machado and Lopes 2004). We should highlight a relative high percentage of (1) flowers offering oil as resource (ca. 10%); (2) pollination by vertebrates (ca. 28%; birds = 15% and bats = 13%); and (3) plant species with floral morphology that keep their resources relatively hidden, i.e., not easily accessed by floral visitors (43%). This trait is a good proxy to evaluate how restricted the pollinator guild of a flower is.

The Caatinga also supports a rare case of double mutualism involving two endemic species: the cactus *Melocactus ernestii* is both pollinated and dispersed by the lizard *Tropidurius semitaeniatus* (Gomes et al. 2014a, b). It has been proposed that seasonality, low water availability, and continuous nectar production by the flowers may attract lizards to visit (and pollinate) flowers in addition to eating fruits (see details of seed dispersal in Sect. 9.2.2) of this cactus (Gomes et al. 2014a, b). Another rare pollination system is pollination by ants (Fig. 9.1i), such as two co-occurring species of *Ditassa* (Asclepiadoideae) (Domingos-Melo et al. 2017). This pollination system was also the focus of a study evaluating how strong seasonality in resource availability in a semiarid tropical environment (the Caatinga) affects the structure of ant–flower networks apparently consisting of two main guilds: generalist ants sharing several floral resources during the dry season and another consisting of highly generalized ants visiting during both seasons (Santos et al. 2014).

Studies on pollination networks in the Caatinga vegetation also included an investigation involving oil flowers and oil-collecting bees. This small network has been revealed to be more nested than all other pollination networks examined in the world, and it has also been proved to be modular (Bezerra et al. 2009) and with taxonomic variation associated with vegetation types (Mello et al. 2012). The oil flowers of the genera *Byrsonima* and *Banisteriopsis* and the oil bees of the genera *Centris* and *Epicharis* are the most important species attending these plant-pollination networks, the latter attending as both hubs but also as connectors (Mello et al. 2012).

Local networks including bees and flowers in general can involve a large number of species, for example, 80 species of bees visiting the flowers of 83 plant species, with an average of 16 plant species visited each month (Santos et al. 2012). It has been proposed that (1) flower-visiting bees more strongly separate their trophic niches than their temporal niches, with most bee species focusing their activities at specific hours of the day; (2) in extreme environments, such as the Caatinga, abiotic conditions seem to play an important role in structuring the community of flower-visiting bees (Santos et al. 2012); and (3) the prevalence of generalist interactions, resulting in a nested functional network, which provide resources for the persistence of rare species contribute to system stability (Pigozzo and Viana 2010). Cross-network analyses also revealed that (1) social bee–plant and social wasp–plant interaction networks are nested with similar topologies, such as asymmetrical and modular structures; and (2) the exotic social bee *Apis mellifera* is important in both interaction networks, suggesting the importance of more detailed studies to measure the invasiveness level *of A. mellifera* in bee communities of Brazilian vegetation domains (Santos et al. 2010).

Moving to pollination across secondary forest regeneration, preliminary but interesting patterns have been proposed: (1) both mature and regenerating forest stands support a higher proportion of species and individuals with inconspicuous or small flowers, which are white or green (Sobrinho et al. 2016); (2) species with more specialized strategies (e.g., offering oil and brood or mating places/floral tissues) are not present in agriculture-related regenerating stands); and (3) pollination by diverse small insects and bees dominate all plant assemblages across all habitat types, but regenerating stands following agriculture diverged more clearly from mature forest stands, that is, they supported a higher frequency of species pollinated by bees and a complete absence of species pollinated by beetles, birds, and vertebrates (chiropterophily + ornithophily) (Sobrinho et al. 2016). Finally, functional diversity of reproductive traits and pollination systems are higher in old-growth forest areas than in regenerating forest stands (Sobrinho et al. 2016). Such impoverishment has already been observed in rain forests (e.g., for the Brazilian Atlantic Forest; Girão et al. 2007; Lopes et al. 2009; Tabarelli et al. 2010). Independent of the underlying mechanism, this may promote the collapse of plant and pollinator populations and modify the natural regeneration course or the dynamic of vegetation remnants, allowing the establishment of poor assemblages in terms of species richness, ecological interactions, and trophic structure.

9.2.2 Seed Dispersal

Most information about seed dispersal in the Caatinga vegetation refers to seed dispersal syndromes, considering both local and regional floras, instead of information from classical seed dispersal investigations on focal plant species. However, combining syndrome-based analyses with information on life-history traits (from species to family level) available in the literature allows a basic description of the main vectors involved in both primary and secondary seed dispersal in this SDTF biota. Although the Caatinga woody flora supports a reasonable number of endemic and narrow-distributed species, woody floras are usually dominated by species and individuals from only a few families of any spatial scale, particularly the Fabaceae, Euphorbiaceae, Bignoniaceae, Apocynaceae, and Cactaceae. Accordingly, abiotic primary seed dispersal, including gravity, wind, and ballistic seed dispersal, is the predominant mechanism, usually accounting for over 70% of the species and plant individuals recorded in local plant assemblages, with dry legumes as the predominant fruit type (Griz and Machado 2001; Barbosa et al. 2003). Vertebrate gut-dispersed seeds are most related to small- and medium-sized berry- or drupe-bearing species (seeds <1 cm in length), which can be considered as primarily bird-dispersed species (Griz and Machado 2001). We refer to species within the Myrtaceae, Malphigiaceae, Rubiaceae, Sapindaceae, and Erythroxylaceae. Such wet season-dispersed species (Griz and Machado 2001) tend to become increasingly more frequent as the average annual rainfall increases (Tabarelli et al. 2003).

Only a few species can be considered as being primarily dispersed by mammals, that is, those with large seeds protected by hard coats and associated with fleshy fruits, such as those from *Spondias*, *Zyziphus*, and *Syagrus* species. There are some records of common marmosets and howler monkeys (Moura and McConkey 2007; Amora et al. 2013) operating as fruit consumers and anecdotal observations reporting fruit consumption by other generalist mammals such as felids, foxes, armadillos (Moura and McConkey 2007; Vaz et al. 2012), and eventually by domestic cows and goats (Leal et al. 2003). The Cactaceae represents a particular and important feature of the Caatinga seed-dispersal profile as this family is highly diverse (ca. 80 species and subspecies; Zappi et al. 2012), with species covering a wide range of fleshy-fruit size. Fruits of Cactaceae are generally fleshy with a great number of seeds embedded in a structure that is denominated funicular pulp (Taylor and Zappi 2004).

Globular species bearing small fleshy fruits (i.e., *Melocactus* species) have been reported to support saurochory (Gomes et al. 2014b; Fig. 9.2a), while large fruits such as those from the columnar *Cereus and Pilosocereus* are consumed by a wide range of animals, from reptiles, birds (Fig. 9.2b), and primates (primary dispersal) to carnivorous opportunistic mammals (Gomes et al. 2014a, b, 2016) and ants (Leal et al. 2007) as secondary seed dispersers. Saurochory provides short-distance seed dispersal, that is, 6.5 ± 3.0 m distant from parents as in the case of *Pilosocereus gounellei* seeds dispersed by the striped lava lizard (*Tropidurus semitaeniatus*; Gomes et al. 2016). Seeds ingested and defecated also experience increased germination rates as compared with undispersed seeds (Gomes et al. 2016). As the Caatinga biota supports over 30 species of frugivorous bats (E. Bernard, personal communication), this group is a potential key seed-dispersal group, but information on seed dispersal is still missing.

A very frequent dispersal mode in the Caatinga is myrmecochory, or seed dispersal by ants (Leal et al. 2015a, 2017), which is especially prevalent in the Euphorbiaceae (Fig. 9.2c–d), the second largest plant family in the Caatinga flora (Moro et al. 2014). More than 100 woody species from the genera *Cnidoscolus*, *Croton*, *Jatropha*, and *Manihot* (about 70% of the Euphorbiaceae species) have their

Fig. 9.2 Seed dispersal, ant–plant protective mutualism, and herbivory in the Caatinga. (**a**) *Tropidurus semitaeniatus* eating a fruit of *Melocactus ernestii* (Cactaceae)*;* (**b**) *Paroaria dominicana* eating fruits of *Cereus jamacaru* (Cactaceae); (**c**) *Dinoponera quadriceps* carrying a *Jatropha mutabilis* (Euphorbiaceae) seed; (**d**) *Pheidole fallax* removing elaiosomes of a *Jatropha mollissima* (Euphorbiaceae) seed in situ; (**e**) *Camponotus* sp. visiting the extrafloral nectary of *Chlroleucon foliolosum* (Fabaceae); (**f**) *Dorymyrmex thoracicus* visiting extrafloral nectary of *Pityrocarpa moniliformis* (Fabaceae); (**g**) *Pseudomyrmex gracilis* visiting extrafloral nectary of *Tacinga inamoena* (Cactaceae); (**h**) *Camponotus* sp. chasing a ladybug in an open flower of *Tacinga inamoena* (Cactaceae); (**i**) a giant grasshopper in *Senegalia bahiensis* (Fabaceae); (**j**) a Pieridae larvae eating leaves of *Senna occidentalis* (Fabaceae); (**k**) a Noctuidae larvae eating leaves of *Senna occidentalis* (Fabaceae); (**l**) *Atta opaciceps* cutting pieces of *Tacinga inamoena* (Cactaceae) cladodes (Credits for images: (**a**) kindly provided by Zelma G.M. Quirino; (**b**) kindly provided by Vanessa G.N. Gomes; (**c**, **j**, and **k**) kindly provided by Carlos Henrique F. Silva; (**d**) kindly provided by Inara R. Leal; (**e**, **f**, **g**, and **h**) kindly provided by Fernanda M.P. Oliveira; (**i**) kindly provided by Pedro E. Santos Neto; (**l**) kindly provided by Felipe F.S. Siqueira)

caruncle-bearing seeds dispersed exclusively by ants (Leal et al. 2015a, 2017). Although many ant species are attracted to diaspores, the dispersal service provided by them is highly variable and related to behavioral and morphological differences between the ant species (Ness et al. 2009; Leal et al. 2014b). In particular, large-bodied solitary foraging ants typically offer superior dispersal services because individual workers can quickly collect seeds, transport them over relatively long distances, and deposit them isolated or in small groups in external nest refuse piles (Ness et al. 2004; Leal et al. 2014b). Conversely, small-bodied, recruit-foraging ants are typically low-quality dispersers because they often feed on the elaiosome in situ without transporting the diaspore, or use a mass-recruiting system to remove diaspores, usually only over very short distances, and deposit them in large groups into nest refuse (Andersen and Morrison 1998; Lôbo et al. 2011; Leal et al. 2014b). The most important high-quality disperser ant species in the Caatinga are those of *Dinoponera* (which are able to remove diaspores >20 m; Fig. 9.2c), *Ectatomma*, and *Camponotus*, whereas species of *Solenopsis* and *Pheidole* (Fig. 9.2d) are the most common low-quality dispersers (Leal et al. 2014b). LCAs (species of *Atta* and *Acromyrmex*) are also classified as low-quality dispersers despite their relatively large body size and ability to transport seeds long distances because they usually cut or bury all seedlings growing on or near their nests (Silva et al. 2007).

The interactions of ants with euphorb seeds have been described in detail, including the removal rate and distance, seed fate, seed germination, and seedling growth rate (Leal et al. 2007, 2014b). The rate of seed removal varies among sites, but was frequently very high (e.g., >70% after 12 hours) for all seven species studied by Leal et al. (2007). Approximately 80% of removed seeds are transported to ant nests. Dispersal distances can exceed 25 m, but mean distance is much shorter, varying from 1.2 m (Leal et al. 2014b) to 5.3 m (Leal et al. 2007). Even with this short distance, ant dispersal substantially exceeds that of ballistic dispersal (Leal et al. 2007). Within the nest, ants remove the elaiosome and retain the cleaned seeds inside the nest or, more frequently, deposit them in the vicinity of the nest entrance, including refuse piles and nest mounds (Leal et al. 2007). Although seeds become clustered close to nest entrances, they experience a higher chance of escaping from predation than seeds deposited in areas away from nests (Lôbo et al. 2011; Arcoverde 2012).

The deposition of transported seeds on ant nest improves seed germination for most species evaluated in Leal et al. (2007). This may be a peculiarity of Euphorbiaceae and other caruncle-bearing seed species, as their elaiosome (also referred to as micropylar aril) covers the micropyle, the structure responsible for seed imbibition (Gorb and Gorb 2003). Caruncle removal by ants may facilitate seed imbibition, and consequently enhance seed germination (Leal et al. 2007). In the case of *Cnidoscolus quercifolius*, a higher germination rate in nest soil is followed by an increased seedling growth rate, due to the higher nutrient content and cation exchange capacity of nest soil (Leal et al. 2007). Additionally, soil penetrability is three times higher in ant nests than in random sites (Leal et al. 2007). Thus, ant nests may provide a deep, soft, nutrient-enriched, and moist substratum that promotes seed germination and enhances seedling performance, particularly at sites covered by shallow and rocky soils, which are very common in the Caatinga.

Myrmecochory is strongly affected by human disturbance. Leal et al. (2014c) investigated the effects of chronic anthropogenic disturbance on myrmecochory in Caatinga vegetation. Using five surrogates of chronic disturbances (density of people and livestock, and proximity to urban centers, houses, and roads) combined in an index they demonstrated that overall ant disperser composition varied markedly with disturbance. The abundance of the two key high-quality disperser ants (*Dinoponera quadriceps* and *Ectatomma muticum*) decreased with disturbance, whereas a range of low-quality dispersers (species of *Pheidole*, *Solenopsis*, *Camponotus*, and *Crematogaster*) increased (Leal et al. 2014c). These disturbance-mediated changes in seed disperser composition reduced ant dispersal services in terms of number of ant–seed interactions, number of removals, and removal distances. The influence of chronic anthropogenic disturbance on two post-dispersal services provided by *Dinoponera quadriceps*—protecting seeds from predators and promoting seedling establishment—was also observed (Arcoverde 2012). Although ant nests presented lower seed predation and higher seedling richness and densities than control areas, no relationship with anthropogenic disturbance was detected. This result indicates that although disturbance markedly reduces rates of seed removal by *D. quadriceps* and the distances seeds are removed, post-dispersal services are maintained even in areas under a higher level of chronic disturbance pressure.

9.2.3 Ant–Plant Protective Mutualism

Protection mutualisms occur when a mutualist defends its partner against natural enemies (Bronstein 2015). In terrestrial ecosystems ant–plant symbioses are ubiquitous examples of protection mutualisms, in which plants provide nesting space and food for symbiotic ants in exchange for ant defense against herbivores (see reviews in Rico-Gray and Oliveira 2007 and references therein). Ant–plant protective mutualisms range from symbiotic obligate systems in which the plants house and feed the ants (e.g., *Acacia cornigera*; Janzen 1967) or only house ants without food provided (e.g., *Mayeta guianensis*; Vasconcelos 1991), known as myrmecophytism, to those loser relationships in which ants live away from plants but visit them for food, in most cases extrafloral nectar (Boucher et al. 1982; Bronstein 1998). While there are no myrmecophytic plants in the Caatinga, extrafloral nectary (EFN)-bearing plants are very diversified and abundant in this ecosystem (Leal et al. 2015b) and their interaction with ants seems to be a key component of Caatinga biodiversity.

Plants bearing EFNs in the Caatinga include mostly species from Fabaceae and Euphorbiaceae, the two richest and most abundant families of this domain, but species from Anacardiaceae, Capparaceae, Passifloraceae, and Turneraceae are also documented (Melo et al. 2010; Leal et al. 2015b; Reis 2016). A recent study recorded 15% of woody species (21 of 141) and 39% of individuals (2.243 of 5.678) as bearing EFNs in the Catimbau National Park (Reis 2016). Most of the EFN-bearing species (15; 71%) and individuals (73%) in this study belonged to Fabaceae (Reis 2016; Fig. 9.2e–f). In some cases, just one species can represent more than 50% of the local flora, such as *Croton sonderianus* (Euphorbiaceae) in Parnamirim region (Pernambuco state) with 3267 individuals (61% of total individuals surveyed by Leal et al. 2015b). The origin of EFNs in the Caatinga can be substitutive, where the secretory structure presents other functions (e.g., trichomes, stipules, hydathodes), or non-substitutive, for those glands with typical EFN function (Melo et al. 2010). In terms of structure, EFNs are extremely variable, from simple glandular trichomes (*Cenostigma* spp.) and cryptic non-structural (or amorphous nectaries, as in *Libidibia ferrea*) or structural secretory tissue embedded within EFN-bearing plant parts (*Hymenaea courbaril*) to highly individualized EFNs in the form of conspicuous, complex vascularized or non-vascularized glands on the surface of the bearing organ (Melo et al. 2010; Reis 2016). These conspicuous individualized EFNs include various forms—such as plane (*Anadenanthera colubrina*), elevated (*Senna* spp.), embedded (*Pityrocarpa moniliformis*; Fig. 9.2f), stalked (*Chamaecrista pilosa*) or not stalked (*Piptadenia stipulacea*)—and positions on the plants (leaf blade, petiole, rachis, sepals, and bracts) (Melo et al. 2010; Reis 2016).

A large number of ant species visit EFNs in the Caatinga, from typical arboreal genera such as *Azteca*, *Brachymyrmex*, *Camponotus* (Fig. 9.2e, h), *Cephalotes*, *Crematogaster*, *Linepithema*, and *Pseudomyrmex* (Fig. 9.2g) to soil nesting ants that frequently visit plants such as *Dorymyrmex* (Fig. 9.2f), *Ectatomma*, *Gnamptogenys*, *Pheidole*, and *Solenopsis* (Leal et al. 2015b; Silva et al. unpublished data). *Camponotus crassus* is one of the most common ant species attending EFNs, in some cases accounting for more than 80% of all ant-attending observations (Leal et al. 2015b). At the Catimbau National Park we have observed 29 ant species attending 20 EFN-bearing plants (Silvino-Silva et al. unpublished data). These ants actively collect extrafloral nectar on plants during both day and night, and have been observed to attack simulated herbivores (termites) in both periods also (Durval et al. unpublished data). However, the taxonomic composition of ant-attending assemblages changes markedly from one period to another. The diurnal ant fauna at EFNs of *Pityrocarpa moniliformis* is dominated by the ants *Azteca* sp. A, *Cephalotes pusillus*, and *Crematogaster crinosa*, while the species *Crematogaster elevens*, *Ectatomma muticum*, and *Camponotus vitatus* are the most frequent nocturnal visitors; only *Camponotus crassus* were active both day and night (Durval et al. unpublished data).

The influence of human disturbance on EFN-bearing plants and their ant attendants have been also investigated in Caatinga vegetation. Leal et al. (2015b) observed that some EFN-bearing plant species that decrease in abundance as disturbance increases are also less attended by visiting ants. This indicates that disturbance reduced the ability of those plant species to attract ants, probably due to a reduction in extrafloral nectar quantity or quality. In fact, preliminary results indicate that the secretion rate of *Pityrocarpa moniliformis* EFNs decreases as disturbance increases (Oliveira et al. unpublished data). Although EFN production is considered to be physiologically 'cheap' for plants, it still requires resources that could be allocated to other plant functions, and plants consequently regulate nectar production according to environmental conditions (Heil et al. 2000; Strauss et al. 2002). In particular, extrafloral nectar secretion can be negatively affected when plants experience low water supply or high temperatures; both conditions commonly observed in disturbed habitats (see Murcia 1995). Plants under water stress close their stomata to avoid water loss, and, given that EFN glands are often modified stomata (Heil 2011), any factor affecting stomata functioning will also affect EFN nectar secretion. Therefore, the decline in ant attendance could be related to a reduction in EFN secretions at disturbed sites due to physiological stress.

9.3 Antagonistic Interactions

9.3.1 Herbivory

Few studies have investigated herbivory in the Caatinga and most of them address how herbivore insects of individual plant species (e.g., Coelho et al. 2012; Oliveira et al. 2010; Ribeiro et al. 2013; Dourado et al. 2016) and, more rarely, plant communities (Dantas de Paula et al. 2011; Santos-Neto 2016) respond to environmental stress, obviously because the semiarid climate under which Caatinga vegetation conditioned. The most common groups of herbivores in the Caatinga are leaf-chewing (e.g., Coleoptera, Orthoptera, Lepidoptera e Phasmatodea), sap-sucking (mostly Hemiptera), and wood-boring insects (Coleoptera) (Oliveira et al. 2010; Santos-Neto 2016). The abundance of these herbivores is higher during the beginning of the rainy season, but leaf damage increases as the rainy season proceeds (Oliveira et al. 2010), which is in common with other dry forests (Janzen and Waterman 1984; Filip et al. 1995; Boege 2005).

Studies on plant anti-herbivory defensive traits are even rarer in the Caatinga. We were able to find only two studies relating leaf traits to herbivore damage. Oliveira et al. (2010) found no significant relationships between leaf damage and both total phenolic content and leaf toughness in individuals of *Handroanthus spongiosus*. Dourado et al. (2016), studying six common species from the Caatinga, found lower leaf damage in perennial species than in deciduous ones and in species with higher leaf toughness, while chemical defensive compounds (alkaloids and saponins) were not related to plant damage. These results indicate that mechanic defenses are more effective against herbivores than chemical ones and that an analysis of multiple defensive traits (the defense syndrome) must be more informative for determining the mechanisms driving herbivore attacks (Dourado et al. 2016).

LCAs sensu stricto (genera *Atta* and *Acromyrmex*, Myrmicinae) are important herbivores in the Caatinga (Siqueira 2017; Tabarelli et al. 2017). They are among the most polyphagous and voracious herbivorous insects, cutting up to 15% of the standing leaf crop (Wirth et al. 2003; Urbas et al. 2007) and up to 50% of the species of a given forest flora (Vasconcelos and Fowler 1990; Wirth et al. 2003) in their colony's territory each year. Accordingly, LCA herbivory impacts plant fitness, demography, and community structure (Wirth et al. 2003; Leal et al. 2014a; Corrêa et al. 2016). In addition to herbivory, LCA affect their environment via construction and maintenance of colossal nests that may remove more than 40 tons of soil to the surface (Moreira et al. 2004). LCA open canopy gaps above their nests (Corrêa et al.

2010) that cause drastic shifts in microclimatic conditions, particularly in light availability, soil temperature, and soil water potential (Meyer et al. 2011). By modifying the forest environment *Atta* nests can act as ecological filters for plant recruitment (Meyer et al. 2011), and are considered a major disturbance with the potential to alter the structure and plant species composition of tropical forests (reviewed in Farji-Brener and Illes 2000; Leal et al. 2014a).

There are eight species of LCA in the Caatinga, five from *Acromyrmex* (*A. balzani*, *A. landolti*, *A. octospinosus*, *A. rugosus*, and *A. subterraneus*) and three from *Atta* genera (*A. laevigata*, *A. opaciceps*, and *A. sexdens*) (see Chap. 13). The herbivory patterns of *A. opaciceps*, the only LCA species endemic to the Caatinga, were studied in detail in the Catimbau National Park where colonies harvested more than 40 plant species (Siqueira 2017). The most abundant and widely distributed species in the Catimbau region, *Croton argyrophyllus* and *Cenostigma* microphylla, were also the species most frequently collected by *A. opaciceps* colonies (Siqueira 2017). The herbivory rate was estimated to be more than 30% of leaf biomass in their foraging areas (Siqueira 2017). This number makes LCA the most voracious herbivore in the Caatinga region, with a potential to affect plant reproductive success as demonstrated for humid forests and savannas (Wirth et al. 2003; Urbas et al. 2007; Costa et al. 2008; Corrêa et al. 2010; Leal et al. 2014a). In addition to herbivory, edaphic engineering by LCAs can affect Caatinga vegetation dynamics (Siqueira 2017; Tabarelli et al. 2017). We refer to soil movement and deposition on nest mounds and, more importantly, the presence of external nest refuse dumps composed of organic waste in nests of all LCA species (Siqueira 2017; Tabarelli et al. 2017), both altering soil conditions around the nests and probably patterns of seedling recruitment and growth as documented for humid forests and savannas (Corrêa et al. 2010; Meyer et al. 2011, 2013; Leal et al. 2014a).

LCAs are amongst the few group of organisms that proliferate in anthropogenically modified tropical landscapes (Leal et al. 2014a; Tabarelli et al. 2017). Various studies have documented the proliferation of LCA, especially of *Atta*, in modified habitats such as (1) pastures (Fowler 1983) and plantations (Oliveira et al. 1998); (2) forests at early successional stages (Silva et al. 2009); (3) remnants of forests embedded in open matrices (Rao et al. 2001); (4) roadsides (Vasconcelos et al. 2006); and (5) forest edges (Wirth et al. 2007; Dohm et al. 2011). The causes for this proliferation involve the relaxation of both top-down and bottom-up controls in a process of ecological release (Terborgh et al. 2001). The release from top-down forces occurs because in disturbed areas colonies suffer fewer attacks by predators (Wirth et al. 2008) and parasitoid phorid flies (Almeida et al. 2008) than in non-disturbed areas. With regard to bottom-up control, the relaxation of LCA population is driven by the proliferation of pioneer species in disturbed habitats (Laurance et al. 2006; Santos et al. 2008) and the facts that these plants are less well defended against herbivores (Coley et al. 1985) and more palatable to and preferred by LCAs (Farji-Brener 2001; Wirth et al. 2003; Falcão et al. 2011). Such hyper-abundance of LCAs fundamentally alters their global impact as herbivores and ecosystem engineers on forest stands and the landscape level when compared with undisturbed systems.

In addition to humid forests such as the Atlantic and Amazon, we have observed a proliferation of LCAs in the Caatinga (Siqueira et al. 2017; Tabarelli et al. 2017). Apparently, LCA species such as *A. laevigata*, *A. opaciceps*, and *A. sexdens* benefit from the proliferation of herbs and pioneer woody species (e.g., *Croton argyrophyllus*, *Poincianella microphylla*, *Pityrocarpa moniliformis*), which dominate regenerating forest stands following the abandonment of agricultural fields (i.e., slash-and-burn agriculture), pasture lands, and roadside vegetation (Siqueira et al. 2017; Tabarelli et al. 2017). In fact, colony density sharply decreased from 15 ± 2.92 ha^{-1} in the 50-meter zone along roads to only 2.55 ± 1.65 ha^{-1} at distances up to 300 meters (Siqueira et al. 2017), a trend in line with previous findings from tropical rain forests (Dohm et al. 2011), Cerrado savanna (Vasconcelos et al. 2006), and the arid steppe of Patagonia (Farji-Brener 1996). Among the factors driving nest density we identified (1) road proximity; (2) lower vegetation cover; and (3) higher chronic disturbance (Siqueira et al. 2017).

Although the Caatinga biota supports native large-bodied vertebrates operating as folivores, particularly two species of ungulates/deer species, by far goats, both the exotic goat species (*Capra hircus*) and local breeds (e.g., moxotó, parda sertaneja, canindé), represent the predominant herbivore since their introduction by Europeans in the sixteenth century (Leal et al. 2003). There are now 8.6 million animals, most of them raised extensively by small farmers and feeding on Caatinga vegetation. As browsers, a significant part of the goat diet in the Caatinga consists of woody plant species and herbaceous dicots, including leaves, fruits, flowers, fruit/seeds, bark, and litter (Leal et al. 2003; Bakke et al. 2010). Anecdotal reports inform a lower content of tannins and other anti-herbivore defenses among senescent leaves of Caatinga woody flora (Parente et al. 2012). Moreover, goats usually feed on the majority of woody species available, including highly unpalatable ones in the absence of proper foliage in the dry season (Parente and Parente 2010; Parente et al. 2012). Herb biomass and leaves from woody plant species create nearly 4000 kg of dry matter/ha/year, but only 10% (400 kg) is available for animal grazing (Araújo Filho et al. 2002); however, herbivory rates by goats are still not available. Frequently, the stock rate is mentioned as at a level of overgrazing (more than three animals per hectare) (Guimarães Filho and Góes 1998). Negative impacts on soil attributes, plant populations, vegetation structure, and ecosystem functioning have been already reported as reduced plant growth, reduced leaf, flower and fruit production, reproduction failure, soil compaction, seed ingestion and deposition in unsafe sites, and reduced herb cover and soil litter cover and soil carbon stocks (Resente et al. 2004; Santos et al. 2010; Espirito Santo et al. 2012; Schulz et al. 2016).

9.4 Conclusions and Future Directions

Although we are far from having a comprehensive view of plant–animal interactions in the Caatinga vegetation, it is already possible to highlight some patterns relative to pollination, seed dispersal, ant–plant protective mutualism, and herbivory. The Caatinga and other SDTF share several characteristics such as the prevalence of a biotic pollination system, particularly by small insects and bees, and abiotic seed dispersal (Griz and Machado 2001; Barbosa et al. 2003; Machado and Lopes 2004). Among zoochoric plant species, ornitochory is the most frequent strategy (small drupes and berries) with vertebrate–frugivorous fauna relying on a few taxonomically related species (i.e., within the Cactaceae and Anacardiaceae families) (Griz and Machado 2001; Barbosa et al. 2003). As EFN-bearing plants are frequent among Fabaceae species (the most diverse and abundant family in SDTF) (Pennington et al. 2009; Moro et al. 2014), ant–plant protective mutualisms based on EFNs is expected to be frequent in SDTF (Melo et al. 2010; Leal et al. 2015b). Obviously, most interactions are seasonal, such as the dispersal of fleshy diaspores during the rainy season (Machado et al. 1997).

Reduced frequency of wind-pollinated species, a high frequency of specialized pollination modes, and the presence of a highly diverse vertebrate-pollinated plant community and ant-pollinated species are likely to distinguish the Caatinga from other neotropical SDTF (Machado and Lopes 2004; Sobrinho et al. 2016; Domingos et al. 2017). A high frequency of oil-flower species may also be a peculiarity of the Caatinga flora (Bezerra et al. 2009). Certainly, a distinctive feature of the Caatinga refers to the relative richness of true myrmecochorous species (Leal et al. 2015a) and those supporting saurochory (particularly in the Cactaceae) (Gomes et al. 2014a, b, 2016). Although some SDTF in Mexico can support a great diversity of Euphorbiaceae and Cactaceae, true myrmecochorous and saurochorous flora is apparently not as diverse as in the Caatinga. Such distinctness is probably more related to the evolutionary history of the Caatinga flora than the occurrence of ecological filters operating exclusively in the Caatinga biota. Unfortunately, herbivory remains largely unexplored in the Caatinga vegetation. Among promising topics are the (1) impact of goat browsing, including litter consumption; (2) proliferation of LCAs in human-modified landscapes; and (3) massive, regional-scaled migration of Pieridae butterflies during the rainy season.

Like other SDTF, much more research is required relative to the basic ecology of plant–animal interactions in the Caatinga vegetation and this topic remains as a research priority (see Sanchez-Azofeifa et al. 2014). However, some applied issues have already achieved priority since this biota has experienced increasing levels of human disturbance, including both acute (habitat loss and fragmentation) and chronic disturbance (firewood collection, livestock production based on native vegetation) (MMA and IBAMA 2011; Ribeiro et al. 2015). The Caatinga is also threatened by climate change (i.e., up to a one-third reduction in the precipitation levels during the current century) (Magrin et al. 2014) and we already have evidence of negative effects of reduced rainfall on plant assemblages (Rito et al. 2017). Collectively, these pervasive drivers have been proposed to alter the nature, frequency, and persistence of several mutualistic interactions in SDTF (Leal et al. 2014b, 2015b, 2017; Sobrinho et al. 2016). For instance, we refer to those involving endemic and narrow-distributed species or those relying on highly seasonal resources, which are associated with plant phonological events controlled by climatic variables, that is, potential mismatches (see Quesada et al. 2011; Sobrinho et al. 2016; Leal et al. 2017). Moreover, many plant traits/strategies supporting particular interactions are phylogenetically clustered or present across few taxa, such as the elaiosome-bearing seeds, EFN-bearing plants, and ground-level berries consumed by lizards. Mutualistic interactions involving rare partners are usually more vulnerable to human disturbances (Gomes et al. 2014a, b; Leal et al. 2014c, 2015b, 2017; Sobrinho et al. 2016). On the other hand, some antagonistic interactions are apparently benefited by human disturbance, such as LCAs and goat herbivory (Leal et al. 2003; Siqueira et al. 2017; Tabarelli et al. 2017). Disrupted/altered interactions are expected to cascade on multiple biological levels, from the population to ecosystem level, including resilience patterns (Leal et al. 2014a). Translating interactions in terms of impacts on forest dynamics (e.g., over-browsing causing arrested forest regeneration), ecosystem function and services (e.g., crop pollination), and the sustainability of the socio-ecological systems of the Caatinga (i.e., integrated studies) clearly represents an essential approach in the context of conservation/restoration planning and mitigation/adaptation-related better practices.

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Part III
Ecosystem Services

Chapter 10
Water as Capital and Its Uses in the Caatinga

**Eunice Maia de Andrade, Deodato do Nascimento Aquino,
Luiz Carlos Guerreiro Chaves, and Fernando Bezerra Lopes**

Abstract Due to climate and local geology, the only source of water for the entire Caatinga is rainfall. Annual rainfall averages 773 mm, and 70% of this amount may precipitate in a single month. The rainfall regime in the region is more strongly affected by the great spatio-temporal variability of the rains than by the total amount of rainfall precipitated annually. This variability results in several microclimates, from a desert climate in the central region to a rainy climate along the coastal areas and mountainsides due to orographic effects, with alternating drought and flood years. The scarcity of water in the region is also linked to the physical environment, such as shallow soils, high evaporative demand, the reduction of vegetative cover, and social organization. The waterways that make up the drainage network of the Caatinga are almost entirely intermittent or ephemeral, and throughout the dry season water is available from artificial lakes and artificial perennial use of rivers. These constitute the main source of water for many uses, making the prevention and control of pollution in these sources essential to ensuring a safe water supply. This natural asset has many uses, from soil and vegetation development to climate thermoregulation. In fact, water, soil, and vegetation act in a complementary way; if the existence of vegetation is dependent on water availability, then vegetation is crucial to the infiltration of water into the soil and the maintenance of water quality.

Keywords Semiarid hydrology • Natural resources • Best management practices • Rainfall regime • Water production

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10.1 Introduction

Much discussion has occurred concerning the reduction of water availability worldwide and whether it is a result of global population growth or the degradation of bodies of water through human action (Gachango et al. 2015). In addition, water availability has an important contrasting component, agriculture, which is responsible for the production of the fiber and biomass needed to meet the food and energy requirements of humans and animals (Boval and Dixon 2012). Faced with this situation, a model needs to be defined that considers the conservation and proper management of natural resources as essential components of exploiting the natural capital of a biome (Giraudeau et al. 2014) and which should consider the carrying capacity and suitability of the natural resources of each region (Lopes et al. 2009). This paradigm becomes more important in semiarid regions of the world, such as the northeast of Brazil, where natural resources (water, soil, and vegetation) are limited as a result of the climatic conditions of the region (Souza and Fernandes 2000). As a result of the prevailing crystalline geological basement of the Brazilian semiarid region, water reserves originate from rainfall that is concentrated over a few months of the year, along with intermittent surface runoff (Farrick and Branfireun 2015). This process was crucial to the formation of the deciduous forest and the caatingas, the predominant type of vegetation in the Brazilian semiarid region (Sampaio et al. 2005; Pennington et al. 2000). The classical models of man's use of natural resources have failed because they separate socio-economic issues from the environmental features inherent to a region (Nelson et al. 2009). In addition to knowledge of environmental and socio-economic dynamics, it is also necessary to identify any conflicts that may exist between development goals and the carrying capacity of the natural resources that make up the Caatinga region.

Although a new paradigm has been developed regarding the use of this natural asset, which has economic value because of the direct and indirect benefits it generates for the human population (Braat and Groot 2012), much still remains to be done. For example, low levels of social organization and joint action occur on the part of rural residents. This situation compromises the production of food for these residents, especially those of low economic status, who depend completely on the availability of natural resources in the region (Buainain and Garcia 2013). In 1980, Duque was already discussing the preference for isolated action among the people who inhabit the Caatinga.

We are living in a time in which actions and decision making must be in line with local environmental reality and consider the goods and services generated by natural assets. Therefore, this chapter discusses the production and uses of water as capital in the Caatinga.

10.2 Rainfall Regime of the Caatinga

The Caatinga is characterized by abundant solar energy, a water deficit, and low relative humidity, which contributes to the high evaporation rates of water bodies and wet surfaces. Its geographical area is bounded by the 800-mm annual isohyet. In this regard, the Caatinga is very similar to the semiarid northeastern region, which is also known as the drought polygon (Pereira Júnior 2007).

The rainfall regime is more strongly affected by the high spatio-temporal variability of the rains than the total rainfall precipitated annually (Andrade et al. 2016b). The average annual rainfall in the region is 773 mm (Table 10.1), and 70% of this amount may precipitate in a single month (Andrade et al. 2010). The rainy season does not begin or end at a fixed time.

Although 21% of the region receives annual precipitation of less than 600 mm and 0.6% of the region receives less than 400 mm (Fig. 10.1, Table 10.1), 75% of the area lies between the 600 and 1200 mm isohyets, and 1.7% of the area receives an annual total greater than 1200 mm. This spatial variability in rainfall results in distinct microclimates in the Caatinga region, ranging from a desert climate in the central region to a rainy climate along the coastal area (Fig. 10.1) and in the mountains due to the orographic effect. In these regions (*Precipitation* > 1200 mm), there are records of annual rainfall above the 1800 mm isohyet, as in the case of the city of Guaramiranga in the state of Ceará.

Due to its proximity to the equator (2°54′–16°18′ S), the Caatinga has only two distinct seasons, a wet season and a dry season, with dry years frequently alternating with years of flooding. The region is subject to the influence of subtropical high-pressure areas linked to the semi-permanent South Atlantic anticyclone (Guerreiro et al. 2013), which is in turn influenced by the Hadley (meridional) and Walker (zonal) circulations (Ferreira and Mello 2005). This produces a rainfall regime that depends on geographical position (Fig. 10.2). In the northern part of the Caatinga region, the rainy season occurs between January and May, reaching a maximum from March to April, when the Intertropical Convergence Zone (ITCZ) migrates towards the southern hemisphere and reaches latitudes up to 10° S. The upward

Table 10.1 Average annual rainfall in the Caatinga

Isopleth (mm)	Area (%)	Weighted rainfall (mm)
<400	0.6	24
400–600	21.9	109.5
600–800	38.6	270.2
800–1000	30.2	271.8
1000–1200	7.1	78.1
>1200	1.6	19.2
Total	**100.00**	**772.8**

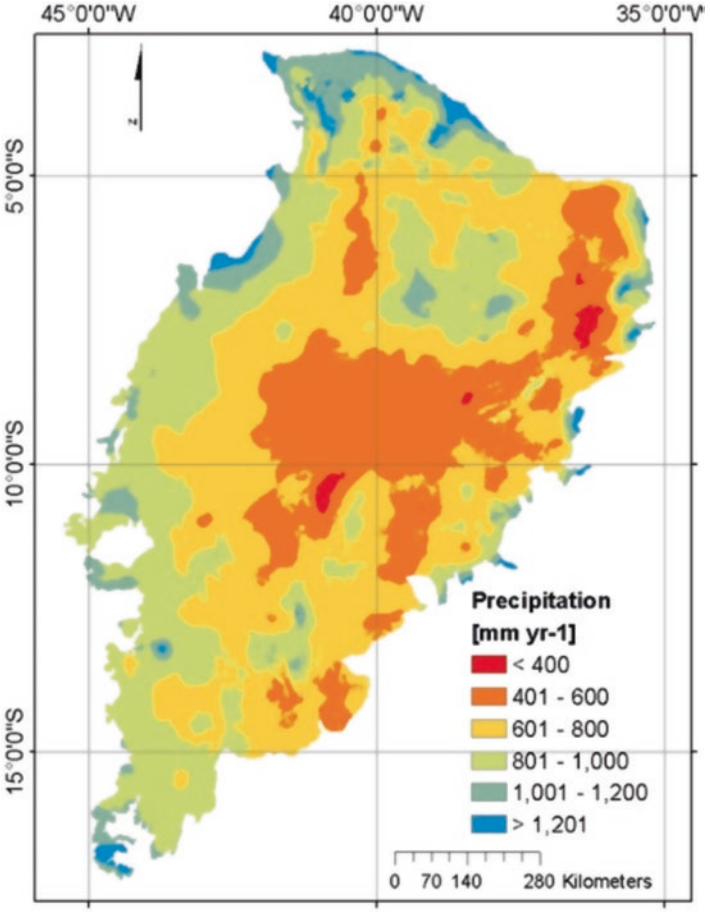


Fig. 10.1 Isohyets in the Caatinga

movement of the air associated with the ITCZ generally gives rise to intense precipitation that is convective in origin and has no definite periodicity (Sun et al. 2006; Alves et al. 2009). This behavior results in a rainfall pattern that is climatically anomalous, with highly variable spatial and temporal distributions (Bates et al. 2008).

In the southern region of the Caatinga, the rains begin in October and are concentrated in December and January. These rains are caused by cold fronts advancing toward the equator and reaching latitudes below 10° S (Ferreira and Mello 2005). To the east (Fig. 10.2), the rainy season begins in May, continues until August, and is concentrated in June and July. These rains are mainly induced by easterly waves, which consist of moist air masses moving from the coast of Africa to the east coast of Brazil (Torres and Ferreira 2011), where they join the sea breeze that advances over the continent via the process of advection. When oceanic and atmospheric

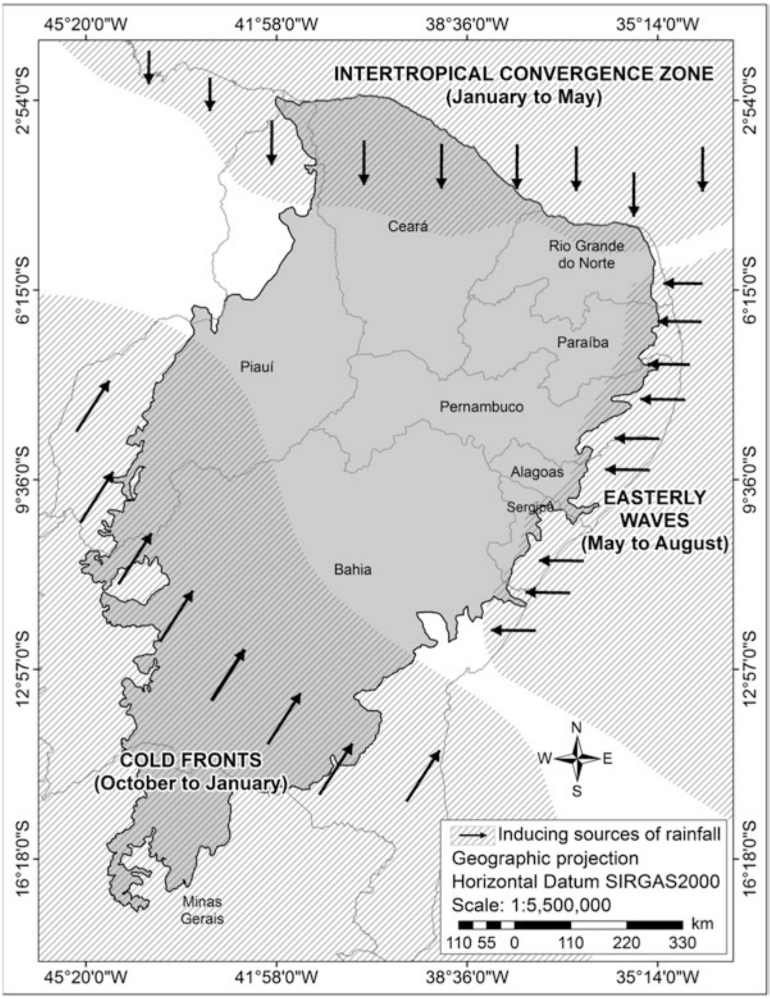


Fig. 10.2 Predominant sources of rainfall regimes in the Caatinga

conditions favor the increased displacement of the air masses, these air masses advance over the central and northern parts of the Caatinga region. In such cases, the rainy season can last until July or August (Guerreiro et al. 2013).

The rainy season has a unimodal distribution, with 60% or more of the total precipitation being recorded over 3 months (Fig. 10.3). Also, the lower the annual rainfall depth, the greater the contraction of rainfall events. At the three rainfall stations with the lowest annual rainfall depths, Petrolândia, Campos Sales, and Macau, precipitation is mainly induced by the ITCZ because the rainiest months occur between February and April. In contrast, the rainfall distribution recorded at the Bom Jesus da Lapa station shows that rainfall events there are generated by cold fronts

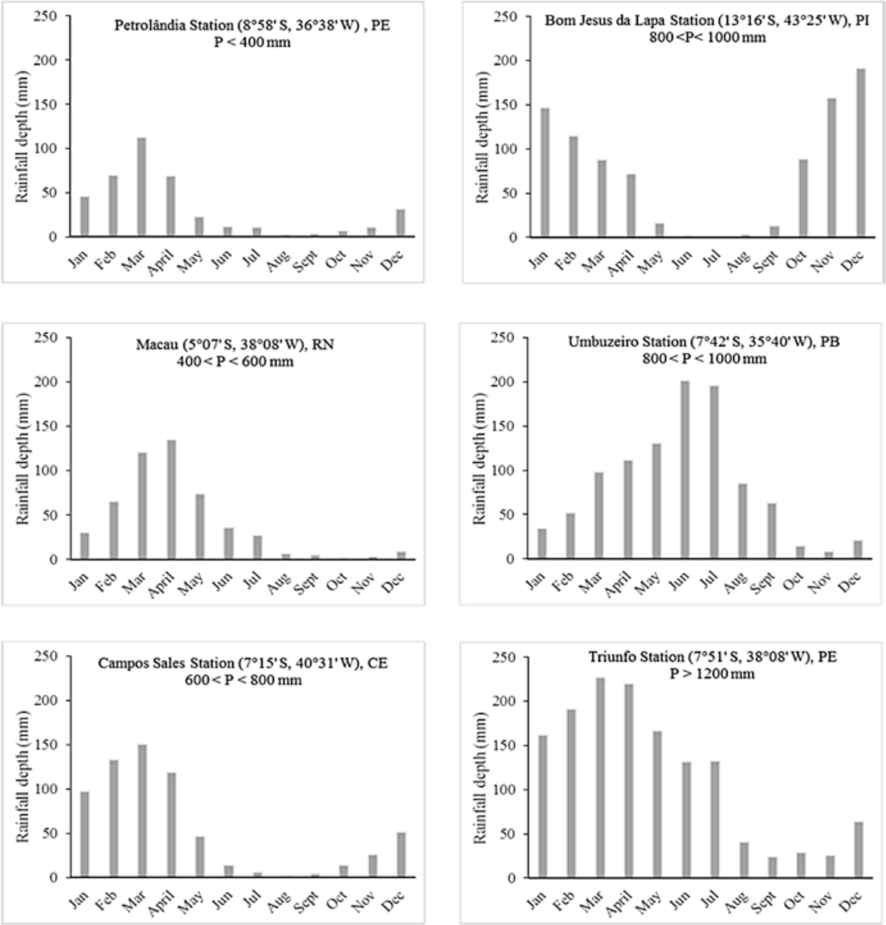


Fig. 10.3 Historical series of total monthly rainfall at six rainfall stations in the Caatinga

(Fig. 10.3), and the rains occurring at the Umbuzeiro station are mainly induced by easterly waves, with the maximum rainfall depths being recorded in June and July.

The greatest water shortages in the Caatinga region begin on the northern coast of Rio Grande do Norte and move toward the central area of the Caatinga. This void, located on the western side of Rio Grande do Norte and running in a north–south direction (Fig. 10.1), is determined by the leeward effect of the Borborema plateau, along with the presence of dry air masses. Between the latitudes of 8° S and 11° S, little rain falls (Fig. 10.1) because of the weak influence of the ITCZ and the polar fronts in the region, that is, the ITCZ or polar fronts do not always arrive with air masses that are humid enough to generate large amounts of rainfall.

The uncertainties of the rainfall regime are not limited to spatial variability. Rainfall is also characterized by high inter-annual variability (the existence of drought) and intra-annual variability (the existence of consecutive dry days [CDDs]

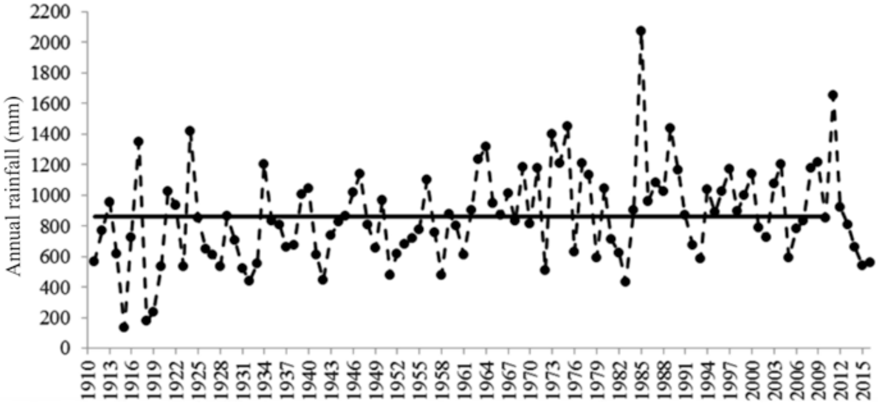


Fig. 10.4 Historical series (1910–2015) for the rainfall station at Iguatu, Ceará

during the rainy season) (Guerreiro et al. 2013; Andrade et al. 2016b; Santos et al. 2016). It is common for the total annual precipitation at any one station to vary by more than 1000% (Fig. 10.4) from one year to the next, as is the case at the Iguatu station in Ceará. For that station, the annual historical series shows records of 133 mm for 1915 and a yearly accumulation of 1348 mm 2 years later (1917). Variability of this magnitude was also seen from 1983 to 1985, when the total precipitation varied from 433 to 2075 mm. These results indicate the uncertainty of events in the Brazilian semiarid region, even on an annual scale (Guerreiro et al. 2013).

Studies of these uncertainties show that the entire Caatinga displays the vulnerabilities associated with rain-fed agricultural production or pasture (Andrade et al. 2016b). Intra-annual vulnerability is present even in regions with total annual rainfall exceeding 1200 mm, demonstrating that water vulnerability should not be limited only by annual rainfall. For a better understanding of how these events are distributed throughout the year, a monthly analysis was carried out on a historical series (1961–2015), which was part of a total series of 106 years. The complete series was not used due to the unavailability of data on a monthly scale.

Of the months that make up the rainy season, January to May, only January shows discrepant data (Fig. 10.5), and, with the exception of May, the median tends to move towards the first quartile. This pattern shows that monthly rainfall depths of less than the median have values that are close to one another and that monthly rainfall depth values greater than the median are dispersed, showing greater variability, along with a trend toward the occurrence of extreme monthly events. Lima et al. (2008) also found that for the rainiest months, no discrepant data were registered.

The precipitation that occurred in March and April also shows that 50% (median) of the total rainfall for these 2 months was higher than the annual total for years of severe drought (Fig. 10.5). In contrast, the months representing the dry season (June–December) show the existence of isolated events with high temporal

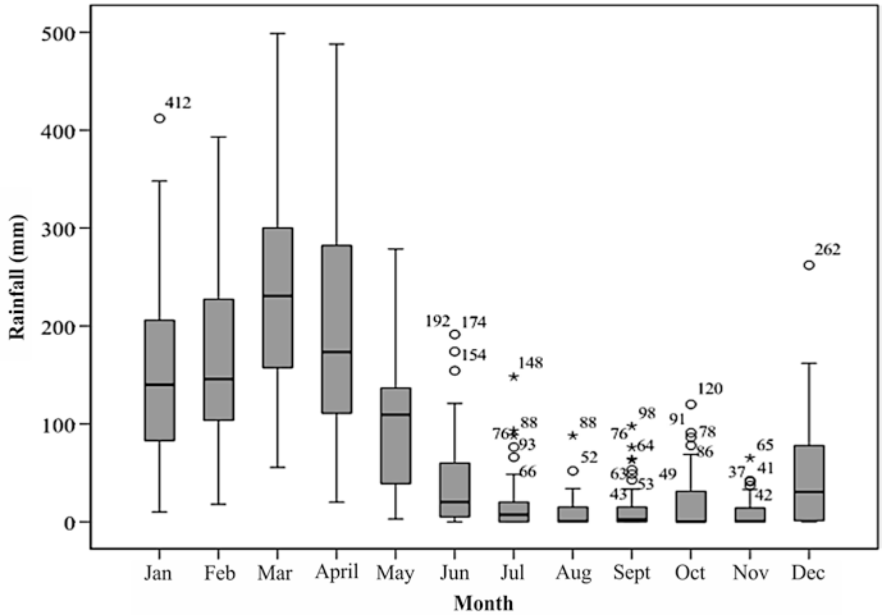


Fig. 10.5 Monthly distribution of the historical series (1961–2015) of annual rainfall for the Iguatu station

variability in that extreme events are present for every month. As seen in Fig. 10.5, no rainfall was recorded from July to November in 50% of the investigated years because the median value is zero. This demonstrates that using only average values as indicators of the rainfall regime in the Caatinga should be avoided. It is recommended that other indicators be considered, such as the monthly and annual distribution of events, the occurrence of CDDs, and extreme events. The only certainty of the local reality is the uncertainty with which rainfall events are distributed over time and space. In addition to the uncertainty of rainfall, the matrix of hydrological behavior contains shallow soils (Romero and Ferreira 2010) and a drainage system of ephemeral rivers (Campos 2011). This results in a low level of water being stored in the soil.

10.3 Geology and Soils

The Caatinga lies inclined over crystalline rocks from the Precambrian (gneisses, granites, and schists), which represent the predominant geological units in the eastern part of the northeast, with the exception of the sedimentary basins located along the coast (Saadi 1993) and the western part of the region. The evolution of the landscape in the Northeast is based on the pedimentation ramps having been subjected

Fig. 10.6 Inselbergs in the town of Quixadá, Ceará

to climatic changes in Quaternary (Maia et al. 2010), and the pediplains of the backlands are the result of a vast, slow process of erosion under very humid conditions, followed by intense aridity. In the Brazilian semiarid region, one proof of the existence of a period of high precipitation and runoff in earlier times is the presence of pebbles on the land and interfluves in the headwaters (Maia et al. 2010). This process began in Lower Tertiary, followed by phases of more recent pediplanation that were contemporary with the deposition of the Barreiras Group. Isolated traces of younger surfaces are found, which is characterized by plateaus, mountain ranges, and inselbergs (Fig. 10.6). The geological basement of the Caatinga region consists mainly of metamorphic and igneous rocks, which make up approximately 70% of the basement and are commonly described as crystalline.

Geological and climatic processes, together with the action of organisms, gave rise to the soils of the Caatinga. The result of these interactions can be seen in the high diversity of soil types, which form a true mosaic in which soil classes can vary even over short distances. Although the soils are complex and have varying characteristics (Sampaio 1995), it can be said, based on Jacomini (1996) and EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) (2013), that 70.3% of the Caatinga territory is divided into four classes of soil: latosols (24%), litholic neosols (18.2%), argisols (15.2%), and luvisols (12.9%).

The common occurrence of latosols in the Caatinga is due to the very nature of the region, specifically the action of the climate on the bedrock. These are deep soils with low-activity clay, high aluminium content, and low levels of nutrients. The latosols are mostly located in the southern and southwestern part of the Caatinga, which corresponds to Bahia and the southern Piaui; the other three predominant classes are shallow soils with high-activity clay (2:1) that are not very deep (<50 cm) but are fertile. In general, these soils have stony surfaces or upper layers and a strong tendency toward erosion. Rocky outcroppings are common in the area and are almost always associated with litholic neosols but also occur as inclusions in other soil classes (Embrapa 2013). The greatest concentrations of argisols, litholic neosols, and luvisols are located in the northeastern region of the Caatinga, corresponding to the states of Ceará, Rio Grande do Norte, Paraiba, and Pernambuco.

The excess heat and light inherent to tropical semiarid regions results in the rapid mineralization of organic matter, with the fertility of the soil being a result of its alkalinity and base richness (Romero and Ferreira 2010). Methods of exploiting these soils should therefore cause the least possible disturbance of the biological environment and reinforce the contributions of organic matter by maintaining a live cover consisting of nitrogen-fixing plants and a mulch of crop stubble, manure, and various sources of green fertilizer (Duque 1980).

10.4 Vegetation

The combination of the predominant soils, rainfall regime, energy availability (2800–3000 h year^{-1}), and high rates of potential evaporation, which range from 1500 (coastal regions) to 3000 mm year^{-1} in the continental area (Molle 1989; IICA 2002), has resulted in various plant typologies (Neri et al. 2012.), predominantly seasonally dry tropical forest (Pennington et al. 2000). From a phytosociological point of view, the density, frequency, and dominance of the species are determined by variations in topography, soil type, and rainfall (Sampaio et al. 2005; Prado 2008; Moro et al. 2016).

As for resilience, the plant species that make up the Caatinga display physiological adaptations to their environmental conditions. Knowledge of these adaptations is indispensable in understanding the functionality of the region, which represents the largest area of seasonally dry tropical forest in South America (Miles et al. 2006; Pennington et al. 2000). Among plants of the Caatinga, closing the stomata in an attempt to maintain favorable levels of water content in their tissues for as long as possible is one of the first lines of defense against drying out (Silva et al. 2004). This mechanism of stomatal closure at the hottest times of the day constitutes a strategy used by many species that inhabit arid and semiarid regions to prevent excessive loss of water through transpiration (Chaves et al. 2016). Hence, this behavior is a form of adaptation or acclimatization by the plants to the water deficit they face, maintaining transpiration to a low level and keeping stomatal opening to the minimum necessary to assimilate a sufficient amount of CO_2 to continue with the photosynthetic process, though at a reduced capacity (Sena et al. 2007). This physiological process leads to improved water-use efficiency (WUE) (Medrano et al. 2009), and high WUE allows plants to remain alive under conditions of water stress for longer periods.

The reduction in the number of leaves seen in various species of plants in the Caatinga that are subjected to water stress is believed to be another strategy for survival under adverse conditions by virtue of the reduction of water loss through transpiration and thus a greater resistance to drought (Santiago et al. 2001). In addition to leaf senescence, there are reports in the literature of plants in the Caatinga that are subjected to severe water deficits tending to invest more in the elongation of the roots than that of shoots in order to absorb water from the deeper zones of the soil (Barbosa et al. 2000). Root architecture and roots' ability to exploit the deeper, more humid layers of the soil, together with a higher root to shoot ratio, are important characteristics among plants in the Caatinga that face water deficits (Scalon et al. 2011). Understanding these mechanisms is important because most of the global predictions concerning climate change highlight ever more frequent and extensive drought events (Magrin et al. 2014), which would lead to changes in the behaviors of some species and an increase in desertification in some regions (Santos et al. 2014).

10.5 Water Availability

The semiarid region of Brazil is characterized by a high water deficit, and it is possible for rivers to remain naturally dry for more than 18 months, which illustrates the low water availability in the region. Of the total rainfall occurring in the Caatinga, 88% is transformed into real evapotranspiration, 9% becomes runoff, and only 3% becomes groundwater flow. This demonstrates a negative water balance, and water availability is restricted to the rainy season, as can be seen in Fig. 10.7.

The semiarid region of Brazil is affected by water shortages, which are aggravated by domestic, industrial, and agricultural pollution (Rebouças 1997). Inasmuch as the global demand for water grows, the availability of fresh water decreases. Therefore, maintaining the water supply not only in terms of quantity but also in terms of quality will be a major challenge for society.

In arid and semiarid regions located at low latitudes, such as the Caatinga region, artificial lakes (Fig. 10.8) and the artificial perennial use of rivers are the main sources of water for domestic, industrial, and agricultural use, making the prevention and control of pollution in these water sources essential in ensuring the water supply. In the Caatinga, 74% of the lakes are artificial (reservoirs) and 26% are natural. This is due to the characteristics of the rainfall regime, geology, and soils, as well as the haphazard removal of natural plant cover for the construction of artificial lakes (Molle 1994).

Considering that in the basins of intermittent rivers, the natural availability of surface water is zero, storage reservoirs allow the inter-annual regulation of natural runoff and ensure the availability of a constant annual volume. In this case, flow rates, which are regulated by the reservoirs, represent the availability of surface water. For perennial rivers, the minimum natural flow rates correspond, in principle, to the availability of water (CEARÁ 2008). In terms of the territorial distribution of

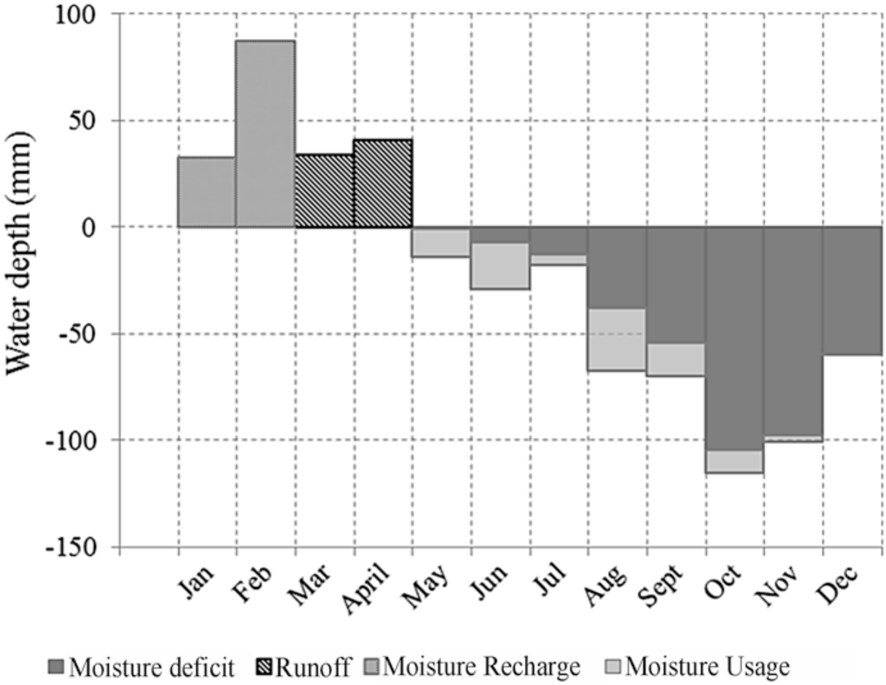


Fig. 10.7 Water balance for the town of Campos Sales, Ceará

surface water in the states of the Caatinga, Ceará stands out as having the highest concentration (1349), equivalent to 38.39% of the total, in contrast to the state of Sergipe, which has a total of only 18 reservoirs, corresponding to 0.51% of the total (Table 10.2).

The distribution of water body types in each state of the Caatinga (Table 10.2) shows the greatest number of natural bodies appearing in the state of Bahia (571), mainly due to the formation of the canyons by the São Francisco River, which are more expressive in the southwest part of the state. In the states of Ceará, Rio Grande do Norte, and Paraiba, artificial reservoirs dominate, highlighting the policy of reservoir construction in these areas to help the population of the backlands to live with the natural water scarcity that exists in the Caatinga (Bezerra et al. 2009). As seen in Fig. 10.8, in the state of Rio Grande do Norte, the reservoirs are concentrated in the central-west and much of the south of the state, where a basement of crystalline rocks predominates, while the center-north and the entire coastal area of the state are formed from sedimentary rocks and soils (Angelim et al. 2007).

Groundwater can occur naturally or artificially in a form that can be extracted and used by man. Groundwater has always been used as a water source by the populations of arid and semiarid regions since the early days of ancient civilizations (Zektser and Everett 2014). To take a simplistic view, due to its geological features,

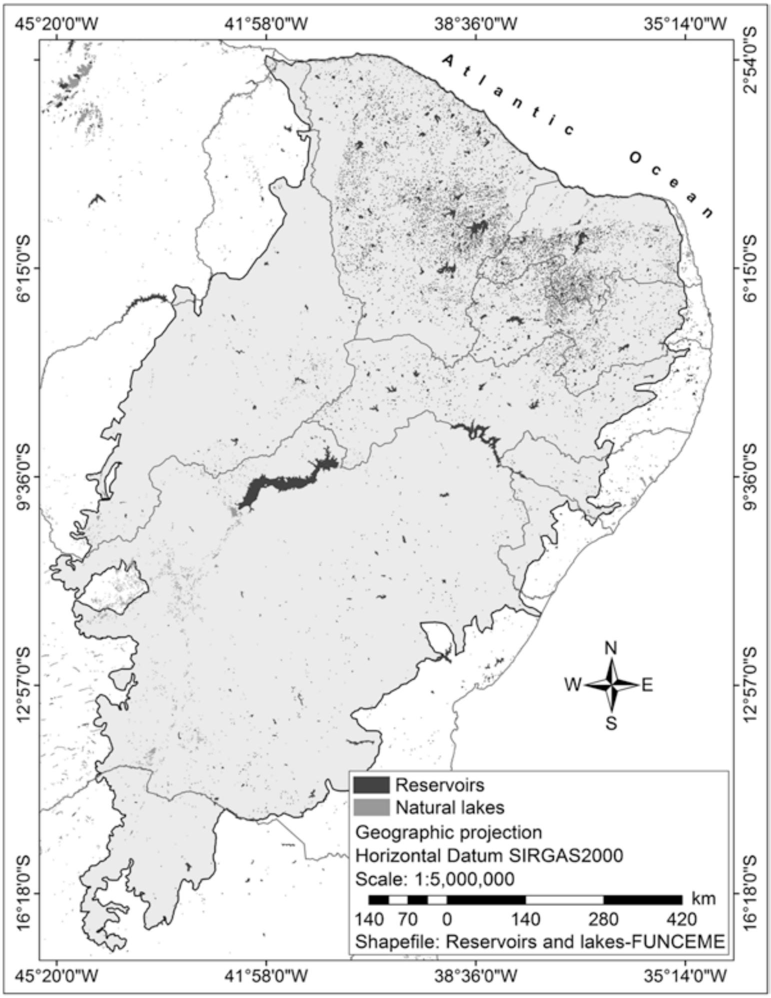


Fig. 10.8 Lakes and reservoirs with water surface of over 5 hectares along the elevation of the spillway in the Caatinga Biome

the Caatinga territory is predominantly composed of two groups of rocks that make up the hydrogeological provinces: crystalline and sedimentary.

In the region with a crystalline basement, groundwater occurs in fractures and discontinuities in the rock, which results in discrete reservoirs of limited size (Deyassa et al. 2014). The use of these sources is always associated with a high level of risk because little information exists about their exploitation and recharge flow rates. However, since the 1950s, underground reservoirs have assumed a prominent role in addressing water-related problems (Rebouças 1999). Researchers such as Feitosa and Feitosa (2011) believe that the potential volume of water to be extracted from these rocks can meet the demands of the diffuse population of the Caatinga.

Table 10.2 Lakes and reservoirs with water surface of over 5 hectares in the Caatinga

	Water reservoir/area					
State	Total	Area	Natural	Area	Artificial	Area
Alagoas	32	28	10	5	22	23
Bahia	718	3988	571	361	147	3627
Piauí	182	257	116	100	66	158
Sergipe	18	69	6	2	12	67
Ceará	1349	2036	143	160	1206	1876
Paraíba	413	495	7	3	406	492
Pernambuco	189	1073	5	2	184	1071
Rio Grande do Norte	613	720	52	83	561	637
Total	**3514**	**8666**	**910**	**716**	**2604**	**7951**

Table 10.3 Wells in the Caatinga

	Wells in the Caatinga			
State	Area (km^2)	Number of wells	Area per well (km^2)	Geology
Alagoas	28,000	1652	17	Sedimentary
Bahia	565,000	23,546	24	
Piauí	25,200	28,651	9	
Sergipe	22,000	5550	4	
Paraíba	56,000	18,953	3	Crystalline
Ceará	149,000	21,996	7	
Pernambuco	90,000	27,035	4	
Rio Grande do Norte	53,000	10,035	5	

These authors estimate that with a median flow rate of 1 m^3 h^{-1} and a pumping regime of six hours per day, 720,000 m^3 could potentially be exploited, which would allow for the consumption of 200 L day^{-1} per person for 3.6 million users. However, due to the salinity of the water (sodium chloride), the percentage of groundwater that is suitable for human consumption in the crystalline region is between 20 and 30% (BRASIL 2005). Limitations on the use of groundwater are related not only to quantity but also to quality.

Unlike the crystalline basement, the sedimentary basement shows a high potential for water storage, and the largest groundwater reservoirs are found in the sedimentary aquifers of the Caatinga territory (Ministério de Minas e Energias 2004). The aquifers of Parnaíba, Potiguar, Jatoba, Recôncavo, and Tucano-Urucuia are important among these reservoirs. The number of wells in the Caatinga is shown in Table 10.3. The state of Piauí has the largest number of wells among the Brazilian states of the Caatinga region; there are 28,651 wells, representing the greatest groundwater potential in the region as a result of being formed from the Parnaiba sedimentary basin. The remaining states of the region, such as Pernambuco, Ceará, and Paraíba, also contain large numbers of wells despite the predominance of the crystalline basement, which, in principle, has a low potential for exploitation because hydraulic conductivity is low, as are the average porosity, permeability, and opening of voids (Manoel Filho 2000).

Based on the ratio between the area of each state of the Caatinga region and the number of wells, the states of Bahia and Alagoas have the largest areas per well; that is, on average, there is a well for every 24 and 17 km^2, respectively. Paraíba has the lowest well to area ratio, with a well for every 3 km^2 on average, followed by Pernambuco and Sergipe, which both average four wells per km^2.

The Caatinga requires further hydrogeological study in order to obtain knowledge of the actual potential of the groundwater there. Only by having precise knowledge about its potential will it be possible to arrive at a plan for the use and development of the region that ensures the rational usage and sustainable availability of water.

10.6 Management of the Caatinga for Water Production

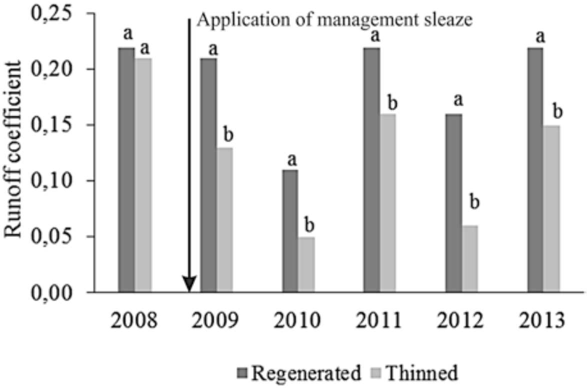
As a natural form of capital, water has various uses, from the development of the soil and vegetation (formation and conservation) to acting as a thermoregulator of the climate. In fact, water, soil, and vegetation act in a complementary and associative way, helping to sustain the environment. In the same way that the soil acts as an important reservoir of water with which to meet the consumptive demands of vegetation, the plant cover and its diversified structure are important in the process of water storage in the ground. If the existence of vegetation is dependent on water availability, the same vegetation determines water's infiltration into the soil and the maintenance of water quality.

The water generated in a river basin, in addition to meeting the hydric requirements of the system, also meets the requirements of agricultural production, watering livestock, and human demand. The benefits derived from this water by maintaining the wetlands in dry tropical forests allow these ecosystems to provide very significant services in dry areas where drought is present for at least 8 months of the year (Marengo et al. 2016). The conservation of forest remnants, especially in the semiarid region, therefore contributes to the protection of surface and underground water sources, improving water availability and conservation in areas where availability is limited (Douglas et al. 2005; Farrick and Branfireun 2015). In addition to the conservation of soil, water, and plant resources, there is also the need for the production of fiber and protein needed to meet the basic food requirements of humanity.

To the extent that natural resources are managed with disregard for their ability and capacity for support human life, these resources begin to run out, and degradation sets in. In view of this, there is a need to define and test models of the exploitation of this natural asset in which the sustainability of ecosystems is maintained as close to a state of homeostasis as possible (Palácio et al. 2013). Thinning is among the management alternatives suggested to increase the production and storage of water in soils of the tropical semiarid region (Rodrigues et al. 2013; Andrade et al. 2016a). This technique consists of the selective control of woody species, in which some tree and shrub individuals are removed from the vegetation, reducing both the density of the plants and the ground cover of the woody stratum (Pimentel 2010).

Fig. 10.9 Period when thinning was being undertaken in the Caatinga

Fig. 10.10 Annual runoff coefficients in watersheds of caatingas given regeneration for 35 years and thinning for 6 years (Andrade et al. 2016a). Thinning was undertaken after the rainy season of 2008



Management via thinning, the selective removal of trees and shrubs, should be adopted to reduce competition for water, light, and nutrients, creating more room for the growth of small herbaceous species (Savadogo et al. 2008). Herbaceous ground cover is an important factor in defining the pattern of water movement in a watershed (Garcia-Ruiz et al. 2008). When carried out correctly, thinning inputs crop residues into the soil (Fig. 10.9). Together with the emergence of herbaceous undergrowth, thinning promotes the reduction of surface runoff (Fig. 10.10), an

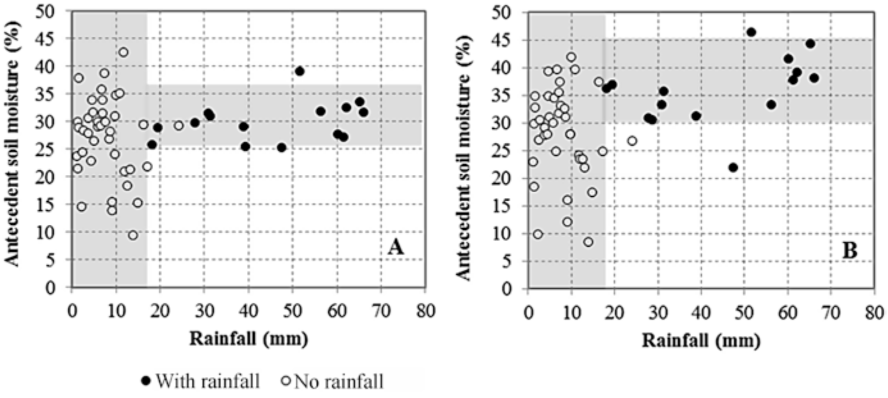


Fig. 10.11 Soil moisture during the rainy season by type of land use: caatinga under regeneration for 35 years (**a**) and caatinga under thinning for 5 years (**b**)

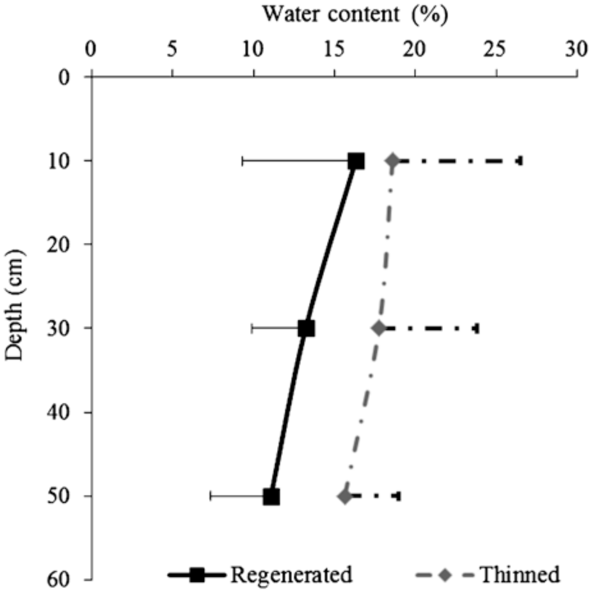


Fig. 10.12 Gravimetric moisture in the soil profile under conserved and thinned caatinga from April 2013 to March 2014 (Aquino 2015)

increase in infiltration, and, consequently, a larger percentage of water being stored in the soil (Figs. 10.11 and 10.12), as discussed by Rodrigues et al. (2013) and Andrade et al. (2016a).

The significant reduction in surface runoff after the application of thinning (Fig. 10.10) results in greater water retention and storage capacity in the soil. The production dynamics of herbaceous biomass and its relationship to changes in the humidity of an inverted neosol under two different types of land use (caatinga preserved for 35 years and caatinga thinned for a period of 6 years) showed that thinning contributes more greatly to the maintenance of moisture in the soil (Figs. 10.11 and 10.12). In the regenerating caatinga area, the runoff process begins with soil moisture content of 25% (Fig. 10.11), while in the thinned area, surface runoff begins when the soil moisture content becomes greater than 30%. The water storage capacity of the soil of the caatinga under regeneration was 10%, while for the thinned caatinga, this value reached 15%, showing that management with thinning resulted in a 5% increase in soil moisture. These results were confirmed by Aquino (2015), who identified greater soil moisture at depths of 10, 30, and 50 cm with thinning (Fig. 10.12). The reduced surface runoff and greater soil humidity result in increased biomass (Palácio 2011) and a reduction of soil and nutrient loss (Lobato et al. 2009).

Although research shows that thinning can be used to promote the sustainable use of natural resources in the Caatinga, further research is needed before thinning can be defined as an integral part of the natural system in tropical drylands. Defining the threshold of sustainability in a model for the use and exploitation of natural resources is crucial in defining the conservation or degradation of the environment.

10.7 Concluding Remarks

To understand the availability, support, and services that water can offer in environments with irregular climate regimes and a negative water balance (evaporation greater than precipitation), a holistic view, in which the territory, human beings, and natural resources of the environment are interwoven, is crucial. In seeking to meet the demand for various types of water usage, the strategies to be adopted must consider the environment and its peculiarities. It is time to change the strategy of transferring techniques that are successful in regions with sub-humid or dry-temperate climates to tropical dry regions. Decision-making must be in line with the reality of each location. In this context, any action involving water resources in the Caatinga region should consider the uncertainty of the rainy season, which is defined more by its irregularity than by actual water scarcity; population growth; the need for increased food production; and the model of natural resource exploitation used. The population that inhabits this region requires water. Therefore, future challenges must involve a better understanding of the natural system and the associative management of water as a natural asset, viewing man's demand for water and fiber as an integral part of the natural system. This vision, together with integrated action, can widen the threshold of sustainability in dryland ecosystems.

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Chapter 11
People and Natural Resources in the Caatinga

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Abstract The interaction of people with the natural environment is ancient. Humans have great power to transform the natural environment and to interfere with the food chain and the processes that enable the renewal of populations of other species. The needs and demands for subsistence and economic growth convert natural systems to social-ecological systems. This chapter aims to highlight the findings of studies on the interactions of human populations with animal and plant resources in the Caatinga. In this type of ecosystem, seasonal and inter-annual variations in the rainfall pattern and the unpredictability of the total annual rainfall as well as the length of each season and the occurrence of interrupting events in the duration of each season in time and space have great influences on ecosystem functioning and the life dynamics of human populations. The collection of forest products and the hunting of wild animals of the Caatinga generate transformations in habitat conditions and often diversify the types of forest microhabitats. This ultimately affects not only the life cycle of resource use but also the dynamics of other species and over the medium- and long-term, the sustainability of human practices and the dynamics of the entire social-ecological system. Thus, we discuss the role of people in ecological processes and identify gaps that need to be filled for a change in perception and the integration of humans in ecological studies.

Keywords Ecological anthropology • Ethnobiology • Ethnobotany • Ethnoecology • Ethnozoology • Human ecology

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11.1 Introduction

The human population in the Caatinga is large (approximately 28.6 million people in 2010) and has a rich culture, but the region is unfortunately also home to many low-income inhabitants (earning between one and two times the minimum salary—or approximately US$300; IPEA 2010). The large number of people living in the region and their economic conditions force many local communities to use plant and animal resources to meet their needs (in terms of both subsistence and additional needs). This situation indicates that some Caatinga species are not only economically important but are also useful for the population (Figueroa et al. 2005; Ferraz et al. 2006; Ramos et al. 2008a, b; Monteiro et al. 2010).

Many Caatinga plant species have food (e.g., *umbu—Spondias tuberosa* Arruda; see Lins-Neto et al. 2010; Almeida et al. 2011), ornamental (e.g., *ipê-roxo—Tabebuia impetiginosa* [Mart. ex DC.] Standl.; see Barreto et al. 2005), or medicinal value (e.g., *aroeira—Myracrodruon urundeuva* Fr. All.; see Almeida et al. 2006; Monteiro et al. 2006a; Albuquerque et al. 2007, 2008; Melo et al. 2009; Monteiro et al. 2011a). In addition, Caatinga plants are used to feed livestock (several herbaceous plants, e.g., *Pavonia cancellata* [L.] Cav.; see Batista et al. 2005), in apiculture (several woody and herbaceous species, e.g., *Hyptis suaveolens* [L.] Poit.; see Santos et al. 2005), and as timber (e.g., *Caesalpinia pyramidalis* Tul.; see Figueroa et al. 2005). The timber may also be used in fences, for civil construction, and as firewood (Figueroa et al. 2006; Nascimento et al. 2007; Ramos and Albuquerque 2007; Santos et al. 2008; Nascimento et al. 2009).

The products derived from Caatinga plant species can be exploited and sold by people either directly (such as seeds, fruits, roots, bark, and leaves) or indirectly, after some processing (e.g., oils, potions, jewelry, cages, baskets, bags, wooden spoons, and ox carts). The diversity and intensity of plant resource use reflects the knowledge and the characteristics of the social structure of the local human communities that interact with the environment (Souza et al. 2008; Albuquerque et al. 2011a, b; Monteiro et al. 2011b). The number of studies carried out in the Caatinga has significantly increased since the beginning of this decade. Before then, studies were essentially descriptive, reflecting a common trend in Brazilian ethnobotany (e.g., Oliveira et al. 2009).

As with plants, people who live in the Caatinga have developed a strong relationship with domestic and wild animals. The exploitation of domestic animals, particularly cattle, goats, and sheep, was established during the occupation of the Caatinga by European settlers in the late sixteenth century (Ribeiro 1995; Ab'Saber 2003; Andrade 2005). Since then, livestock has been found in the Caatinga, representing one of the most important activities for the family farmers of the Brazilian semiarid region (Furtado 1967). The number of cattle, and especially that of sheep and goats, has grown in the region, and animals have become resistant to periodic droughts, but when prolonged, death is common in many of the herds, particularly cattle. From an ecological perspective, the livestock sector has been identified as a degradation factor for the vegetation of the Caatinga (Leal et al. 2005). Despite the negative effect of livestock, the raised animals are used in different ways by the local people, especially in supplying meat, milk, and eggs as well as serving as draft animals as a means of transporting people or cargo and in cultural festivals such as rodeos (Barboza et al. 2007; Souto et al. 2011a, b).

The exploitation of wildlife by hunting was practiced by the first inhabitants of the Caatinga (Melo 2004) and has continued over the years, despite changes in the laws associated with these activities, which have culminated in the prohibition of this activity in all of Brazil (Alves et al. 2009c). The Caatinga has a great richness of wild vertebrates when compared with other semiarid areas of the world, and these animals are used in different ways by the peoples of the region (see Chaps. 4, 5, 6, 7, and 8). Many of these vertebrates are caught by hunting and fishing, activities that have been described in recent ethnozoological studies conducted in the region (Alves et al. 2009a, 2012a; Barbosa et al. 2011; Fernandes-Ferreira et al. 2012; Melo et al. 2014). Such studies have resulted in at least 120 publications (scientific articles, books, and book chapters) and have revealed some patterns in the form of interactions between the local populations and various animal taxa.

The aim of this chapter is to discuss how people interact with Caatinga animal and plant resources. This chapter shows that the diversity and intensity of the use of plant and animal resources reflect the knowledge and characteristics of the social structure of local communities that interact with the environment.

11.2 How Do People Interact with Resources in the Caatinga?

Beyond the biological diversity and ecological processes, the Caatinga presents a great cultural richness due to its occupation by diverse ethnic groups, which are distributed throughout almost all regions. In a general sense, the ethnic groups may be divided into indigenous, *quilombola* (i.e., descendants of black slaves brought to Brazil from Africa during the colonial period who live in isolated communities in some regions), and rural communities.

Although being strongly disturbed by historical occupation processes and irrational use, the caatinga vegetation constitutes an important subsistence resource for these communities, which also collect products that are necessary to maintain and replicate their practices (see Albuquerque et al. 2007). The distinct ethnic groups explore the biological resources differently as a function of their social, cultural, economic, and/or ecological aspects (Silva and Andrade 1998; Sampaio 2002; Silva 2003; Albuquerque et al. 2005a, 2007, 2011a, b; Silva et al. 2006).

From the local communities' point of view, plants may play several roles, but the use of wood is the most commonly recorded (Albuquerque et al. 2009). Several studies have been conducted concerning the uses of native Caatinga species as wood, but relatively few systematic investigations have been performed. Initially, the main objective of such studies was to describe useful plants; from 2000 until now, the studies have tended to address the processes and patterns of use of those resources through the formulation of questions and specific hypothesis. In general, studies have focused on the role of plant species in medicine (Santoro et al. 2015), fodder (Ferraz et al. 2005, 2006; Nunes et al. 2015), rural construction (Lucena et al. 2007), as fuel (Ramos and Albuquerque 2012), and as food and medicine for people (Cruz et al. 2013, 2014; Albuquerque et al. 2007).

People use approximately 390 species of medicinal herbs and trees (see Albuquerque et al. 2007). Trees constitute the most important component in terms of biodiversity and use intensity (Albuquerque 2006). Although herb species richness is higher than that of trees, the local communities tend to mainly use herbs for animal feeding (Santos et al. 2009, 2014; Nunes et al. 2015). It is important to note that many herbaceous species are identified by the communities as having biological activity, which deserves pharmacological study (Silva et al. 2013; Almeida et al. 2011).

Nascimento et al. (2013) recorded approximately 170 species that are known as a food source for humans in the Caatinga, and 15% of them are native or spontaneous. Curiously, less than 10% of the native species (Nascimento et al. 2011) are cited as food for people (Cruz et al. 2013, 2014), most likely due to the absence of specific studies, their lack of importance, or even the interpretation by local people that eating these plants is a signal of poverty (Albuquerque 2006). It is important to note that many species have a higher nutritional value for humans when compared to plants that people eat more frequently (Nascimento et al. 2011). There are 17 species used that are considered as emergency foods (famine foods, i.e., consumed only in periods of low food availability), which take too much time to prepare and have a high carbohydrate concentration (Nascimento et al. 2012).

Beside the richness of useful species, only 65 species (mainly trees) seem to attract the attention of local human communities, and approximately 61% of them constitute a group of highly versatile plant species (Albuquerque et al. 2009). Albuquerque (2006) argues that this high versatility of Caatinga plants is typical in regions that exhibit lower biological diversity, and is a result of the development of strategies to address uncertainty (related to resource availability) and to optimize the natural resources that are available. These strategies have ecological implications, such as the pressure caused by use of tree species, mainly of the perennial organs, which are continuously available over time, which is referred to as the hypothesis of climate seasonality (Albuquerque 2006). This hypothesis also explains the lower extraction pressure on herbaceous species by local human communities.

These versatility nucleuses may eventually be found in almost all types of plant uses. This means that, in spite of the relative plant richness that is available for human use, people may concentrate their use on a reduced group of species. Therefore, functional redundancy is much more common within Caatinga plants, promoting a highly resilient social-ecological system because the plants that are not part of the more commonly used group may constitute resilience reserves (see Albuquerque and Oliveira 2007; Ferreira Júnior et al. 2012; Santoro et al. 2015).

This preference may be illustrated by the use of Caatinga plants as fuel. Approximately 60–70 species are known as being good for use as fuel, but fewer

Fig. 11.1 Some game mammals of the semiarid region of Brazil. (**a**) *Euphractus sexcinctus* (Linnaeus, 1758); (**b**) *Conepatus amazonicus* (Lichtenstein, 1838); (**c**) *Kerodon rupestris* (Wied, 1820); (**d**) *Tamandua tetradactyla* (Linnaeus, 1758) (Photo credits: (**a**) and (**c**) John Philip Medcraft; (**b**) and (**d**) Wedson Medeiros Silva Souto)

than 50% may be present in domestic storage, and approximately 10% are considered to be preferred because of their fuel qualities (Ramos et al. 2008a, b; Ramos and Albuquerque 2012). Undoubtedly, the demand for wood is one of the greatest pressures on Caatinga vegetation, and we know very little about the factors that drive the use and management dynamics of this resource by local communities. The availability of plants is related to their frequency of use (Ramos et al. 2015), suggesting that foraging behavior is oriented toward available resources, even when local preferences exist. However, strategies and decisions for resource collection are determined not only by the environment but also by socio-economic factors.

Regarding animals, hunting continues to occur in the Caatinga, and the people use animal resources in various ways, demonstrating the economic and cultural significance of local fauna to the people in this region. One of the most fundamental uses of game animals in this region is to meet nutritional needs (Fig. 11.1). The meat of wild animals constitutes an important protein source for several rural and urban communities (Alves et al. 2012a). These resources are even more important during seasonal drought periods, especially the more prolonged periods, when a good portion of the livestock herds dies from hunger and thirst (Alves et al. 2009a; Albuquerque et al. 2012a, b; Mendonça et al. 2016).

Following a common trend in various places where hunting occurs, mammals are the preferred targets of hunting (Alves et al. 2016a, b; Barboza et al. 2016; Mendonça et al. 2016). This is because medium- and large-sized wild mammals furnish greater quantities of meat, which is much desired by local residents (Alves et al. 2012a). However, human activities and the exploitation of natural resources in the Caatinga, including rapid deforestation, increasing urbanization, and the continued intensification of hunting, has led to instabilities in the population structure of game animals, mainly those of large size such as mammals (Barboza et al. 2016). As a consequence, the populations of several important vertebrate species seem to have declined (Albuquerque et al. 2012a, b; Alves et al. 2012a; Barboza et al. 2016), and many of the game mammals preferred by hunters no longer occur in the region (Alves et al. 2016a, b). This situation is attested to by older local hunters, who confirm the occurrence of species before they were hunted in the region and the current local extinction of many them in several locations, including medium- and large-sized species such as *Mazama gouazoubira* and *Cabassous tatouay* (Alves et al. 2016a).

With the decline of populations of large-sized species or their local extinction, the focus of hunters has moved to other species. Recent studies reveal that the game mammals that are currently most affected in the region are the six-banded armadillo (*Euphractus sexcinctus*), nine-banded armadillo, skunk (*Conepatus amazonicus*), and anteater (*Tamandua tetradactyla*) (Alves et al. 2016a; Barboza et al. 2016). In addition to these species, small-sized species with fast reproduction are still being hunted in high numbers, especially the Brazilian guinea pig (*Galea spixii*) and rock cavies (*Kerodon rupestris*) (Alves et al. 2016a, b). Although these latter species are small-sized, the large number of specimens that can be caught compensates for their small biomass.

Birds are the second group of preferred vertebrates that have been hunted in the Caatinga region (Fig. 11.2). In recent years, the hunting pressure on birds seems to have increased (Albuquerque et al. 2012a, b; Fernandes-Ferreira et al. 2012). This can be related to the population decline of preferred species (as discussed earlier), which places hunting pressure on smaller-sized mammals and other vertebrate groups that were previously less exploited (Alves et al. 2016a, b). This trend was observed by Mendonça et al. (2016) in a study on the annual consumption of wild animals by the families of hunters in the semiarid region of Paraiba (northeast Brazil). These authors recorded a higher consumption of birds than mammals but an equal biomass consumed for both. Even though there are fewer mammals than birds in the Caatinga, mammals have a larger biomass on average, meaning that despite the population decline of some mammalian species, the game importance of these two groups is equal.

Of the birds that occur in the Caatinga, species from the families Columbidae and Tinamidae are more often hunted for use as a protein source by the local people (Albuquerque et al. 2012a, b). Moreover, Anatidae and Cracidae have also been extensively hunted (Alves et al. 2009a; Bezerra et al. 2012a, b; Fernandes-Ferreira et al. 2012). The main bird species that are hunted are as follows: the columbids *Zenaida auriculata*, *Patagioenas picazuro*, *Claravis pretiosa*, *Columbina picui*, *C. minuta*, *C. squammata*, *C. talpacoti*, and *Leptotila verreauxi*; the tinamids *Nothura maculosa*, *Crypturellus tataupa*, and *C. parvirostris*; and the species *Penelope*

Fig. 11.2 Some bird game species in the semiarid region of Brazil. (**a**) *Dendrocygna viduata* (Linnaeus, 1766); (**b**) *Dendrocygna bicolor* (Vieillot, 1816); (**c**) *Nothura boraquira* (Spix, 1825); (**d**) *Penelope jacucaca* (Spix, 1825) (Photo credits: John Philip Medcraft)

jacucaca (Cracidae) and *Cariama cristata* (Cariamidae) (Fernandes-Ferreira et al. 2012; Alves et al. 2013a).

In addition to being relatively abundant, birds are more easily found and hunted than mammals (Bezerra et al. 2012b). They are captured by a variety of hunting techniques, including several non-selective traps (Alves et al. 2009a; Bezerra et al. 2012a, b; Fernandes-Ferreira et al. 2012), which are particularly used during drought periods, when birds typically aggregate in the vicinity of water bodies (Alves et al. 2009a; Bezerra et al. 2012a), thereby allowing the capture of a large number of specimens. The diversity of hunting techniques is not limited to birds and can be applied to mammals and reptiles. Techniques are chosen according to the target game species and the aim of its use. The most common are weapons, hunting dogs, and different kinds of traps (Alves et al. 2009a).

Few reptilian species ($n = 13$) have been recorded as food items in the semiarid region (Alves et al. 2012b). The lizard *Salvator merianae* is the main game reptile (Alves et al. 2009a, 2012b). Its meat is used as a source of protein by local populations (Marques and Guerreiro 2007; Alves et al. 2012b) and may be sold on a small scale in urban areas. Marques and Guerreiro (2007), for example, recorded the sale of meat of this lizard in public markets in the city of Feira de Santana, Bahia state. Other reptiles can also be eaten, such as the lizard *Iguana iguana* and snakes *Boa constrictor* and *Crotalus durissus*, although less frequently (Alves et al. 2012b). Amphibians are also rarely eaten in the Caatinga; the northeastern pepper frog (*Leptodactylus vastus*, Lutz 1930) is the only amphibian recorded as being used for food (Alves et al. 2012b; Mendonça et al. 2014).

Fishing is another important protein source for the inhabitants of the Brazilian semiarid region. However, the socio-economic importance of this activity has been decreasing in recent decades, reflecting the climatic instability that affects the region, with the occurrence of prolonged droughts that reduce the volume and quality of water stored in reservoirs in the region (Santos et al. 2016; Santos and Alves 2016). In addition to the water problem, native ichthyofauna in the semiarid region have been seriously reduced by the introduction of exotic species, habitat destruction, and the elimination of some native species by pesticides (Silva and Araújo 1996; Gurgel and Costa 1994; Rosa et al. 2003; Gurgel-Lourenço et al. 2013). Despite the climatic and ecological problems that affect the fish fauna of the Caatinga, fishing in this region has historical importance, particularly for populations that live around the large water reservoirs and rivers of the region, mainly the São Francisco and Parnaíba rivers (Santos and Alves 2016).

The importance of fishing for local peoples has decreased in recent years due to environmental degradation. The large rivers of the region, such as the São Francisco, have experienced profound changes in recent decades, leading to hydrological alterations and flooding of the territories of traditional populations, causing a decline in fish stocks (Santos et al. 2016; Santos and Alves 2016). Such factors have led to a situation in which fishing has less importance for these populations than in the past (Santos and Alves 2016), which is a clear example of how environmental degradation has affected the subsistence culture of local communities, and this is certainly occurring for other rivers of the region as well.

In addition to providing a source of food, animals are widely used in popular medicine and play a significant role in the healing practices of the Caatinga people (Alves 2009). The medicinal fauna of the region includes different taxa of vertebrates and invertebrates (Alves 2009). Among the latter, bees in particular supply different products for common medicinal use among the local people, especially honey, which is one of the most used animal products in the region and can be administered as pure honey from one plant species or from a combination of various plant species (Alves 2009; Alves et al. 2011). Other invertebrates (e.g., termites) are also used in popular local medicine, but vertebrates are mostly used for medicinal purposes, particularly fish, reptiles, and mammals (Alves 2009). Medicinal products are also used for the treatment of livestock diseases (Barboza et al. 2007; Confessor et al. 2009; Souto et al. 2011a, b, 2012).

Some vertebrate groups in the Caatinga that are not important as food, such as reptiles, have medicinal importance. While only four species of reptiles have been reported as a source of protein, at least 23 species of reptiles are known to be used in local popular medicine (Alves et al. 2012b). *Salvator merianae*, *C. durissus*, *I. iguana*, and *B. constrictor* are the most common reptile species to be used for medicinal purposes in the region (Alves et al. 2012b; Mendonça et al. 2014). In particular, *S. merianae* and *B. constrictor* have wide applicability in traditional Brazilian medicine (Ferreira et al. 2009a, b, 2011; Alves et al. 2012b). Recent works have investigated the use of the fat of these two species, and these studies have shown that these products may be effective in treating some illnesses (Ferreira et al. 2009b, 2011).

Mammals of the Caatinga also represent an important source of medicinal products. A recent review indicated that products derived from 39 mammal species are used for medicinal purposes (Alves et al. 2016a, b). These animals are hunted for their meat, and the non-edible components are used for other purposes. Birds and fishes are also used in the popular medicine of the region (Alves 2009; Bezerra et al. 2013), but the number of species is smaller than that of mammals and reptiles. In addition to their use in rural communities, products derived from these medicinal animals are also sold in public markets in many urban areas of this region (Almeida and Albuquerque 2002; Alves et al. 2008, 2009b, 2010a).

Another cultural practice that involves the fauna of the Caatinga is the use of wild vertebrates as pets (Alves et al. 2010b). Birds are the principal animal group exploited for this purpose in this region (Fig. 11.3) (Alves et al. 2010b, 2013a, b; Licarião et al. 2013). Bird-keeping is a widespread activity, not only in small cities and villages in the countryside but also in large urban centers in this region (Fernandes-Ferreira et al. 2012; Alves et al. 2013b), which has sustained a continuous illegal trade of birds in regional markets (Alves et al. 2013b) or even among the wild bird keepers themselves as a way of circumventing laws that prohibit such activities (Alves et al. 2013a). Some bird families (Emberizidae, Columbidae, Icteridae, and Psittacidae) in particular include the taxa of wild birds kept and traded as pets in the semiarid areas. Fernandes-Ferreira et al. (2012b), for example, reported that birds of the families Emberizidae and Icteridae represent 40% of the wild birds raised and sold in the countryside of Ceará. Similarly, Alves et al. (2010b) reported that birds in the families Emberizidae and Columbidae are those most commonly used as pets in Catolé do Rocha, a municipality in the Paraíba semiarid region.

There are many reasons for the observed preference for species in these families. Birds of the family Emberizidae, for instance, include species that have popular appeal due to their colorful plumage; they are also granivorous (being far easier to maintain in captivity) and small-sized (allowing a large number of them to be kept together in small cages) (Frisch 1981; Sick 1997). In the case of the Psittacidae, their beauty, docility, and ability to imitate human voices are characteristics that contribute to the popularity of this group of birds as pets. Generally, the choice of bird species that are kept as pets is influenced by interspecific (beauty of plumage and quality of song) and intraspecific factors (sex, as males are usually more valuable because they are better singers, and how long they have been domesticated, because domesticated birds sing more than recently captured birds) (Alves et al. 2013a, b; Bezerra et al. 2013; Fernandes-Ferreira et al. 2012; Licarião et al. 2013).

In addition to birds, some species of wild vertebrates belonging to other taxa may be used mainly as pets, especially the red-footed tortoise (*Chelonoidis carbonaria*) and common marmoset (*Callithrix jacchus*). The red-footed tortoise is an animal

Fig. 11.3 Examples of wild birds used as pets in the semiarid region of Brazil. (**a**) *Paroaria dominicana* (Linnaeus, 1758); (**b**) *Icterus jamacaii* (Gmelin, 1788); (**c**) *Sporophila albogularis* (Soix, 1825); (**d**) *Sicalis flaveola* (Linnaeus, 1766); (**e**) *Forpus xanthopterygius* (Spix 1824); (**f**) *Eupsittula cactorum* (Kuhl, 1820); (**g**) *Cyanocorox cyanopogon* (Wied, 1821); (**h**) *Turdus rufiventris* (Vieillot, 1818) (Photo credits: John Philip Medcraft)

that is relatively docile, easily captured, and easy to maintain in captivity. All of these characteristics make this species one of the most popular native reptiles kept as pets in the Caatinga region (Alves et al. 2012b), reflecting a situation that occurs across all of Brazil (Alves et al. 2012c). In addition, a popular belief that the presence of *C. carbonaria* helps ward off respiratory illnesses favors their use as pets (Alves 2009; Alves et al. 2012b). Marmoset monkeys are widely domesticated across their entire area of natural occurrence and are commonly kept as pets in the Caatinga region (Alves et al. 2016a, b). These monkeys are also illegally sold as pets in the region (Alves et al. 2016a, b).

Although they are more commonly used as food, popular medicines, and pets, Caatinga vertebrates may also be a source of products that are used for magic-religious purposes and as ornamental pieces (horns, hooves, eggs, and furs) (Alves et al. 2009a, 2012b, 2016a, b; Bezerra et al. 2012a, 2013; Fernandes-Ferreira et al. 2012; Barboza et al. 2016).

Conflicts between people and wildlife represent another important type of interaction between humans and fauna in the Caatinga (Fig. 11.4) (Alves et al. 2009a; Mendonça et al. 2011; Alves et al. 2012b; Mendonça et al. 2014). The reasons for conflicts include attacks on livestock, risks to human life, destruction of crops, and risk of disease transmission (Alves et al. 2009a; Mendonça et al. 2011). These conflicts mainly involve terrestrial vertebrates, including mammals (particularly carnivores), birds (granivores or falconiforms), and reptiles (particularly snakes) (Alves et al. 2009a, 2016a, b; Albuquerque et al. 2012a, b; Fernandes-Ferreira et al. 2013).

In relation to snakes, the local people are used to killing not only venomous but also non-venomous species and even those amphibians that have a similar body shape, such as amphisbaenians (Alves et al. 2014). Santos-Fita et al. (2010), for example, documented that all inhabitants of a semiarid area of Bahia state have strong negative reactions in relation to snakes, always killing them if possible. According to Alves et al. (2012b), the main reasons for the conflicts that lead to the killing of snakes include attacks on livestock and risk to human lives.

Such conflicts also include other vertebrate groups, including medium- and large-sized carnivorous mammals, such as *Leopardus tigrinus*, *Puma yagouaroundi*, *Puma concolor*, and *Cerdocyon thous*, which are killed because they prey on domestic animals (Alves et al. 2009a, 2016a, b). Rodents and some mammalian species of medium size that feed on crop products are also killed (Mendonça et al. 2011; Alves et al. 2016a). Some granivorous birds are hunted for this same reason. Falconiforms, which can attack livestock, especially calves, lambs, and goat kids, are also killed when possible.

11.3 The Role of Seasonality in the Use of Plant Resources

The choices people make concerning the use of plants in the Caatinga seem to be greatly conditioned, on a local scale, to plant responses to climatic seasonality; other variables such as the social structure and economy are also important

Fig. 11.4 Examples of vertebrate species involved in conflicting relationships in the semiarid region of Brazil. (**a**) *Puma yagouaroundi* (É. G. Saint-Hilaire, 1803); (**b**) *Cerdocyon thous* (Linnaeus, 1766); (**c**) *Caracara plancus* (Miller, 1777); (**d**) *Boa constrictor* Linnaeus, 1758 (Photo credits: (**a**), (**c**), and (**d**) John Philip Medcraft; (**b**) Alexandre Vasconcellos)

(Albuquerque 2006). On a regional scale, there is a correlation between rainfall and the total species richness; however, this correlation is not observed for useful species (Santos et al. 2008). These results indicate that the richness of useful species may be closely related to the total biodiversity, but not in a linear way.

Data show that preferred plants, or those that are the most commonly used, are those whose availability is not affected by the local seasonal pattern (Albuquerque and Andrade 2002a; Albuquerque et al. 2005b; Albuquerque 2006; Lucena et al. 2007, 2012), as was previously suggested. The spontaneous herbaceous layer is the most affected by severe drought conditions, when the populations drastically diminish in number. Therefore, there is a preference for shrub and arboreal plants, from which human populations mainly obtain wood (for several uses) and/or stem bark for uses in local medicine (Albuquerque et al. 2005b; Albuquerque 2006; Monteiro et al. 2006b; Silva et al. 2006). Generally, herbaceous species are of major importance only because of the necessity of feeding domestic animals during the rainy season, even though these plants are potential sources for human food and medicine.

An example of the preference for items that are available year-round is the use of stem bark from *Myracrodruon urundeuva* (*aroeira*, Anacardiaceae) and *Anadenanthera colubrina* (*angico*, Mimosaceae) as anti-inflammatory agents. Indeed, this bark has a high concentration of phenolic compounds, justifying its local use (Monteiro et al. 2006a, b). However, high concentrations of these substances have also been found in leaves during some periods of the year, sometimes with even higher values than those recorded for stems (Monteiro et al. 2006b). These data show that the continuous availability of bark may induce its preference by people independent of the fact that the phenolic concentrations of leaves are similar or even greater than those of bark.

In the set of plants used for medicinal purposes in the world, there is a predominance of exotic herbs and/or plants from managed habitats, a fact that led Voeks (2004) to suggest that traditional medicines are based on a disturbance regime. However, in contrast to what has been proposed by some authors (Stepp and Moerman 2001; Voeks 2004), this high richness does not necessarily imply people's preference for those plants. In the Caatinga, for example, people often prefer to use native plant species rather than spontaneous or cultivated plants (Albuquerque et al. 2005b). Similar results have also been recorded in other arid and semiarid areas of the world (Estomba et al. 2006).

The apparent low importance of herbs for the local communities of the Caatinga may also be explained by the quantity of available information concerning these plants or by the seasonal pattern discussed earlier. From a total of 624 herbaceous Caatinga species (Araújo et al. 2002; Silva 2005; Costa et al. 2007), at least 16% are cited by people as being useful in local medicine (Sales and Lima 1985; Agra 1996; Rocha and Agra 1996; Cabral and Agra 1998; Silva and Andrade 1998; Costa-Neto and Oliveira 2000; Albuquerque and Andrade 2002a, b; Almeida and Albuquerque 2002; Silva 2003; Marinho 2004; Trovão et al. 2004; Lucena 2005; Almeida et al. 2006). Moreover, at least 15% of these herbs are known as medicinal plants in other human communities in Brazil and around the world. Although these proportions seem to be impressive, it is necessary to consider whether these species are, in fact, used by people because knowledge about plant properties does not prove their use, as was noted by Albuquerque et al. (2005b) for a local community in the Caatinga. In this study, people knew many medicinal herb species with broad uses but preferred to use native tree species, even if they had to cover large distances to find them. This curious pattern described by Albuquerque et al. (2005a) suggests that there is an inverse relationship between collection and distance in relation to the resource sources that have been observed in many studies. Soldati and Albuquerque (2012), using *Anadenanthera colubrina* as a model, noticed that there was no relationship between extraction events and the distance from the main populations. Therefore, foragers seem not to optimize resource collection by selecting closer extraction sites.

If the climatic seasonality and ecogeographic conditions of a region regulate the relationships between people and plants, it is expected that their influence can be expressed in several ways. Gottlieb et al. (1996) suggest that, even if one considers local ecological processes, some sets of secondary metabolites are shared by plants that are ecogeographically related. Thus, a high level of plant phenolic compounds (polyphenols), for example, is expected to be produced in areas of high incidence of sun energy. Indeed, a study in the Caatinga corroborated this hypothesis. Almeida et al. (2005) studied a diversified sample of medicinal plants (including herbs, shrubs, and trees) and recorded that they all presented phenolic compounds. In an attempt to comprehend the choice criteria for the selection of plants by people, the authors investigated local preferences and the chemical composition of plants. They found that herbs (and other plants presenting short life cycles) are not more important for local medicine and do not present higher incidences of bioactive compounds of low molecular weight (e.g., alkaloids). These results indicate that cultural and ecological factors influence local strategies of plant selection and use by local people. The comprehension of these processes may contribute to the more rapid advance of studies related to the conservation and investigation of biodiversity (Albuquerque et al. 2012a, b).

During the process of the development of local medical systems based on the use of medicinal plants, local communities had to address the fact that the environment limits the incidence of certain classes of compounds. A possible strategy would be to include exotic plants in the Caatinga ecosystem and to offer frequent and careful management services. Indeed, exotic plant species are very common in the Caatinga pharmacopoeia, which led Albuquerque (2006) to formulate the diversification hypothesis. This hypothesis interprets the presence of such plants as being part of a conscious and active strategy to improve the chemical diversity of local pharmacopoeias. Some studies seem to corroborate this hypothesis (Alencar et al. 2010; Silva et al. 2015).

11.4 People and Ecological Processes in the Caatinga

Land use history and the manner in which people relate themselves with plant resources influence the ecological processes in the Caatinga. The establishment of pastures and the expansion of agriculture have been recognized by ecologists and biologists as disturbances that modify the structure and diversity of the ecosystem (Leal et al. 2005). Similarly, the proximity to cities and the construction of roads, for example, may predict the fragmentation and loss of habitats (Santos and Tabarelli 2002). Although Caatinga areas are subjected to all of these anthropogenic pressures, there is little information regarding the local processes of the interactions between people and the environment (especially animals and plants), which could be used as a basis for generalizations regarding human impacts on this important ecosystem. Broad-scale events overlap local events on a smaller scale, which are a result of human actions on specific resources and are not recorded or quantified. In

Amazonia, for example, some areas of 'primary' vegetation seem to be a result of manipulation by indigenous groups (Chazdon 2003). These data led us to believe that human impacts on tropical forests may be less apparent than previously thought and may have effects that are even less perceptible. Thus, it is necessary to abolish the idea of virgin or pristine forests and change the notions of climax and stability into a model of flux and dynamism (Chazdon 2003).

We believe that adopting this model and including the human role in the ecosystem (not only as a destroyer but as a niche constructor like other species) is a strong, very important, and necessary paradigm shift. Most of the time, people are selective in the resources and areas they forage. The fact that people interact with different natural resources, exhibit preferences for particular species, and carry out selective cutting and collection may generate even more unexpected effects upon the dynamic and ecological processes in plant communities that are not necessarily negative.

Selective plant cuttings, for example, may modify the survival and mortality rates of plant populations (Figueroa et al. 2006, 2008; Araújo and Albuquerque 2011), alter pollinator sharing (Araújo et al. 2007; Neves et al. 2011), or even affect neighboring populations with which they are ecologically related (López-Acosta et al. 2014; Andrade et al. 2015a, b). However, there are few studies that have evaluated these aspects in the Caatinga and which join the approaches used in plant ecological investigations (e.g., the investigation of population structure and dynamics) with those of resource use and management by people (e.g., ethnobotany). Although human actions on forests are always seen as destructive, local practices of plant use may constitute good models (see Florentino et al. 2007) to evaluate these complex resource interaction dynamics. Nascimento et al. (2009), for example, observed that the use of wood from native species for the construction of fences (for the delimitation of rural properties) can lead to pressures placed upon a particular species group. On the other hand, the practice of using native plants in live fences may function as a source of germplasm and diaspores of these species and connect landscape elements. The impacts of these actions in community dynamics are practically unknown.

People do not manage only individual species in the Caatinga; they create different landscape mosaics that serve different necessities. In addition to wood extraction (used for fuel, the ecological impacts of which are not well understood), people collect medicinal stem bark (for subsistence or commercial purposes) and fruits. We know, for example, that the extraction intensity and frequency of these barks vary among species and that their regeneration ability also varies as a function of particular features of species or the environment (rainfall, for instance; see Monteiro et al. 2010; Ferreira Júnior et al. 2012).

For several years, our group has been using a fruit tree species from the Caatinga as a model to understand the ecological and evolutionary effects of human activities on plants. *Spondias tuberose* (Anacardiaceae), locally known as *umbu*, has high economic and cultural importance in the Caatinga. It is considered to be a sacred tree (Lins Neto et al. 2010), most likely because it produces flowers and fruits during the dry season, providing food for animals and people during a period of very low resource availability. The *umbu* trees are maintained in disturbed areas, even when other tree species are excluded. People search for its fruits in different areas based on their flavor, size, and amount of pulp (Lins Neto et al. 2010). Additionally, we have recorded morphological variation among *S. tuberosa* populations subjected to different forms of landscape management, and we found that local communities have been contributing to the maintenance of this phenotypic diversity (Lins Neto et al. 2012). We confirmed the relationship between genetic diversity maintenance and landscape management practices, and we concluded that this plant species is experiencing an incipient domestication process (Lins Neto et al. 2013a).

No variation in plant phenology was observed in *umbu* populations subjected to different landscape management methods (Lins Neto et al. 2013b), although it is possible that some species of the Caatinga exhibit temporal displacement of their phenological events in anthropogenically impacted areas that have suffered clear cutting for use in agriculture, modifying the time of occurrence of seed rain to the renewal of the soil seed bank (Souza et al. 2014). However, the native pollinator guild may differ among *umbu* (*S. tuberosa*) populations, and native pollinators may sometimes be replaced by exotic species without apparent consequences to its short-term reproductive success (Almeida et al. 2011).

In addition to causing changes in landscapes and promoting the incipient domestication of species of high interest in the Caatinga, land use and the interaction between humans and vegetation resources induce changes in the conditions under which plants establish in each habitat. Such changes may result in the emergence of new microhabitats, with light, temperatures, and wind speeds that differ from those of the original microhabitats (Andrade 2016). These new abiotic conditions interfere with the metabolism and growth of plants, the renewal dynamics of populations, and the ecological processes involved in the maintenance and operation of the ecosystem.

Soils of open areas experience higher temperatures and dry faster in the dry season, which leads to an increase in the respiration rate of plant roots (Shi et al. 2011). Seed germination and the growth and establishment of plants require species to have the ability to adjust to new conditions created by human activity. Seeds that need light to germinate are favored, and the opposite occurs for those that require more shading. However, after germination, growth is limited more quickly due to water restriction, which is the main factor that affects the dynamics and ecological processes of the Caatinga (Andrade et al. 2012), but this also occurs in other dry environments (Augustine 2010).

Over the successional process of open areas of the Caatinga after their use has been abandoned, it is often possible to note differences in the species diversity of the new forest that is established or in the diversity of species that are stored in the soil seed banks (Lopes et al. 2012; Mendes et al. 2015). There is also an absence of some species that occurred in the forest prior to human intervention and the presence of many other species that were not previously recorded (Souza et al. 2014), indicating that the interaction between man and the forests can also lead to increased diversity. The absence of certain species considered late successional possibly occurs due to physiological constraints imposed by the new conditions (light, temperature, humidity, and wind speed) of the microhabitat combined with low a frequency or even lack of such species in the seed rain that renews the seed stock stored in the soil seed banks.

With the advancement of the successional process, it is expected that microclimate conditions are re-established and late species return to become established, but the time necessary for this to occur is unknown. For example, in Caruaru, Pernambuco, monitoring Caatinga areas subjected to a single human intervention, or the use of land for agriculture through manual clear-cutting without the use of fires or pesticides and maintained at least ten meters away from the original Caatinga forest, showed that 21 years after abandonment, the effects of human intervention could still be seen in the floristic composition (Lopes et al. 2012), seed rain and phenology (Souza et al. 2014), soil seed bank dynamics (Mendes et al. 2015), and the renewal of woody and herbaceous populations (Andrade et al. 2015a, b; Andrade 2016). Long-term studies monitoring the regeneration of the Caatinga with other histories of use but with a single episode of human action are non-existent. However, the results of studies comparing anthropogenically impacted areas of different ages or subjected to more than one episode of anthropogenic intervention also show differences in the composition and structure of the new forest and the ecophysiological behavior of plants (Fabricante et al. 2012; Falcão et al. 2015), which leads us to expect greater complexity in forest resilience in areas with multiple histories of use and with a greater frequency and intensity of disturbance (Andrade et al. 2003; Ribeiro et al. 2015).

11.5 Integrating Humans in Ecological Studies

There are several fields of study that investigate the relationships between people and nature using different theoretical perspectives. The most important fields are most likely human ecology, ethnobiology (especially ethnobotany), and ethnoecology. Although most studies are descriptive, there is a growing tendency for studies to attempt to comprehend the relationships between people and nature (see Albuquerque et al. 2015; Albuquerque and Alves 2016).

Such studies have a strong relationship with plant population ecology because both are concerned with sustainable development, which should be guided by a balanced view of conservation. A frequently asked research question with respect to the sustainability of resource use is, “How much can we take from a resource while still ensuring that it can be renewed naturally by the growth and reproduction of its population?” Unfortunately, in northeast Brazil (as in other parts of the world), plant resource use and conservation are moving in opposite directions. Today, there are two important questions that we seek to answer: “How can we manage a given resource without threatening the well-being and quality of life of the people who use it?” and “How can we restore a resource that has already been lost?”

In management and restoration, it is necessary to identify the limiting factors for population growth. These factors can be grouped into at least four levels. The first three levels are the absence of seed production; the absence of seed germination;

and the absence of growth of seedlings and saplings. Problems surrounding the absence of seed production may be due to insufficient pollination, inbreeding (which leads to the formation of unviable seeds), excessive predation, climatic and edaphic stresses (which affect plant reproduction and seed production), and disease. The absence of germination may be due to the lack of dispersers, an unsuitable environment for germination, excessive predation or disease. The growth of seedlings and saplings may be inhibited by elevated competition for some limiting resource, an inadequate environment for growth, excess predation, climatic or physical stresses, or disease. Finally, the fourth level is that the extraction of resources beyond the self-renewing capacity of plant populations may also limit population growth. Obviously, this last aspect may also be influenced by the other factors mentioned.

How can the incorporation of human behavior data contribute to ecological studies? Such approaches can enable the identification of useful species in a region (and those with future potential uses) (Lucena et al. 2007; Cartaxo et al. 2010; Albuquerque et al. 2011a, b), determine how local communities use each species (Lucena et al. 2008; Almeida et al. 2010), identify preferred sites for resource collection, characterize the ways in which a resource is exploited (Albuquerque and Andrade 2002c; Albuquerque et al. 2005a), reveal the intensity of resource exploitation (Albuquerque et al. 2007; Monteiro et al. 2010), identify alternative management strategies from the perspective of local communities (Florentino et al. 2007; Nascimento et al. 2009), identify conservation priorities (Oliveira et al. 2007; Melo et al. 2009; Albuquerque et al. 2009), identify demands that should be addressed through public policies (Florentino et al. 2007; Nascimento et al. 2009), and demonstrate the awareness of population and socio-environmental conflicts arising from the establishment of conservation measures (Andrade et al. 2015a, b).

For example, let us consider the use of plants as timber, which is common in northeast Brazil. This type of use is generally destructive and therefore causes a substantial impact on the dynamics of the native population that is exploited (Ramos et al. 2008a, b). We know that timber in the northeast is used and/or sold as firewood, charcoal, and materials for building houses and other objects (Figueroa et al. 2005). The questions that must be addressed regarding the management of plant resources include “Which species are used for each purpose?”, “How are plants collected?”, “How much is collected?”, “What factors affect or determine the collection of a certain plant?”, “Can a plant survive the cutting process?”, and “In a seasonal environment such as the Caatinga, are certain times more favorable for cutting?”

In addition, destructive methods employed in resource collection promote deforestation. As a resource becomes scarce, people search for it in other areas, causing increasing habitat fragmentation and converting the few remaining patches of native vegetation into islands within anthropogenic landscapes. As previously discussed, such a scenario also inevitably causes changes in microhabitats from the edge to the interior of these fragments. At the edge, there is greater light intensity, temperature, and air flow as well as lower humidity. These differences influence the establishment and maintenance of species populations.

Species occurring at the forest edge must tolerate, or at least adapt to, these harsh conditions. An increase in climbing plants is common. These plants affect the growth of woody plants by using them as supports and breaking their branches (Araújo 2005; Araújo et al. 2005). In addition, the forest edge is highly vulnerable to invasion by exotic and ruderal species, increasing the risk of competitive displacement of native species (Andrade and Fabricante 2009). It has also been reported that natural enemies or stronger competitors frequently do not affect these exotic species, likely increasing the probability of invasion (Andrade et al. 2009, 2010). Furthermore, the role of useful exotic and ruderal plants in human communities is poorly understood (Santos et al. 2009).

Exotic species can also carry diseases not experienced previously by native species (Primack and Rodrigues 2001), increasing the mortality rates of native organisms and reducing their population sizes. Thus, deforestation associated with changes in habitat causes the following problems for native plant communities: loss of genetic variability and evolutionary flexibility, an increased risk of local extinction, limited potential for dispersal and colonization, and a decrease in resources for animals as well as for people (Araújo et al. 2007).

Depending on the population size of the exploited plants and the intensity of exploitation, the resource may become increasingly scarce, or even locally extinct, inevitably affecting the people who use it. This scenario occurs because the exploited population becomes unviable when it is reduced to a critical size. Conservation biologists have discussed the need to maintain a minimum population size in natural habitats (termed the minimum viable population [MVP]). This parameter is "the smallest size at which an isolated population has a 99% chance to continue to exist for 1,000 years" (Primack and Rodrigues 2001).

Ethnobotanical studies have addressed some of these questions. For example, the survival of plants after cutting and the effects of the cutting season have been studied by researchers from the Plants of the Northeast (PNE) association in partnership with the Kew Royal Botanic Gardens (London, UK). Figueroa et al. (2006) selected four Caatinga species, *Caesalpinia pyramidalis* Tul. (catingueira), *Mimosa tenuiflora* (Willd.) Poir (jurema-preta), *Mimosa ophthalmocentra* Mart. ex Benth. (jurema-branca), and *Croton sonderianus* Muell. Arg. (marmeleiro), for an experiment replicating the types of cutting methods used by local communities in the dry and wet seasons, including coppicing, pollarding, and crown thinning. The authors aimed to evaluate the effects of these cutting treatments on the survival of these species and found that some species demonstrate reduced survival if they are cut during the rainy season; this reduced survival was evident for jurema-branca and jurema-preta (*M. tenuiflora* and *M. ophthalmocentra*, respectively), which showed higher survival rates after coppicing in the dry season. Regardless of the type of cut, all four species showed the capacity to regrow, especially when subjected to coppicing. Regrowth is important for the habitat restoration of anthropogenically affected areas (Sampaio et al. 1998; Figueroa et al. 2008), a fact that has been confirmed in other dry environments around the world (Negreros-Castillo and Hall 2000; McLaren and McDonald 2003; Luoga et al. 2004; Tewari et al. 2004). This type of information will allow for better planning for the use of vegetation as firewood.

Another practice adopted by the community and one that ethnobotany has shown to be helpful in conservation is the cultivation of home gardens. Home gardens are an agricultural unit with the primary purpose of providing food to supplement a family's diet (Albuquerque et al. 2005a). However, Florentino et al. (2007) showed that home gardens have other uses in addition to food production because they can also provide shade and plants with medicinal, ornamental, and timber uses. Home gardens are generally comprised of exotic and native plants, the latter of which are obtained from fragments of native vegetation near the community. The authors demonstrated that home gardens are important for biodiversity conservation because they reduce the use of destructive methods for the collection of plant products from the remaining native fragments. This reduction is because some native species such as *Piptadenia stipulacea* (Benth) Ducke (calumbi) and *Acacia paniculata* Willd. (unha-de-gato) are maintained in home gardens for use as firewood.

Conservation measures regulating the collection of specific resources from the Caatinga have often been established in response to the pressures of use suffered by resources without previous studies on their sustainability and/or renewal. Such measures usually end up causing dissatisfaction and local conflicts by prohibiting or limiting people's access to the resources used. Consequently, people who make direct or indirect use of such resources or their associated habitats can develop negative attitudes regarding these conservation measures. For example, in the region of Raso da Catarina, Bahia, the licuri palm (*Syagrus coronata*) is used for different purposes, and the collection of its leaves is regulated by Brazilian Institute of the Environment (IBAMA), which allows the collection of only three leaves per plant per year. It is believed that a larger collection reduces the production of fruit, which is the main food item of an endemic bird threatened with extinction, Lear's macaw (*Anodorhynchus leari*). From the viewpoint of artisans using only licuri leavesto make handicrafts, this measure is negative because it forces them to have to collect over a larger area when they believe that the plant can support a larger collection pressure (Andrade et al. 2015a, b). The negative effect of conservation measures has also been recorded in other regions of the world (Karanth and Nepal 2012). Thus, the perception of people cannot be neglected because it ends up generating unfavorable conservation attitudes.

11.6 Final Remarks

Over the past 15 years, we have accumulated a considerable amount of information regarding the interactions between people and the natural resources of the Caatinga. We have progressed in the composition of useful plant lists, but data on the processes that shape the relationships between people and such natural resources are lacking. This is a limiting factor for the improvement of a scientific approach that considers people as a part of the environment rather than only as the main originator of disturbance.

All forms of interactions between the fauna/flora and inhabitants of the Caatinga need to be better investigated, particularly considering their importance in the development of management and conservation plans. In addition to the scarcity of ethnobiological studies concerning important animal groups, there are gaps in our knowledge that need to be filled from a geographical point of view because, even in the states for which a greater number of studies have been performed, these studies are limited to two or three cities and then to the same community within these cities.

Habitat management and conservation are undoubtedly scientific issues closely related to the challenges discussed in this chapter. However, conservation measures that do not consider their effects on the relationship between people and the environment can turn people against them. The perception and sentiments of people regarding such measures need to be determined, aimed at proposing strategies that minimize socio-environmental conflicts and making local populations partners in the implementation of projects or conservation measures. Currently, the number of demographic studies focusing on species that face high exploitation pressures in the Caatinga is small, despite their importance for the establishment of resource management efforts and the identification of strategies that promote habitat conservation. This gap occurs because demographic studies require long monitoring periods. To comprehend the current ecology of the Caatinga based on all processes that generate, maintain, and affect its biodiversity (including people) is also a challenge but is crucial for the modeling of future scenarios for the Caatinga ecosystem.

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Chapter 12
Cultural Services in the Caatinga

Chiara Bragagnolo, Felipe A.S. Vieira, Ricardo A. Correia, Ana Claudia M. Malhado, and Richard J. Ladle

Abstract Cultural ecosystem services (CES) are "non-material benefits people obtain from ecosystems". These benefits include *recreation*, *aesthetic enjoyment*, and *spiritual fulfillment* arising from the interaction between cultural and natural features. In this chapter, we describe the role of the Caatinga—a unique semiarid region located in northeast Brazil—as a source of cultural inspiration, recreation, knowledge, and spiritual significance. Firstly, we define and discuss the current conception of CES, exploring available approaches to measure them. Secondly, we reframe the Caatinga as a biocultural environment, created and maintained by the dynamic interactions between human communities and the landscape. We then identify and discuss the CES provided by the Caatinga, by combining a review of key literature and a novel big data approach based on content analysis of geo-referenced digital photographs. Finally, we critically evaluate the current state of knowledge about CES in the Caatinga, recommending multiple approaches to assess and quantify cultural values. Studies of CES in the Caatinga are only just beginning, but are critically important to demonstrate the enormous contribution of this unique environment to local cultures and the regional economy in the face of increasing land-use competition.

Keywords Cultural ecosystem services • Caatinga • Big data • Social well-being • Protected areas • Cultural heritage • Aesthetic value • Culturomics • *Sertão* • Brazil

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12.1 Introduction

In the Western world view, dryland and desert ecosystems are typically thought of as remote and inhospitable—desolate areas that are generally unsuitable for human habitation. This popular perception is, of course, far from reality. Hyperarid and semiarid ecosystems cover almost one-third of the earth's land area and hold one-fifth of the human population (Welland 2014). The semiarid region of northeast Brazil follows this general trend: covering approximately 735,000 km^2, it contains nearly 27 million inhabitants at average densities of 20–30 people/km^2 (Gariglio et al. 2010). Much of this population is engaged in small-scale agriculture and low-intensity exploitation of natural resources and is therefore highly dependent on a wide variety of supporting, provisioning, and regulating ecosystem services.

Perhaps less appreciated is the role of the Caatinga[1] as a source of cultural inspiration, recreation, knowledge, and spiritual significance for both local inhabitants and the many visitors that are drawn to this biologically and culturally unique region. These socially important attributes represent cultural ecosystem services (CESs) and are the subject of this chapter, which is divided into four main sections. The first section defines CESs and discusses how they can be measured. The second section describes the Caatinga as a biocultural environment, with meanings and values derived from the history of interaction between human communities and the landscape. The third section identifies and discusses the CESs provided by the Caatinga, using a combination of published studies and big data approaches. The chapter concludes with a critical evaluation of the current state of knowledge about CESs in the Caatinga and the prospects for future research in this area.

12.2 Cultural Ecosystem Services: Definition and Measurement

12.2.1 Definition

CESs have been defined as "non-material benefits people obtain from ecosystems such as recreation, aesthetic enjoyment, and spiritual fulfillment" (MEA 2005a). These attributes have been divided into six broad categories: (1) aesthetic value, (2) recreation, (3) religious and spiritual value, (4) cultural heritage and identity, (5) inspiration, and (6) research and education (MEA 2005a). The underlying rationale is that ecosystems provide locations and opportunities to enhance both individual and social well-being by improving mental health, enhancing a *sense of place*, enriching

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[1] The term 'Caatinga' (a Tupi word for 'white forest') has been variously used to refer to a biome, an ecosystem, a habitat type, and the semiarid climatic region of northeast Brazil. In this chapter we intentionally adopt a broad definition to incorporate human interactions with the biophysical environment in northeast landscapes that contain mixtures of native tropical dry forest, modified habitats, and other vegetation types (e.g., *brejos*).

knowledge systems (traditional and formal), developing social capital, feeding spiritual and religious growth, and providing inspiration for arts and sciences.

Unlike the other categories of ecosystem services, CESs cannot be measured easily in purely economic terms. Rather, their value is related to their contribution to the physical and mental health of individuals, improving quality of life and facilitating self-actualization (MEA 2005c). Such effects arguably have an indirect economic impact in terms of reduced use of health services and increased economic productivity (e.g., increased tourism demand) (Seidl 2014; TEEB 2010). Many studies have demonstrated the importance of contact with nature for health and social relations (Burls 2007; Pröbstl-Haider 2015; Romagosa et al. 2015). Conversely, cutting the cultural ties that bind people to ecosystems often leads to the loss of cultural identity and decreases opportunities to enjoy natural and cultural landscapes (Groot et al. 2005; Soga and Gaston 2016). The loss of traditional knowledge systems can also have negative effects on human health (e.g., through reduced use of medicinal plants) and on landscape and natural resource management. This may particularly be the case in dryland ecosystems where cultural identity, heritage, and traditional knowledge have been profoundly shaped by the challenging climatic conditions (Safriel and Adeel 2005).

Drylands have also been a source of inspiration for scientific studies, enlarging our knowledge of paleo-environments (e.g., Oliveira et al. 1999), biological adaptations to extreme environmental stresses (e.g., Santos et al. 2014), and ecology of arid and semiarid regions (e.g., Rocha et al. 2004), among others. They have also inspired great literature and epic histories (from the *Bible* to Paulo Coelho's modern masterpiece *The Alchemist*), as well as providing the backdrop to classic films (e.g., *Lawrence of Arabia*, *The Living Desert*). More broadly, arid regions are often the loci for spiritual elevation (especially in Abrahamic religions), with the extreme conditions frequently providing the context for intense religious experiences (Jesus's 40 days and nights in the Judaean desert, Moses leading the Israelites through the Desert of Paran on the border of Canaan, etc.). More generally, groves and tree species frequently have spiritual significance to dryland peoples because of their relative rarity, high visibility in the landscape, and ability to provide shade. Finally, drylands are increasingly becoming places for cultural tourism (e.g., historical and religious sites) and ecotourism (e.g., safari tours) (Picon-Lefèbvre and Chaouni 2011).

12.2.2 Measurement

Despite the importance and ubiquity of CES, quantifying their (monetary and non-monetary) value and assessing the potential impacts of their loss remains challenging (MEA 2005a). Perhaps the best established approach is estimating utilitarian value through contingent valuation techniques (Hernández-Morcillo et al. 2013), especially through the assessment of 'willingness to pay' or 'willingness to accept' (compensation) (Hanemann 1991; Farber et al. 2002). However, methodologies based on assessment of monetary value are often unsuitable for CES, because markets do not always exist for services with a non-utilitarian values such as spiritual fulfillment, cultural identity, etc. (MEA 2005b; Milcu et al. 2013). Consequently, quantitative valuation of CES has often been limited to attributes with clear financial components such as recreation, tourism (Jim and Chen 2006; Barrena et al. 2014) and, more recently, artistic expressions (Coscieme 2015).

An alternative approach is to assess how people and societies perceive the different benefits associated with CES. Such social/psychological approaches are typically based on deliberative methods (i.e., semi-structured questionnaires, stakeholder interviews, and participatory techniques) and have been increasingly adopted to assess non-utilitarian CES such as national/regional identity and *sense of place* (Asah et al. 2014; Bieling 2014).

Social survey-based approaches to CES assessment are widely used, flexible, and often result in quantitative metrics, some of which relate to financial value. However, they are costly to design and implement, lack standardization (Bragagnolo et al. 2016), and are geographically restricted. This makes scaling up, mapping, and comparison of CES studies highly problematic. One potential solution is through the association of quantitative/qualitative indicators with land-use properties, potentially allowing the visualization of different services at a variety of spatial scales (Plieninger et al. 2013; Paracchini et al. 2014).

An alternative approach is to utilize the increasing reach of the internet for large-scale (e.g., regional/national/global) analysis of CES. Such methods adopt a big data methodology, inferring human interest and sentiment towards the environment from the digital representation of words and images. The formal study of human culture through the analysis of changes in word frequencies in large bodies of texts (*corpora*) is known as culturomics (Michel et al. 2011) and research in this area has recently exploded due to the rapid spread of digital media and the digitization of a significant proportion of the world's historical written resources. Culturomic approaches are increasing being applied to conservation challenges (reviewed in Ladle et al. 2016), including the assessment of CES. For example, the relative internet representation (a proxy of cultural interest) of species can be calculated (using automatically retrieved data) and converted into maps of cultural value based on the species assemblage at any given location (Ladle et al. 2016). Such maps have the power to reveal the cultural 'hotspots' (and cold spots) of interest in species: places that contain high frequencies of culturally important animals and plants.

Closely related to culturomics is the analysis of digital photos posted on file-sharing sites such as Flickr®, social networks such as Facebook, and microblogging platforms such as Twitter. Many of these photos have been taken with smart phones and contain geographic data from the phone's global positioning system (GPS) function, potentially allowing researchers to map human interactions with nature at finer spatial resolutions (Richards and Friess 2015). As with culturomics, there are still many technical challenges to overcome, the most problematic aspects being how to automatize the collection of data and systematically analyze/classify image content. The increasing sophistication of machine learning tools suggests that this may eventually be overcome (Sonka et al. 1993), opening the way for large-scale analysis of human interactions with nature. For now, such studies are still performed at small spatial scales (e.g., within a protected area) and heavily rely on human interpretation of images.

12.3 The Caatinga as a Biocultural Environment

The relationship between human culture and the natural environment is mutual and dynamic. While human societies and their value systems have developed in relation to the landscapes they encountered, they have also shaped and influenced these same landscapes (MEA 2005a). Accordingly, most ecosystems are biocultural environments that are the product of the spatial and temporal interactions between cultures and landscapes, influencing social interactions, knowledge systems and intellectual development, heritage values, artistic and spiritual fulfillment, among others (Groot et al. 2005).

Thus, one of the main differences between CES and other ecosystem services is that the benefits are highly dependent on cultural context and value is therefore a strictly relational property. For example, topographically complex landscapes are often associated with scenic beauty, which is both aesthetically appealing and, for some people, spiritually fulfilling. Such attitudes now seem to be almost universal in western societies, although this was not always the case. Indeed, pre-industrial Europeans considered mountain regions as ugly and dangerous before the pervading cultural influence of the late eighteenth-century Romanticism movement (Nicolson 1997).

It should also be noted that many of the most appreciated conservation landscapes have been heavily influenced by humans (e.g., the English Lake District) and important components of CES, such as spiritual meaning, only emerge through a long history of human interaction with the surrounding landscape. Thus, to demonstrate the cultural value of the Caatinga to its inhabitants and to national/international visitors, it is necessary to know something of the (i) biophysical attributes of the landscape; (ii) history of human interactions with the natural environment; and (iii) current cultural context.

12.3.1 The Biophysical Environment

Sitting in a flattened depression, the Caatinga is a large semiarid region in northeast Brazil with a climate suitable for tropical dry forest. The geomorphology and soil chemistry is largely a consequence of a surface layer of cretaceous sandstone that sits on a basement of Pre-Cambrian crystalline rock (Ab'Sáber 1977). The natural landscape consists of a mosaic of seasonally dry tropical forest and xerophytic, deciduous, semiarid thorn-scrub (Leal et al. 2005; Pennington et al. 2009; Chap. 2), much of which has been highly modified due to the effects of grazing, firewood collection, exploitation of non-timber forest products, and small-scale agriculture (Leal et al. 2005; Santos et al. 2011; Ribeiro et al. 2015; Chaps. 13 and 14). Open scrub forest is probably the most frequently encountered vegetation type in the contemporary landscape and the tall Caatinga forests that probably predominated in pre-Colombian times are now scarce and fragmented (Sampaio 1995; Prado 2003; MMA 2007).

The Caatinga's climate exerts an enormous influence on both the landscape and the people that live within it (Redo et al. 2013). Climate variability is high, with frequent droughts of more than 11 months (Ab'Sáber 1977). Even in climatically typical years most of the rainfall (50–70%) is concentrated in three consecutive months, with the frequency of dry months increasing from the periphery to the center (Prado 2003). Many of the taller trees only produce leaves and flowers during this short wet season and for the rest of the year the landscape can appear leafless and almost lifeless. Some predictions indicate that anthropogenic climate change will increase the frequency and intensity of droughts in the Caatinga (Salazar et al. 2007), expanding areas of desertification (Vieira et al. 2015) and negatively affecting local livelihoods (Novaes et al. 2013). The increasingly marginal economics of cattle farming under such uncertain climatic conditions is leading to high levels of land abandonment, further altering the appearance of landscape.

In addition to the thorn-scrub and tall dry forests, there are also small patches of humid forests known as *brejos* that can be found on the windward slopes of raised sandstone plateaus (*chapadas*) and the higher mountain ranges (>500 m) that receive >1200 mm of rainfall (Prado 2003). More than 30 *brejos* are known, all of which contain unique floras with close affinities to both Atlantic Forest and Amazon floras (Andrade-Lima 1981; Santos et al. 2007).

12.3.2 History of Human Interactions with the Caatinga

Current research indicates that human impacts in the Caatinga may date back more than 25,000 years, when the first hunter-gatherers are thought to have penetrated the region (Heredia 1994). Those first humans would have found an ecosystem almost unrecognizable from that of today, replete with a diverse megafauna of giant sloths, wild horses, and giant armadillos (Gallo et al. 2013). It is still unclear whether humans played a direct role in the rapid demise of these enormous animals, although there is fossil evidence that some species, such as the giant ground sloth *Eremotherium laurillardi*, were eaten (Dantas et al. 2014). Nevertheless, on the basis of the stone tools associated with archeological sites it is unlikely that these early peoples of the Caatinga region engaged in the systematic hunting of the megafauna (Heredia 1994).

It is important to note that the climate experienced by these early inhabitants of the Caatinga was probably considerably more humid than that of today; prevailing semiarid conditions began to form about 10,000 years ago (Ab'Sáber 1977). There is abundant archeological evidence of hunter-gatherer societies throughout the present-day Caatinga region (reviewed in Martin 2008). Even at low densities, these early societies are likely to have significantly influenced the abundance and distribution of food species. As might be anticipated, the richest evidence for ancient human occupation of the Caatinga comes from the *brejos* (Prado 2003).

After the arrival of Europeans in 1500, the Caatinga was increasingly converted into pasture. The first cows were imported from the Cape Verde Islands and had to become adapted to semiarid conditions. The animals were initially allowed to roam free across enormous areas which were progressively converted into farms. Post-colonial establishment was through a *latifúndio* system based on a mutual dependence between larger-scale land barons and small-scale subsistence farmers. The vertex of this organization was occupied by the Portuguese Crown which, as the founding landowner, provided large plots (*sesmarias*) to favored nobles. The nobility typically placed their animals under the management of wranglers/stockmen (*vaqueiros*) who were often paid in animals or primary goods such as salt, encouraging them to raise their own livestock and colonize unoccupied areas of the semiarid backlands. The backlands were also colonized by escaped African slaves from the extensive sugar cane farms along the Atlantic coast. These diverse ethnic groups mixed extensively with indigenous peoples to create the typical phenotype of the Brazilian dryland people: short of stature, slim, and dark-skinned (Nozoe 2006; Ribeiro 2013; Matta Machado 2017).

Water scarcity and droughts have been a recurrent constraint on the development and progress of the Caatinga region, periodically forcing poorer people to migrate in search of better conditions. Since the late nineteenth century, droughts in northeastern Brazil have been a national issue, often requiring government intervention. However, since the *latifúndio* system inevitably led to a society based on clientelism (a social order based on patronage of a major land owner, locally known as the *Corenel*), government actions were often poorly implemented and subject to extensive corruption, establishing a 'drought industry' that diverted money to favored places and people (Ribeiro 2013).

12.3.3 Current Cultural Context

The present-day Caatinga is a densely populated region containing approximately 27 million inhabitants (Gariglio et al. 2010). There is high cultural and ethnic diversity, including the scattered remnants of the original indigenous Amerindian populations. At the turn of the century it was estimated that about 20,000 ethnic Amerindians lived in northeast Brazil, distributed among approximately 35 ethnic groups (Athias and Machado 2001). There are also communities known as *Quilombolas* that are mainly composed of the descendants of escaped slaves. However, the largest group of rural residents is of mixed ethnic origin, often claiming ancestry from Amerindian, African, and European forebears.

In 2007 the Brazilian semiarid region[2] contributed about 12% to the national gross domestic product (GDP), and in 2008 the regional GDP per capita was about three times less than the national average (MMA 2010; Buainain and Garcia 2013). The regional economy is still based on agriculture and livestock, with more than 30 million head (about 50% of which are cattle) (IBGE 2006). Rural areas in the Caatinga are divided between big landowners and small-scale farmers (often tenants), who respectively contribute 14% and 31% of the agricultural production of the region (Gariglio et al. 2010).

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[2] Geographically delimitated on climatic criteria and used as a basis for structural funds supporting rural development and drought relief.

The Caatinga region remains one of the least developed areas of Brazil. In 2007, 52% of Brazilian illiterates were concentrated in northeastern Brazil (MMA 2010), and in 2010 it was estimated that the average monthly wage of about four million families of the Brazilian semiarid region did not reach US$50 (Buainain and Garcia 2013). Nevertheless, during the last two decades the region has experienced a slow, but important, socio-economic transformation mainly driven by pro-poor national programs (e.g., the *Bolsa Familia* social welfare program introduced in 2003) and rural development policies. The net gain of population registered between 2000 and 2010 is in contrast to previous decades when the population was falling due to migration (Buainain and Garcia 2013). Moreover, an increasing development of infrastructure and services and the creation of a regional networks of tourism routes, industries, and small-scale farming has also contributed to economic growth of the region (Buainain and Garcia 2013).

While the economy has shown moderate growth, since 1990 the Caatinga has suffered a continued net loss of natural vegetation (MMA 2007)—although land use cover data are still controversial (Beuchle et al. 2015). Among the major human pressures to the Caatinga biodiversity are hunting, fire burning, unsustainable exploitation of natural resources (e.g., firewood), and overgrazing (MMA 2010; Ribeiro et al. 2015; Chaps. 13 and 14). Furthermore, the increasing frequency and intensity of droughts due to human-induced changes in the bioclimatic equilibrium (see Chap. 15) are putting increasing pressure on both the human and non-human inhabitants (Novaes et al. 2013; Acosta Salvatierra et al. 2017).

12.4 Cultural Ecosystem Services of the Caatinga

To discuss CES of the Caatinga we use a modified classification from the Millennium Ecosystem Assessment (2005a) (broad categories) and Richards and Friess (2015) (detailed categories). The broad categories of CES are aesthetic value, recreation value, spiritual and religious value, cultural heritage and cultural identity value, inspiration, and research and education value.

12.4.1 Aesthetic Value: Appreciation of Nature and Landscape

The main functions of protected areas are to conserve iconic landscapes and species, prevent the loss of biodiversity, and maintain key ecosystem functions (Watson et al. 2014). Thus, the most culturally meaningful and visually impressive landscapes and geological features, as well as the best examples of native vegetation, are typically found within a region's conservation units, especially national parks. The Caatinga follows this pattern, with perhaps the most iconic images coming from Chapada Diamantina National Park (Bahia State). Our photographic analysis (Box 12.1) indicated that almost 70% of geo-referenced photographs could be classified as representing aesthetic appreciation of the landscape (frequently deep-cut canyons and gorges, waterfalls, tracts of Caatinga forest, and *brejos*).

Box 12.1 Assessing Cultural Ecosystem Services (CES) of the Caatinga's Protected Areas Using Flickr®

We analyzed the content of all photos published on the social media Flickr® from 105 state parks and 104 federal parks within the Caatinga. Photos were extracted from the web through an automatized geographic search using a set of custom R scripts. The search returned 5470 images from 58 protected areas (PAs), of which 4121 had content that represented some type of CES. Each photo was designated to a CES category based on Richards and Friess (2015) and MEA (2005c) (Fig. A). A Digital Saliency Index (DSI) was calculated for PAs with more than 100 published photos based on the number of photos in each CES category and the number of users contributing photos to that PA.

'Aesthetic Value' ($N = 2486$) and 'Recreation' ($N = 1243$) were the most represented categories. Unsurprisingly, almost all photos categorized as representing 'Aesthetic Value' portrayed environmental features which appeal to visitors, such as iconic landscapes and species. There was also a high number of users contributing photos representing social activities and sporting recreation ($N = 1063$ and $N = 180$, respectively).

PAs with more than 100 photos (Table B1) included three national parks (International Union for Conservation of Nature (IUCN) category II), seven environmental protected areas (IUCN category VI), and a natural monument (IUCN category III). Almost all these PAs are located in highland, coastal, or fluvial zones, excepting *Serra da Capivara* National Park which contains one of the most representative landscapes of the Caatinga.

The most digitally represented PA in the Caatinga region is the Chapada Diamantina National Park which, together with its northern buffer zone (Marimbus-Iraquara Environmental Protected Area), contributed 42.5% of the total photos analyzed ($N = 1604$) and 36.6% of Flickr® users ($N = 171$). This is not surprising as the region is one of the most visited and appreciated tourism locations in northeastern Brazil. Following the general pattern, aesthetic and recreation value was highly represented in these two PAs.

The high representation of aesthetic and recreation value in all PAs reflects the lower representation of other CES such as spiritual and heritage value, inspiration, and education. This is in part due to systematic bias in photos taken by visitors whose main purpose is, presumably, to enjoy the landscape and engage in recreation. Nevertheless, our method shows how innovative big data approaches can be adopted to map CES. Such data may be particularly useful to support decision-makers in identifying strategic areas of funding (e.g., building watching towers, maintaining access to highly valued landscape and trails, etc.) and may contribute to assessing CES trade-offs, a key factor for on-the-ground valuation of CES.

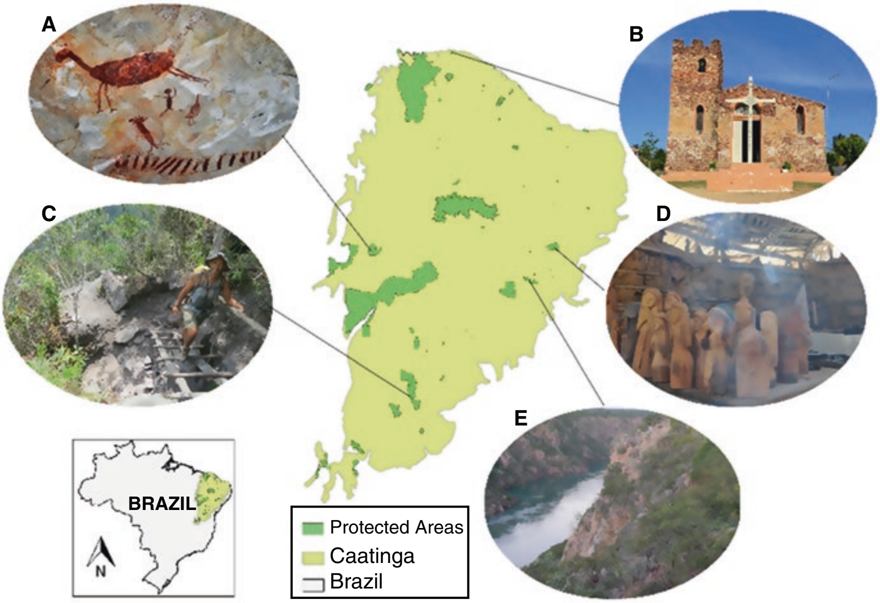

Fig. A Examples of cultural ecosystem services in digital photos of Caatinga protected areas: (**a**) heritage values (Serra da Capivara National Park); (**b**) spiritual values (Lagoa da Jijoca Environmental Protected Area); (**c**) recreation and ecotourism (Chapada Diamantina National Park); (**d**) inspiration (Catimbau National Park); and (**e**) aesthetic values (São Francisco River Natural Monument)

Although better known for its archeological sites, Serra da Capivara National Park (Piauí state) also has impressive outcrops and gorges, including the famous *Pedra Furada* (stone with a hole). This impressive stone arch (Fig. 12.1) is one of the most photographed geological features of the Caatinga and undoubtedly had a deep cultural significance for the original indigenous population of the area. However, not all iconic landscapes are included in national parks. For example, the famous 'stone mouth' (*Boca da Pedra*) of Paraíba is located in a state park of the same name. The 'mouth' itself has been formed by erosion and occurs in an isolated rocky outcrop of about 350 m height. Although the Park covers only 157 ha, it is heavily visited and has become a regional center for adventure sports, especially rock climbing.

The typical vegetation of the Caatinga landscape is perhaps not widely celebrated for its scenic beauty. Nevertheless, it contains several iconic species that are widely known by the local population for a variety of reasons including striking growth forms and culinary/medicinal uses. An example of the latter is the Brazilian plum (*Spondias tuberosa*), known locally as *umbu,* a small tree (<6 m) that produces a delicious round fruit with a leathery shell (Neto et al. 2010). As might be anticipated, many of the native cacti also have strong cultural importance. For example, the friar's crown cactus (*Melocactus bahiensis*) (Fig. 12.2) is extensively used as an

Table B1 Cultural ecosystem services in the most photographed Caatinga protected areas

	Cultural ecosystem services (Digital Saliency Index and relative values)												**Total**	
Protected areas	Aesthetic		Recreation		Spiritual values		Heritage values		Inspiration		Education		Photos (n)	Users (n)
CHAPADA DIAMANTINA NATIONAL PARK	0.70	576 (67%)	0.21	241 (28%)	<0.01	10 (1%)	0.02	7 (1%)	0.02	27 (3%)	0.00	0 (0%)	861	55
MARIMBUS / IRAQUARA ENVIRONMENTAL PROTECTED AREA	0.71	559 (75%)	0.18	128 (17%)	<0.01	3 (0%)	0.04	20 (3%)	0.04	33 (4%)	0.00	0 (0%)	743	116
LAGO DE SOBRADINHO ENVIRONMENTAL PROTECTED AREA	0.49	132 (36%)	0.29	182 (50%)	0.05	3 (1%)	0.01	1 (0%)	0.08	35 (10%)	<0.01	10 (3%)	363	20
SERRA DE BATURITÉ ENVIRONMENTAL PROTECTED AREA	0.69	288 (89%)	0.15	24 (7%)	0.10	9 (3%)	0.00	0 (0%)	0.04	4 (1%)	0.00	0 (0%)	325	61
JERICOACOARA NATIONAL PARK	0.49	145 (46%)	0.43	146 (46%)	0.00	0 (0%)	0.00	0 (0%)	0.06	27 (8%)	0.00	0 (0%)	318	44
LAGOA DA JIJOCA ENVIRONMENTAL PROTECTED AREA	0.49	125 (44%)	0.47	147 (51%)	<0.01	1 (0%)	0.00	0 (0%)	0.03	13 (5%)	0.00	0 (0%)	286	41
SERRA DA CAPIVARA NATIONAL PARK	0.57	86 (34%)	0.38	131 (52%)	0.00	0 (0%)	0.02	28 (11%)	<0.01	6 (2%)	0.00	0 (0%)	251	6
SERRA DA IBIAPABA ENVIRONMENTAL PROTECTED AREA	0.57	123 (51%)	0.16	12 (5%)	0.18	42 (17%)	0.05	19 (8%)	<0.01	5 (2%)	0.01	40 (17%)	241	49
LAGAMAR DO CAUIPE ENVIRONMENTAL PROTECTED AREA	0.42	59 (40%)	0.51	84 (56%)	0.00	0 (0%)	0.00	0 (0%)	0.05	4 (3%)	<0.01	2 (1%)	149	22
CHAPADA DO ARARIPE ENVIRONMENTAL PROTECTED AREA	0.51	81 (68%)	0.38	29 (24%)	<0.01	1 (1%)	0.04	1 (1%)	0.05	7 (6%)	0.00	0 (0%)	119	30
RIO SÃO FRANCISCO NATURAL MONUMENT	0.73	87 (74%)	0.26	29 (25%)	<0.01	1 (1%)	0.00	0 (0%)	0.00	0 (0%)	0.00	0 (0%)	117	22

Grey columns: Digital Saliency Index; white columns: relative number of photos in each protected area

ingredient for cakes and biscuits, as well as being a source of animal feed. Interestingly, it is also thought to protect against evil spirits (Machado et al. 2013) and is consequently a common pot plant in rural areas. The xique-xique cactus (*Pilocereus gounellei*) is also used extensively as a livestock food substitute, especially during drought conditions when other food sources are unavailable. However, the most iconic cactus of the Caatinga is probably the mandacaru (*Cereus jamacaru*), a columnar species that can grow to several meters in height and which

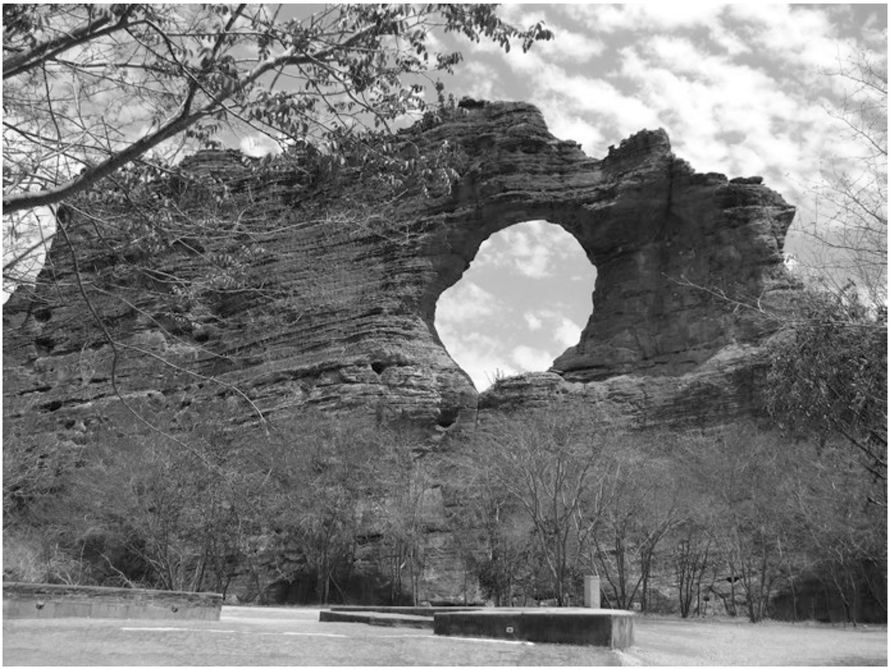

Fig. 12.1 *Pedra Furada* (stone with a hole) of the Serra da Capivara National Park (Piauí state) (Photo: Chiara Bragagnolo)

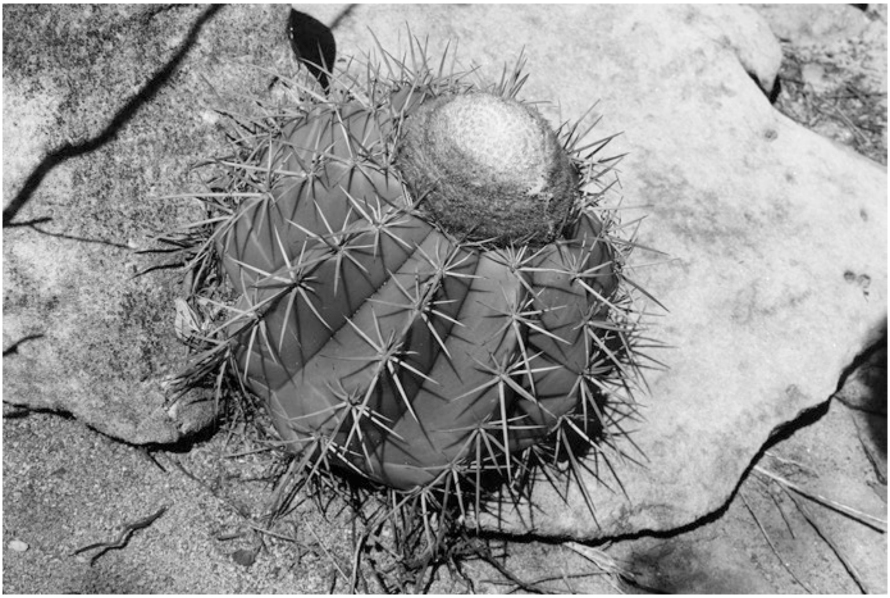

Fig. 12.2 The friar's crown cactus (*Melocactus bahiensis*) (Photo: Chiara Bragagnolo)

dominates in many semi-agricultural landscapes. This cactus is also used as a food source for animals during drought conditions (Cavalcanti and Resende 2006).

The Caatinga provides habitats for some of the most iconic Brazilian animal species, including jaguars (*Pathera onca*) and the ecologically extinct Spix's macaw (*Cyanopsitta spixii*). The macaw became internationally famous as the subject of a Disney film (*Rio*) and a best-selling popular science book (*Spix's Macaw: The Race to Save the World's Rarest Bird* by Tony Juniper). The macaw's natural habitat was the Caraibeira (*Tabebuia aurea*) woodland galleries of the São Francisco River basin in northern Bahia where it fed on seeds of *Caraiba* and various Euphorbiaceae. Never common, a combination of hunting (for trade) and habitat destruction wiped out the last known population in 1990. Spix's macaw and Lear's macaw (*Anodorhynchus leari*)—another rare Caatinga endemic—are among the most culturally visible Caatinga bird species, both in Brazil and internationally (Table 12.1).

Of a much more local significance is the white-naped Jay or *cancão* (*Cyanocorax cyanopogon*), an omnivorous, social, and highly visible member of the Caatinga bird community due to its habit of emitting a loud alarm call whenever approached. It is also a relatively common cage bird in the thriving bird-keeping culture of northeast Brazil (Alves et al. 2010).

Among the mammals, the Brazilian three-banded armadillo (*Tolypeutes tricinctus*) is a Caatinga species that came to global attention more recently when it was unveiled as the mascot for the 2014 FIFA World Cup. To increase environmental

Table 12.1 Most visible Brazilian endemic bird species on Brazilian and international web sites

Rank	Website salience	
	Brazilian	International
1	Red-cowled cardinal (*Paroaria dominicana*)	Spix's macaw (*Cyanopsitta spixii*)
2	Spix's macaw (*Cyanopsitta spixii*)	Jandaya parakeet (*Aratinga jandaya*)
3	Lear's macaw (*Anodorhynchus leari*)	Lear's macaw (*Anodorhynchus leari*)
4	Campo troupial (*Icterus jamacaii*)	Red-cowled cardinal (*Paroaria dominicana*)
5	Golden-capped parakeet (*Aratinga auricapillus*)	Golden-capped parakeet (*Aratinga auricapillus*)
6	Yellow-legged tinamou (*Crypturellus noctivagus*)	Campo troupial (*Icterus jamacaii*)
7	Stripe-breasted starthroat (*Heliomaster squamosus*)	Spot-backed puffbird (*Nystalus maculatus*)
8	Wing-banded hornero (*Furnarius figulus*)	Stripe-breasted starthroat (*Heliomaster squamosus*)
9	White-browed guan (*Penelope jacucaca*)	Yellow-legged tinamou (*Crypturellus noctivagus*)
10	White-naped jay (*Cyanocorax cyanopogon*)	Wing-banded hornero (*Furnarius figulus*)

Data and methods from Correia et al. (2016)

awareness, the mascot was named Fuleco™—a combination of the Portuguese words *futebol* and *ecologia*. Scientists were quick to point out that protected areas in northeastern Brazil included only 8% of the armadillo's distribution and that the species was highly vulnerable to habitat loss and climate change (Melo et al. 2014). After intensive lobbying, the *Tatu-Bola* Wildlife Reserve was established in March 2015, although it was downgraded to become an Environmental Protected Area (sustainable use) months after its creation.

12.4.2 Recreation Value (Social and Sport)

Although there are no systematic data available, anecdotal evidence suggests that hunting is one of the predominant recreational activities practiced within the Caatinga. The lack of data is partly associated with the uncertain legal status of hunting in Brazil: although wildlife hunting and trade is criminalized, the original law and subsequent revisions distinguish between predatory (commercial hunting and poaching) and non-predatory (including hunting for recreation/sport) hunting. Nevertheless, it is by no means simple for an individual to legally hunt in Brazil, and most hunting is almost totally unregulated and practiced illegally (Cullen Jr. and Bodmer 2001; Tabarelli et al. 2010; Constantino 2016).

Still, hunting is an important part of the culture of the people who live in the Caatinga region. Children start hunting birds and reptiles at a young age with slingshots or capture birds in traps (Alves et al. 2009). Adults use a range of methods that are adapted to the type of prey and are more likely to eat or sell their quarry. Nevertheless, a recent study in the Caatinga region recorded that 77% (82/106) of hunters were also motivated to hunt for leisure/entertainment (Alves et al. 2009). Closely related to hunting is the practice of bird-keeping,[3] a leisure activity that is widespread throughout northeast Brazil. A recent study of bird keepers in the Caatinga (Alves et al. 2010) found that the most frequently kept species were the red-cowled cardinal (*Paroaria dominicana*), Caatinga parakeet (*Aratinga cactorum*), campo troupial (*Icterus jamacaii*), white-throated seedeater (*Sporophila albogularis*), rufous-bellied thrush (*Turdus rufiventris*), and ultramarine grosbeak (*Cyanocompsa brissonii*). Bird cages are frequently hung in the front of residences and it is not uncommon to see men walking or cycling with their birds in the early morning sun.

Bird watching and bird photography is still in its infancy in northeast Brazil, although it should be noted that there is enough demand to sustain a specialist tourist enterprise (http://nebrazilbirding.com/) that caters for Brazilian and, especially, international tourists. Other forms of nature tourism are also available, especially in Chapada Diamantina National Park where hiking and guided tours are a major tourist draw. Recent years have also seen a steep increase of interest in mountain biking in the park, with several tourist operators offering a variety of options.

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[3] It is also technically illegal to keep wild animals in Brazil.

12.4.3 Spiritual and Religious Value

Worldwide, humans have attached spiritual and religious value to many natural places, generally known as sacred natural sites (SNS). SNS are often aligned with conservation, contributing to the protection of sacred places from exploitation and degradation (Wild and McLeod 2008). The Caatinga hosts several SNS, most of which contain elements of nature providing shelter from the harsh physical environment, such as waterfalls, lakes, caves, mountains, and *brejos*. Rock paintings and engravings are also common across the Caatinga, providing direct evidence of prehistoric rituals and cultures (Pessis et al. 2014). More recently arrived religions have also adopted natural features. For example, *Pedra da Boca* State Park hosts the *Pedra da Santa*, a sacred place which Catholic pilgrims used to celebrate their rituals. *Morro de Urucum* (Ceará state) is another example of a sacred rocky mountain whose summit hosts a Catholic church. Other sacred Catholic caves are spread through the backlands of Bahia state, such as *Gruta do Sagrado Coração de Jesus* and *Gruta do bom Jesus* (Fernandes-Pinto and Azevedo 2015).

12.4.4 Cultural Heritage and Cultural Identity

Culture is the multifaceted manifestation of the interaction between individuals and their environment through art and science, food, architecture, systems of values, customs, traditions, beliefs, education, language, family nature and social relations, and behavioral norms (Tylor 1871). Cultural identity refers to a sense of belonging perceived by individuals who share the same culture. Brazilian people are a melting pot of roots and races which have been adapted to different ecological and climate conditions, giving rise to five distinguishable cultures with a clear geographical distribution across the country (Ribeiro 2013). One of these cultures, the so-called *cultura sertaneja* (backlands culture) developed from the adaptation of humans to the biophysical conditions characterizing northeastern Brazil.

The identity of *sertanejos* (people from the northeastern semiarid region) has been mainly shaped by adaptation to the very extreme physical conditions (soils with low fertility, droughts, cactus thorns, etc.). Leather is perhaps the main symbol of this culture as cowmen and ranchers used to wear leather clothes (jackets, coats, trousers, hats, etc.) to defend themselves from the giant thorns on many of the cacti and legumes (Lewis 1985). The diet of the *sertanejos* is also characteristic, with many local dishes based around sun-dried beef, goat, and especially manioc (used as a substitute for bread).

Social structure and family organization reflect the well-known land-tenure hierarchy based on clientelism, where influential local owners wield considerable social power. Historically, these land owners (*Coroneis*) did not hesitate to use violence to submit people to their rules, often using bands of thugs (*jagunços*) to enforce their wishes. The harshness of this semi-feudal system often incited people to banditry, such as the famous *cangaceiros* (*Robin Hood*-style gangs wearing the dress of cowmen and well-armed) patrolling the highways of backlands in the 1930s with the mission of redistributing wealth to the poor (Chandler 1981; Grunspan-Jasmin 2006). Another characteristic feature of the *sertanejos* is their fervent religiosity, with very high levels of church attendance and a strong tendency towards syncretism.

12.4.5 Inspiration

Literature and artworks may reproduce geographical and spatial thoughts, perceptions, and feelings. At the same time, places can express cultural circumstances and features which may not be recognized elsewhere, being part of inspiration for writers, artists, and musicians. Unsurprisingly, given the high population, many classics of Brazilian literature are set in the semiarid backlands (Leitão Júnior 2012). Specifically, *Os Sertões* (1902) by Euclides da Cunha and *Grande Sertão: Veredas* (1956) by João Guimarães Rosa have been compared with the Iliad and the Odyssey, respectively. *Os Sertões* tells the history of the *Canudo* war at the end of the nineteenth century while criticizing the social and political theories of the time which supported the modernization of the apparently undeveloped and less civilized backlands. *Grande Sertão: Veredas* consists of a long monologue in which the protagonist tells the story of his life using the natural shapes of the *Sertão* (i.e., labyrinthine nets of grass and palms) and its linguistic expressiveness as a metaphor of the complexity of human nature. Many other masterpieces of Brazilian literature (e.g., *Vidas Secas*, *O Quinze*, *Tieta do Agreste*, etc.) have drawn on the lack of development of the *Sertão* (Leitão Júnior 2012), creating a general perception among Brazilians of the northeast as a region where drought, poverty, and corruption are still keeping modernity at arms length.

Another cultural expression of popular literature of northeastern Brazil is the Cordel literature (*Literatura de Cordel*); pamphlets containing novels, poems, and songs originally passed as oral rhyme improvisations. In Brazil this folk literature has been mainly preserved in the northeast region, with many examples inspired by historical events and natural aspects of the backlands (e.g., *cangaceiros* and their leader Lampião, etc.).

The typical music of the Caatinga is known as *baião*, combining bass drums and accordions and with lyrics deeply inspired by the culture and landscapes of the region. The uncontested king of *baião* was Luiz Gonzaga (1912–1989), whose repertoire focused on the rural life of dryland people and their struggles against the unforgiving environment. Finally, most of the arts and crafts of Caatinga are inspired by local products such as leather, straw, seeds, and clay. Typical examples of these crafts include leather clothes and shoes, seed jewelry, straw accessories/tools, and pottery.

12.4.6 Research and Education Value

With its unique fauna and flora and distinct cultural heritage, the Caatinga has long been a source of inspiration for Brazilian and foreign researchers. For example, a search of Scopus returns 1679 documents published between 1977 and 2015 that have the word Caatinga in the article title, abstract, or keywords. Perhaps unsurprisingly, 77.6% of these are classified as Agricultural and Biological Sciences and 18.8% as Environmental Science. Nevertheless, the Caatinga is one of the least researched ecosystems in South America with very low biodiversity-survey effort and fewer research teams than adjacent humid forest ecosystems (Amazonia and Atlantic Forest) (Santos et al. 2011). A recent study observed that 40% of the Caatinga's plant species had not been sampled by site-based surveys, and that most of the recorded species had been collected from only a single site (Moro et al. 2014). Moreover, plant and animal collectors have tended to concentrate their sampling effort on accessible locations, inside protected areas and on sites with high total precipitation but low seasonal rainfall variability.

The Caatinga environment has also provided a rich subject for the development of indigenous and local knowledge systems. For example, there is an extensive traditional knowledge system associated with the use of medicinal plants that has been comprehensively documented by the research group of Professor Ulysses Albuquerque of the Federal Rural University of Pernambuco (e.g., Albuquerque 2006; Albuquerque et al. 2007; Abreu et al. 2015; Chap. 11). Indeed, there are many medicinal plants from the Caatinga that are frequently used as folk medicines (Chap. 11). A good example is the Brazilian pepper tree (*Myracrodruon urundeuva*), known locally as *aroeira-do-sertão*, which is used locally to treat a variety of ailments from gynecological problems to diarrhea (Ferreira et al. 2011).

12.5 Conclusions

The quantitative evaluation of CES is still in a very early phase of development and lacks systematic and well-defined methodologies. Moreover, to our knowledge (with the exception of the Flickr® study presented in Box 12.1) there have been no dedicated studies that have attempted to measure CES in the Caatinga, although there are several studies that clearly identify cultural services such as hunting (Alves et al. 2009) and bird-keeping (Alves et al. 2010). There is clearly considerable scope for further research, either using traditional social science approaches or adopting a range of big data methods that allow a more quantitative and comparative approach to assessing cultural value. We would argue that such studies are essential to strengthen the resilience of the few remaining areas of natural vegetation in the Caatinga in the face of increasing competition from other land uses, especially agricultural development. As politicians and policy-makers are increasingly forced into uncomfortable trade-offs between the needs of people and the environment, quantifying CES may be one of the most effective ways to demonstrate the enormous contribution of the Caatinga environment to local cultures and the regional economy.

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Part IV
Threats

Chapter 13
Impact of Human Activities on the Caatinga

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Abstract Studies to date suggest that most of the native vegetation in the Caatinga has remained relatively intact. In this chapter we have combined information from fire hotspots, roads, and land-use changes to demonstrate that at least 63.3% of the Caatinga is composed of anthropogenic ecosystems. Human impact is higher in the humid and more productive ecoregions (e.g., Brejos and São Francisco-Gurgéia) than in those ecoregions with very dry climates and nutrient-poor soils (e.g., Dunas do São Francisco and Raso da Catarina). The future of the Caatinga's unique biota is conditional on how societies will protect and restore the native ecosystems. We suggest that an urgent conservation program for the Caatinga should be structured around four quantitative targets: (a) zero species loss; (b) zero natural ecosystem loss; (b) all large and mid-size natural ecosystem patches formally protected; and (c) all protected areas connected through conservation corridors composed of a mix of natural and anthropogenic ecosystems. The second and third actions are the most urgent and need to be implemented as soon as possible. The first and fourth actions are long-term ones that will require building capacity at the local level to design and execute sound conservation development programs.

Keywords Land-use change • Deforestation • Agriculture • Fire • Degradation • Desertification • Human impact • Conservation • Biogeography

13.1 Introduction

Humans have altered so much of Earth's systems that researchers suggest that it is time to propose a new geological epoch: Anthropocene (Steffen et al. 2011; Waters et al. 2016). Among the several changes to the planet that humans have caused, the most serious and threatening is the loss of biodiversity and ecosystem services

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caused by irreversible changes in ecological patterns and processes of the terrestrial biosphere (Pimm et al. 2014; Steffen et al. 2015). The most recent estimates indicate that our species has already modified around 78% of the Earth's ice-free land, with 40% in direct use for agriculture or urban settlements and 38% in semi-natural areas embedded within human-made ecosystems (Ellis et al. 2010). This process of human expansion across the planet seems to be endless, as more lands have been incorporated into the production systems that are required to sustain global economic growth (Foley et al. 2011), even though economic growth by itself does not translate necessarily into better living conditions for all (Sachs 2015).

Humans arrived in the Caatinga around Late Pleistocene and Early Holocene (Bueno and Dias 2015). Around 1500, when the first Europeans disembarked in Brazil, the indigenous population in the Caatinga was estimated at 100,000 people (Hemming 1978). Their impacts on the natural ecosystems were restricted to the patches of humid ecosystems found along the few perennial rivers and in the mountain slopes. The process of colonization of the Caatinga was conducted by slaughtering indigenous people to open up space for large settlements dedicated to cattle ranching and subsistence agriculture along the major rivers (Hemming 1978; Andrade 1998; Puntoni 2002). However, during the seventeenth century, settlers learned to clear and burn the caatingas and discovered that it contained stretches of good pasture (Hemming 1978). Since then, settlements have spread out across the whole region and set the basis for the modern cities. The traces of pastures, agriculture fields, roads, fire, reservoirs, cities, and other human infrastructure have accumulated over time as a palimpsest. In 2010, the Caatinga was home to 28.6 million people, and their impacts could be detected everywhere across the region (Chap. 1).

The major outcome of the expansion of human activities across the Caatinga has been the replacement of the natural ecosystems by anthropogenic ecosystems. However, in contrast with the adjacent Amazonia and Atlantic Forest, the Caatinga has no systematic program on a regional scale to monitor and understand the effects of humans on the native ecosystems, so most of the available information on the distribution of the natural and anthropogenic ecosystems across the region is from individual papers that have used different data sets and methodologies. The first paper that tried to estimate the distribution of the native and anthropogenic ecosystems in the Caatinga was by Castelletti et al. (2003). These authors first modeled the areas in terms of road impacts by using different impact zones ranging from 1 to 10 km along the major paved roads. They then combined the results of these scenarios with the areas under agriculture that had been identified in the 1:5,000,000 scale Brazilian vegetation map (IBGE 1993). They concluded that between 30.4% (the most optimistic scenario) and 51.7% (the most pessimistic scenario) of the native vegetation in the Caatinga could be classified as anthropogenic. A few years later and with support from the PROBIO program (Projeto de Conservação e Utilização Sustentável da Diversidade Biologica), a team from different organizations analyzed Landsat images from 2002 and estimated that 37.3% of the Caatinga was anthropogenic (Brasil 2007). By using the baseline created by Brasil (2007), the PMDBBS (Projeto Monitoramento do Desmatamento dos Biomas Brasileiros por Satélite) improved the measurements for 2002 and mapped newly cleared areas for 2008 and 2009. In this new effort, Landsat and CBERS-2B (China–Brazil Earth Resources Satellite 2B) images were used. The results indicated that anthropogenic ecosystems in the Caatinga covered 43.7% of the region in 2002, 45.4% in 2008, and 45.6% in 2009 (Brasil 2011). More recently, Beuchle et al. (2015) assessed land-use changes for the Caatinga in 1990, 2000, and 2010 using Landsat images. They found that anthropogenic ecosystems covered 32.6% of its original vegetation in 1990, 33.9% in 2000, and 36.8% in 2010. In general, these four studies, with the exception of the most pessimistic scenario outlined by Castelletti et al. (2003), suggested that most of the native vegetation in the Caatinga has remained relatively intact. In this chapter, we combined three datasets to produce a new estimate of the geographical distribution of natural and anthropogenic ecosystems in the Caatinga with the aim of supporting conservation and other land-use policies across the region.

13.2 Impact of human activities on the Caatinga: A New Estimate

A comprehensive estimate of the distribution of the natural and anthropogenic ecosystems in a region requires the combination of different indicators, each one representing one type of human pressure. To model the spatial distribution of the natural and anthropogenic ecosystems in the Caatinga in 2010, we integrated three impact indicators (fire hotspots, road impacts, and land-use changes) using ArcGIS. We selected these three indicators because significant scientific evidence links them with ecosystem changes (Forman 2000; Trombulak and Frissel 2000; Castelletti et al. 2003; Barreto et al. 2005). In addition, these datasets for the region are and will be publicly available, so the results of our analyses can be updated and compared over time. We present our results for the whole region as well as by ecoregions, such as they were defined in Chap. 1.

Data about fire hotspots were collected from the dataset made available by the Brazilian Institute of Spatial Research (INPE) through the *Programa de Monitoramento de Queimadas* (https://prodwww-queimadas.dgi.inpe.br/bdqueimadas). We downloaded the location of all the fire hotspots detected during 2010 that were available in the INPE's database. In the Caatinga, fire hotspots are generally associated with small agriculture openings rather than forest fires (M. Tabarelli, personal communication). As a consequence, we added only a 1-km-wide radius around each fire hotspot as a method to estimate the fire impact on the vegetation. For comparison, Barreto et al. (2005) used a 10-km-wide radius around fire hotspots to estimate human impacts in the Brazilian Amazonia.

To estimate the road impact on the Caatinga, we used the most recent map of roads in the region (http://www.dnit.gov.br/mapas-multimodais/shapefiles). Roads are well-known to interrupt ecological flows and have ecological impacts going well beyond the areas used for their building and maintenance (Forman 1995). Roads open human access to pristine vegetation areas, which can accelerate land-use changes and biodiversity loss as well as the expansion of invasive species (Trombulak and Frissel 2000; Ibisch et al. 2016). The road impact, of course, depends on the region. In the case of the Caatinga, Santos (2000) estimated that road effects in the region around Xingó, Sergipe, were around 7 km. In our analysis, we decided to be conservative. Therefore, we used a 1-km-wide radius along the road network to estimate its impact on the landscape.

IBGE (2015) produced maps of land coverage for the entire country by using 250-m MODIS images. In these maps, 14 land-use categories were recognized, of which seven can be considered anthropogenic: (a) artificial (urban) areas; (b) agriculture areas; (c) managed pastures; (d) mosaics of agriculture and forests; (e) forest plantations; (f) mosaics of forests and agriculture; and (g) mosaics of agriculture and grasslands. We combined the areas of these seven categories to estimate the percentage of the Caatinga that had been impacted by deforestation by 2010.

Our analyses indicate that fire hotspots impacted an area of 139,522 km^2, or 15.3% of the Caatinga (Fig. 13.1). This impact is not uniformly distributed across ecoregions, as three regions (São Francisco-Gurgéia, Brejos, and Ibiapaba-Araripe) were relatively more impacted than others (Table 13.1). One potential reason for this spatial pattern is that these three ecoregions have in common large areas of forests and cerrados, two types of vegetation that are more flammable than caatinga woodlands. In addition, because they receive more rainfall than the other ecoregions, they have a large proportion of their areas covered by agricultural fields. Roads are a pervasive component of the Caatinga's landscape, with very few areas that can be considered roadless (Fig. 13.1). We estimated that roads impact 346,267 km^2 or 37.9% of the region. The impact of the roads by ecoregion ranged from 22.4% in the Dunas do São Francisco to 45.6% in the Chapada da Diamantina (Table 13.1). The land-use map indicates that around 311,225 km^2 have been deforested in the Caatinga as of 2010 (Fig. 13.1). This area corresponds to 34.1% of the region. Only a few large areas have no deforestation, mostly in the region's center and along its western borders (Fig. 13.1). The most transformed ecoregion is Brejos (74.7%), followed by Chapada da Diamantina (55.7%), São Francisco-Gurgéia (41.4%), and Planalto da Borborema (41.1%) (Table 13.1). By combining all of the impact maps, we estimated that 63.3% of the Caatinga has already been converted into anthropogenic ecosystems as of 2010 (Fig. 13.1). In general, almost no large natural area remains with the exception of a few areas in the region's center. The anthropogenic ecosystems are dominant in all of the ecoregions except for Dunas do São Francisco and Raso da Catarina (Table 13.1). With 90.1% of its area altered, the Brejos is the region's most impacted ecoregion (Table 13.1).

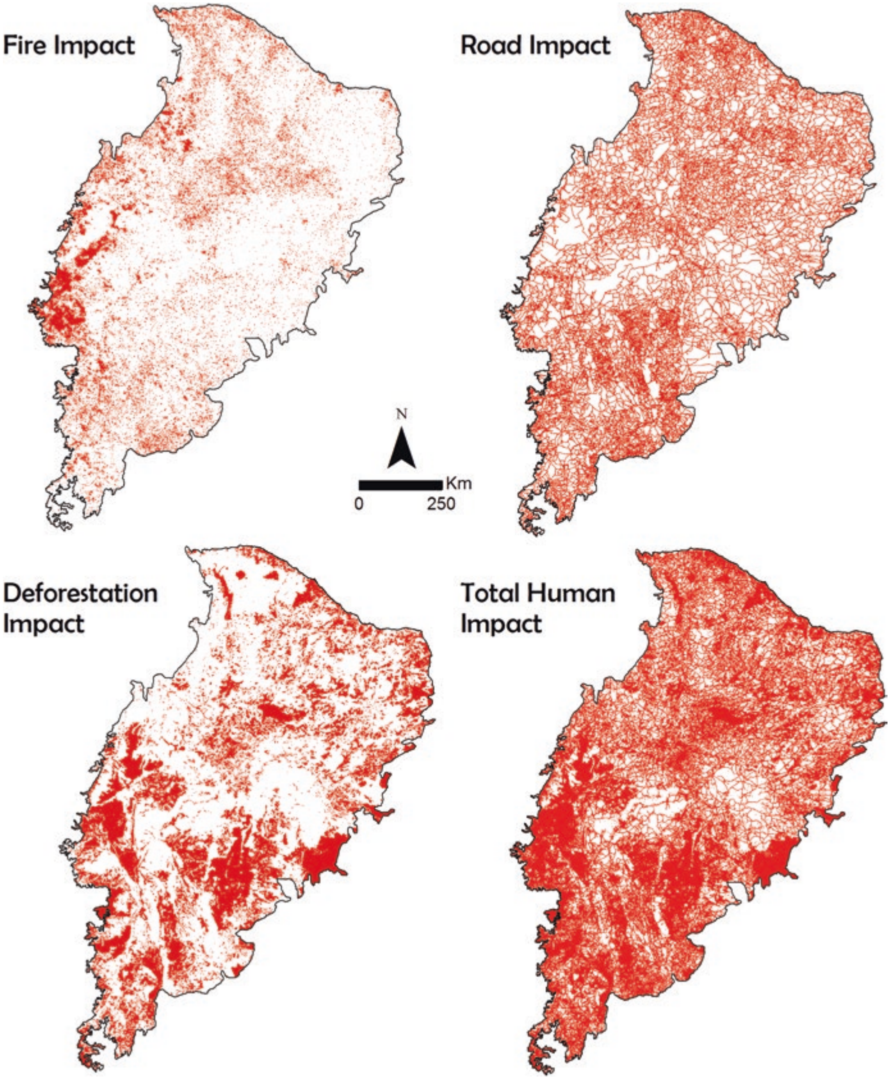

Fig. 13.1 Distribution of the impacts of fire, road, land-use, and total human impacts on the Caatinga as of 2010

13.3 Social–Ecological Consequences of Land-Use Changes

In contrast with previous studies, we found that most of the Caatinga (63.3%) has been modified by human activities. It is the first time that anthropogenic ecosystems are documented to occupy an area larger than natural ecosystems across the region. Although this number is around 11.6% higher than the most pessimistic estimate by Castelletti et al. (2003), it is not surprising. In fact, the Caatinga is currently the

Table 13.1 Total human impact and isolated impact of fire hotspots, roads, and land-use changes across the Caatinga's ecoregions

Ecoregions	Area (km^2)	Region (%)	Fire impact (%)	Road impact (%)	Deforestation impact (%)	Total human impact (%)
Brejos	2412	0.3	24.6	35.3	74.7	90.1
Chapada Diamantina	50,411	5.5	9.2	45.6	55.7	75.7
Ibiapaba-Araripe	69,073	7.6	19.1	36.1	23.4	59.5
Depressão Sertaneja Meridional	285,829	31.3	11.4	37.9	33.1	60.5
Depressão Sertaneja Setentrional	212,308	23.3	14.2	41.6	27.5	61.6
Dunas do São Francisco	26,539	2.9	7.3	22.4	20.0	40.6
Planalto da Borborema	44,287	4.9	3.3	34.4	41.1	62.0
Raso da Catarina	30,708	3.4	4.7	22.7	31.8	48.1
São Francisco-Gurguéia	190,968	20.9	28.1	38.0	41.4	73.3

most densely populated region among South America's tropical seasonal dry forests, with a pressure well beyond the region's carrying capacity (Leal et al. 2005). In addition, recent infrastructure development, the adoption of modern farming technologies, and the expansion of social safety net programs have allowed local populations to improve the ways by which they cope with the frequent droughts and expand their economic activities (Buainain and Garcia 2013; Chap. 1). The result is that human pressure on the natural vegetation has increased rather than declined over time. It has been suggested (Chap. 16) that the productive use of the Caatinga by the local population as native pasture, fallow in itinerant agriculture, and firewood production could lead to the maintenance of a large area of vegetation across the region. However, the vegetation that is left after human use is very poor when compared with the original vegetation that once dominated the region (Sá and Angelotti 2009). It has been also predicted that based on the current trends, the region's vegetation cover will not decrease over time. However, this prediction is not supported by our results.

Anthropogenic ecosystems are the new norm across the Caatinga. As expected, human impact is higher in the humid and more productive areas, in both high plateaus (Brejos and Diamantina) and along the major river valleys (São Francisco-Gurgéia), than in very dry ecoregions, such as Dunas do São Francisco and Raso da Catarina, whose climate and nutrient-poor soils have always constrained human occupation (Velloso et al. 2002). Yet, even the two less impacted ecoregions have more than 40% of their areas occupied by anthropogenic ecosystems, which is a high level of transformation for any tropical region. In general, the distribution of the natural vegetation remnants across the region shows that most of the areas are small and isolated and that opportunities to protect large and roadless areas within the Caatinga are becoming scarce.

The expansion of anthropogenic ecosystems at the expense of natural ecosystems can have negative impacts on the capacity of the regional societies to adapt and cope with the current and future extreme climatic events, which are predicted to become more common in the near future (Chap. 15). The region's economy has been built around products and services provided by nature (Andrade 1998; Chap. 1). However, the large-scale replacement of the natural ecosystems by anthropogenic ecosystems can lead to an irreversible loss of biodiversity, biomass, and ecological processes that altogether undermines the provision of critical ecosystem services (e.g., food, freshwater, and firewood) that local populations require to survive (Silva et al. 2004; Chap. 11). The problem is even bigger if one takes into account that one-third of the Caatinga has a high potential for desertification and that all attempts to control the expansion of the existing four desertification nuclei have not been successful (Sá and Angelotti 2009; Vieira et al. 2015). If the current land-use trend continues, local societies will not have the green infrastructure required to sustain a more sustainable development path (Chap. 18). The decline of some ecosystems services can be reverted through good management and the restoration of anthropogenic ecosystems associated with outright conservation of the few remaining patches of natural ecosystems. While a wealth of appropriate technologies are available to manage anthropogenic ecosystems in the Caatinga (Gariglio et al. 2010; Chaps. 11, 16), the conservation of the region's unique biodiversity requires a sound and ambitious plan.

13.4 Lessons for Conservation

In a nutshell, the future of the Caatinga's unique biota is conditional on how well species will adapt to and thrive with hybrid ecosystems. Different responses are expected, most of them species specific or limited by phylogenetic constraints. Some species are expected to flourish in anthropogenic ecosystems, while others will become locally extinct. The existing macroecological theory (Brown 1995) predicts that, on the regional level, species with small ranges, low populations, and very specialized habitats are the ones that will move fast to the extinction path if they are not protected as soon as possible. In contrast, species that have large ranges and populations and that are able to live in different habitats are the ones with a high likelihood to thrive in anthropogenic ecosystems. The generalist species that adapt well to anthropogenic ecosystems can even enlarge their ranges toward adjacent bioregions, such as Amazonia and Atlantic Forests, following the expansion of human activities across the continent. Very few studies have evaluated how native species will be able to survive in the anthropogenic ecosystems. However, the prospects are not good. For birds, for instance, only 162 species out 548 species will be

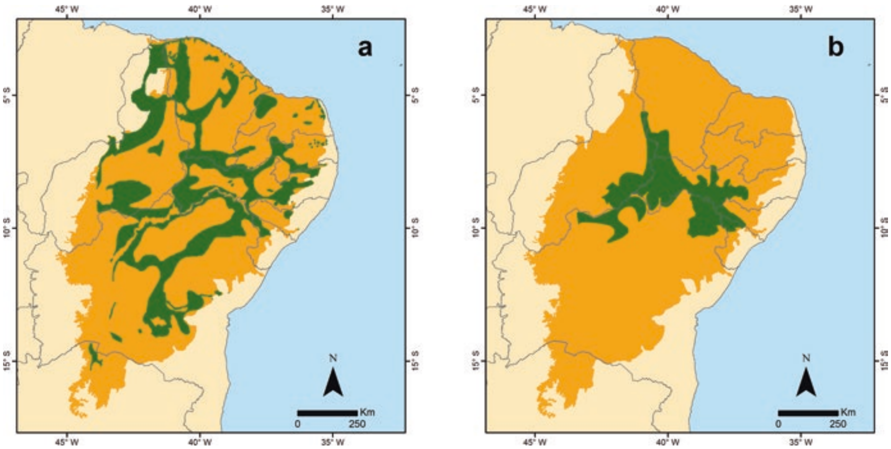

Fig. 13.2 Boundaries of the Caatinga Biosphere Reserve (**a**) and the Caatinga Ecological Corridor (**b**)

able to survive in degraded caatingas under a more unpredictable climate regime (Chap. 7).

In Brazil, as in any other country in the world, the conservation science required to efficiently protect ecosystems always moves slower than the forces that are driving large-scale ecosystem transformation. Therefore, we suggest that governments should launch an ambitious conservation program for the region that can be updated when more scientific knowledge becomes available. The Caatinga has a large-scale science-based conservation plan that was designed together with stakeholders (Silva et al. 2004) and that has been consistently updated (Chap. 17). In addition, the region has two large and comprehensive conservation initiatives that have been formally recognized by the federal government (Fig. 13.2): (a) the Caatinga Biosphere Reserve designated in 2001 with 19,9 million hectares; and (b) the Caatinga Ecological Corridor announced in 2006 with 11.7 million hectares. Therefore, the region's major problem is less about science and planning and more about action on the ground. We suggest that an urgent conservation program for the Caatinga should be structured around four quantitative targets: (a) zero species loss; (b) zero natural ecosystem loss; (b) all large and mid-size natural ecosystem patches formally protected; and (c) all protected areas connected through conservation corridors composed of a mix of natural and anthropogenic ecosystems. The second and third actions are the most urgent ones and need to be implemented as soon as possible. The first and fourth actions are long-term ones that require building of the capacity at the local level to design and execute sound conservation development programs.

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Chapter 14
The Socio-Ecology of the Caatinga: Understanding How Natural Resource Use Shapes an Ecosystem

Felipe P.L. Melo

Abstract The use of natural resources can be a main source of disturbance to natural ecosystems if human populations depend heavily on biomass to attend to their basic needs. However, our understanding of how natural resource use affects natural ecosystems is insufficient. The Caatinga is the most populated dry forest worldwide, and inhabitants depend largely on the exploitation of the natural ecosystem for several purposes such as fuelwood and raising livestock. These constitute 'chronic anthropogenic disturbances' (CAD), the impacts of which, in the long run, may compete with habitat loss and impacts on ecosystem health. In this chapter I present a theoretical framework for the assessment of the impacts of three main sources of CAD on the Caatinga. I discuss how (1) firewood harvesting, (2) raising of free ranging goats, and (3) biological invasion are all linked to changes observed in the Caatinga biota. These sources of CAD are all linked to the socio-economic condition of human populations inhabiting the Caatinga and can be understood and, to some extent, quantified through socio-economic assessments. Finally, I propose a theoretical framework on how the original features of the Caatinga ecosystem may change as a function of the intensity of CAD, leading to two alternative states of both conserved and altered similarity to the original ecosystem. Understanding natural resource use by human populations is crucial to being able to assess the threats to biodiversity and ecosystem functions properly as well as to design conservation strategies to avoid both ecosystem degradation and depletion of human livelihoods.

Keywords Chronic anthropogenic disturbance • Non-timber forest products • Goats • Fuelwood • Biological invasion • Ethnobiology • Biological invasion

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14.1 Introduction

Understanding human-caused disturbance in tropical ecosystems has been a ‘race against the clock’ for ecologists and conservationists. Some research fields such as landscape ecology and restoration ecology have achieved milestones in understanding how habitat structure affects native biotas in human-dominated ecosystems. We can design conservation strategies aiming to protect biodiversity considering landscape features such as amount of habitat, the size of habitat patches, and connectivity among them. However, these approaches usually neglect human presence in the landscapes and how human populations explore natural resources (Torres et al. 2016). Therefore, significant knowledge gaps remain regarding how the human component may shape the future of these landscapes in a world where increasingly more tropical forests are embedded into human-dominated landscapes (Melo et al. 2013). These are the landscapes we will have to manage when aiming to increase both human livelihoods and the likelihood of persistent biodiversity, as very few large areas remain relatively free from human-caused disturbance and hence can be conserved as protected areas with restriction to direct use and exploitation (Ibisch et al. 2016).

The Caatinga in northeastern Brazil is the most populated dry forest of the world, with 28.6 million people living within its limits (Gariglio et al. 2010). These are amongst the poorest people in Brazil and the average Human Development Index is barely above that considered to be medium development (>0.5). Additionally, the Caatinga inhabitants strongly rely on natural resources for subsistence (Cavalcanti et al. 2015). Small-scale slash-and-burn agriculture, as well as free grazing by goats, can be considered the main land use type in the Caatinga, although some specific regions are subject to more intensive use such as irrigated agriculture, mining, and charcoal production (Schulz et al. 2017). This scenario generates a fuzzy mosaic of land uses across this ecosystem that is too complex to be assessed solely by traditional approaches derived from the landscape ecology.

Combining the best analytical tools from both natural and social sciences can be an alternative for evaluating the threats and trends in the Caatinga and other regions that are not suffering from the pressure of an expanding agricultural frontier. These ecosystems are not the main target for agricultural expansion like other more fertile and humid biomes such as tropical wet forests. Therefore, the main source of disturbance in these regions is the direct use of natural resources by inhabitants, which can vary a lot as a function of their socio-economic condition, access to industrialized goods, and market prices of both timber and non-timber forest products. These small-scale disturbances derived from the use of natural resources have been practiced for centuries in the Caatinga but have rarely been assessed properly as an important source of disturbance with the potential to reshape its biotic composition (but see Ribeiro et al. 2015, 2016). Only recently have studies explicitly detected how environmental features related to natural resource use affect plant and ant communities, leading to biological impoverishment regarding both taxonomic and phylogenetic diversity (Ribeiro-Neto et al. 2016; Ribeiro et al. 2015, 2016).

Socio-ecological studies of the impacts of the use of natural resources by smallholders on biodiversity are somewhat biased towards assessing game hunting (Torres et al. 2016), timber production (Shanley et al. 2002), and domestic use of fuelwood (Specht et al. 2015). Drawing a bigger picture of how these sources of disturbance can affect an ecosystem demands interdisciplinary approaches that are rarely found in the literature as they can easily lead to flawed data and weak conclusions.

In this chapter I present a theoretical framework on how to assess the role of human-caused disturbances in the Caatinga ecosystems which could eventually be generalizable to other ecosystems where both the landscape configuration and use of natural resources by human populations are likely to interplay as drivers of the response of the biota to disturbances. I use the results of a long-term ecological project taking place in the Catimbau National Park (https://www.peldcatimbau.org/), a typical sandy Caatinga with all kinds of disturbances from deforestation to overgrazing, including slash-and-burn agriculture and biological invasion. In this chapter, I try to put together pieces of evidence from several studies on the use of natural resources in the Caatinga and some theoretical approaches to better understand and predict the responses by this threatened ecosystem to the most common sources of disturbances taking place in this region.

14.2 The Role of Different Types of Disturbances in the Caatinga

14.2.1 Acute Disturbances

Habitat loss is the main cause of biodiversity loss and the greatest threat to ecosystem services worldwide (Thompson et al. 2017). This fact is not surprising as high deforestation rates are still a horrifying reality for many tropical regions, although reductions or even reversible trends (afforestation + regeneration) can be detected in some specific regions (e.g., China, Vietnam, Costa Rica) (Meyfroidt et al. 2010). Habitat loss is, therefore, an ‘acute’ disturbance as it usually happens very quickly and transforms the landscape in a manner such that one can easily distinguish the original habitat from the other land uses (Fahrig 2003). The scientific literature includes plenty of studies addressing both the effects of habitat loss and fragmentation on biodiversity as well as its socio-economic drivers. Because of this, conservationists have dedicated much of their research and political influence to creating protected areas with the aim of safeguarding as much as possible of the remaining natural habitats (Pimm et al. 2001).

According to non-official estimations, the Caatinga forest has lost up to 63% of its original area as a result of deforestation (Chap. 13). However, we do not know the pace of this habitat loss as this ecosystem is not continuously monitored like other ecosystems in Brazil such as the Amazon Forest and Atlantic Forest. The best official data available recorded deforestation over a period of 7 years (between 2002 and 2009) and registered average annual rates of around 0.2%, accumulating to approximately 2% deforestation during this period. The most recent study actually suggests a net gain in forest cover for the Caatinga in the last decade (Schulz et al. 2017). Probably because the soil in the Caatinga regions is not appropriate for agribusiness unless irrigated, the deforestation rate is below that across the humid tropics. The main cause of deforestation in the Caatinga is the use of tree biomass as firewood for the plaster and mining industries (MMA 2010).

14.2.2 Chronic Anthropogenic Disturbances

Chronic anthropogenic disturbances (CAD) can be defined as the "continuous harvesting of small portions of biomass" (Singh 1998) and the Caatinga forest has been chronically used for a long time and by many different cultures (MMA 2010). There is almost no single plant that is not used by local people for diverse purposes such as medicinal, fuelwood, fences, and housebuilding (Dos Santos et al. 2009). Also, small pockets of slash-and-burn agriculture and free-grazing goats are part of the Caatinga ecosystem as much as its remaining natural habitats, native fauna, and flora (MMA 2010). These scenarios constitute typical examples of how CAD has been affecting the Caatinga ecosystem for centuries. However, there is little to no scientific literature properly assessing the role of this source of disturbance as a driver of changes in biodiversity worldwide, and we are just beginning to understand its effect on the Caatinga biota, specifically plants and ants. For example, Ribeiro et al. (2015, 2016) found that the distance to the nearest city and number of livestock are inversely and directly related, respectively, to the taxonomic and phylogenetic diversity of woody plants. However, all of the available studies use proxies of CAD that are mostly related to accessibility to natural resources (e.g., distance to roads and cities), which may offer insightful clues on the shifts caused by natural resource use dynamics on this ecosystem. However, the drivers of natural resource use, as well as its intensity, need to be better and directly assessed if we are to understand the role of this source of disturbance on the Caatinga ecosystem. In Sect. 14.3, I present data on the potential impacts of three different types of CAD, directly measured in the Caatinga, namely fuelwood harvesting, free-ranging goats, and invasive species. The main goal is to understand the specific role of each of these types of disturbance in the reorganization of the native biota of the Caatinga and to try to draw a bigger picture of their impact on the Caatinga ecosystem.

14.3 Main Sources of Chronic Anthropogenic Disturbances

14.3.1 Fuelwood Harvesting

In the Caatinga ecosystem, fuelwood is the largest source of energy for both the industrial and domestic sectors (Ramos et al. 2008). The gypsum mining industries located in the Caatinga consume 1.5 million m^3/year of tree biomass and other small industries such as brickworks scattered throughout the region must have an important impact, but this is officially unknown along with its methods of harvesting native vegetation (Sá et al. 2009). In total, the domestic consumption of fuelwood by rural population in Caatinga is estimated to be the highest in Brazil (Sá et al. 2009). Therefore, the vegetation in this region is primarily degraded by unsustainable harvesting of tree biomass for both industrial and domestic purposes.

A case study in Catimbau National Park, in Pernambuco state, Brazil, confirmed this trend by assessing the relationship between socio-economic variables and use of fuelwood for 89 households located within this protected area. Briefly, up to 85% ($N = 80$) of the households interviewed in the Catimbau National Park depend on fuelwood for daily cooking, and 99% of this fuelwood is harvested from surrounding vegetation (Cavalcante 2015). The per capita consumption of fuelwood registered in this area reaches 606 ± 457 kg/year of woody biomass (Cavalcante 2015). If we extrapolate the per capita consumption to the entire population of the national park, estimated to be around 1200 people, we came to the astonishing number of 720 tons/year that is harvested only for fuelwood purposes. This is equivalent to the deforestation of up to 10 ha of the Caatinga every year (Cavalcante 2015). This pressure is not randomly distributed across species but focused on those useful as fuelwood, and therefore it is expected to cause severe impacts on specific populations of these species on a regional scale. The outcomes of this pressure are changes in the abundance and taxonomic composition of the remaining caatinga vegetation, as already observed in areas under high chronic disturbance pressure (Ribeiro et al. 2015, 2016).

The issue of fuelwood harvesting is more complex than it appears and has synergisms with both environmental and socio-economic changes experienced by human populations living within the Caatinga. First, some of this fuelwood demand is being met by an increasingly available resource, namely the invasive species *Prosopis juliflora*, which dominates abandoned agricultural areas along the riversides (Wakie et al. 2014). This species meets several demands and purposes beyond fuelwood for cooking, including feeding goats and cattle and fence building. Our data suggest that 20% of the households in the Catimbau use *P. juliflora* as an alternative to native tree species for those purposes, thus reducing pressure on native vegetation (Fig. 14.1).

Socio-economic drivers are also a determinant of whether a household tends to consume fuelwood as well as the amount of biomass harvested. Poorer people are more prone to relying on fuelwood to meet their daily needs for cooking; however, per capita income has been shown not to be a good predictor of biomass consumption

Fig. 14.1 Common scene of women head-carrying loads of fuelwood for cooking. Note the fences built with both native and exotic woody species in the Catimbau National Park, Brazil

(Specht et al. 2015). Many other factors may affect the amount of biomass consumed by rural people, some linked to economic issues (how much income is spent on butane gas) and the availability of human power to harvest fuelwood (Specht et al. 2015). Preferences for certain wood species with high calorific value must represent a greater pressure over high-valued species (Ramos et al. 2008) and these preferences have possibly changed the tree species composition of the Caatinga over the last three centuries to the point that what we see today should be the result of centuries of harvesting of tree species to meet the variable demands of the rural population.

14.3.2 Free-Ranging Domestic Goats

Official data from the Brazilian Government estimated a population of 7.6 million goats in the Caatinga in 2006 (IBGE 2006). However, this estimate is based on registered farms and therefore significantly underestimates the total number of goats being raised in the region. As a comparison, our data estimates 4–6 goats/km^2 for the study area as a whole and 11 goats/km^2 for those habitats preferentially selected by goats (Jameli 2015). This may represent 3–9 million unregistered animals for the region as a whole. Goats and sheep have been reported to cause important impacts on native vegetation elsewhere in the world, mainly on islands (Johnson et al. 1986). Overgrazing by these animals can change the vegetation structure and cause local species extinction (Johnson et al. 1986). Their effect on the Caatinga vegetation has been neglected by both Brazilian authorities and academia to date, despite the fact that government rural development programs have been promoting goat raising for decades.

Considering the Caatinga context, free-ranging goats must be one of the most important disturbance sources for natural vegetation as family-based, small-scale agriculture has been declining in the last decade (Schulz et al. 2017). Minimum-income programs (e.g., 'Bolsa Familia' and rural retirement) implemented by the Brazilian Government have probably pushed subsistence agriculture down as the workforce, once provided by family members including children, is now engaged in formal education as a requirement for assessing these programs. To date, the most cost-effective rural activity for poor households is raising free-ranging domestic goats. Our data for Catimbau National Park show that 80% of the approximately 200 families inhabiting this protected area raise goats as a source of income and protein. None of them employ any costly techniques other than providing a supplementary diet during dry seasons. There is a popular expression used by ranchers that 'goats are raised by nature (or God), not by people.' This summarizes very clearly how they recognize that these goats grow to feed on the natural vegetation with little to no human investment other than watching them to avoid losses.

One common assumption is that free-ranging domestic animals may represent a serious risk to natural environments (Carmel and Kadmon 1999; Schulz et al. 2016). This is supported by a vast set of evidence published elsewhere in the scientific literature. However, virtually no direct evidence exists on the impacts of goats in the Caatinga vegetation. An exception is that Schultz et al. (2016) demonstrated a reduction of soil carbon at shallow depths in the presence of goats. Ribeiro et al. (2016) also suggest that the total number of livestock (number of goats and cattle summed up) has a proportional negative effect on plant communities and affects their taxonomic composition in the Caatinga. Although insightful, these studies measured the effect of goats indirectly and combined with cattle, and conclusions are very limited on the real role of these animals in changes in vegetation. In this section I provide some evidence suggesting that we must be cautious before considering goats to be an important source of disturbance to Caatinga vegetation that is likely to have evolved in coexistence with large herbivores since ancient times (Pennington et al. 2000; França et al. 2015). The thorny caatinga vegetation presents several types of chemical and physical defenses against large herbivores such as spines, sclerophylly, and tannin. Therefore, the Caatinga ecosystem is likely to deal with herbivores in a better way than other seasonally dry tropical forests (SDTFs) where such functional attributes of plants are present but probably not as dominant as in the Caatinga. A first step to better understanding the role of grazing by free-ranging goats is to assess how goats move through caatingas and their range when using native vegetation for feeding.

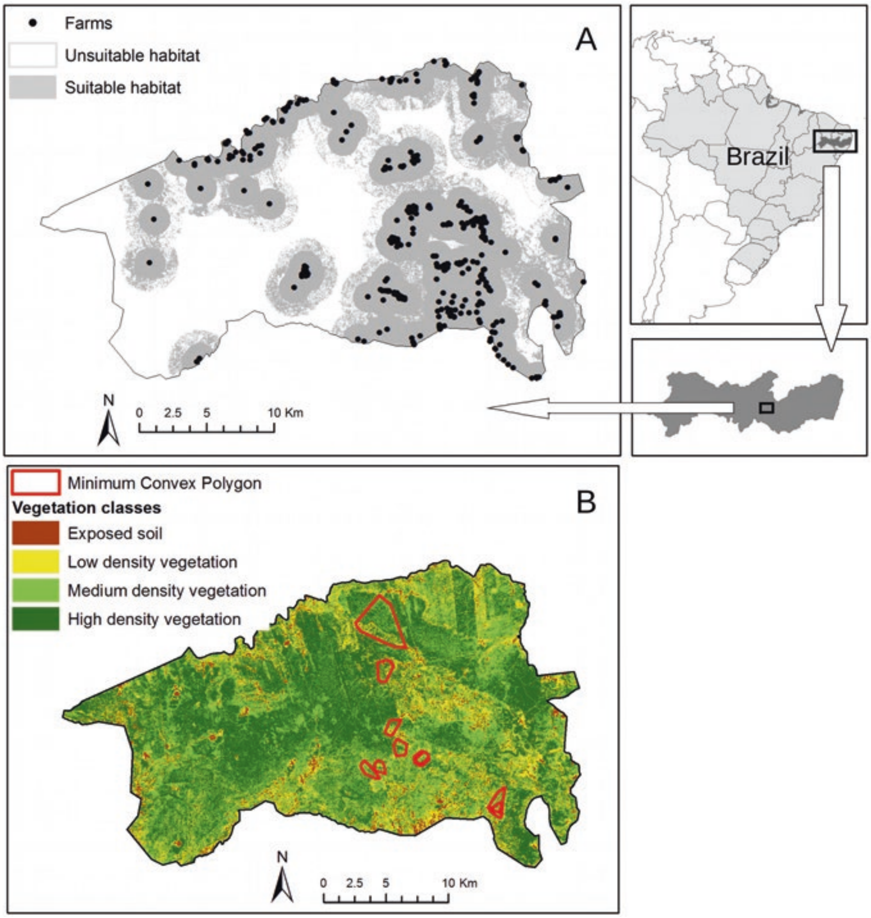

Fig. 14.2 Spatially explicit model of habitat use by free-roaming goats at the Catimbau National Park, Brazil. Distance to human settlements (**a**) and type of vegetation (**b**) are the predictor variables and suggest goats usually forage close to humans in regenerating areas dominated by pioneer species (Adapted from Jameli 2015)

Using small global positioning systems (GPS), we tracked ten free-ranging domestic goats for up to 14 days with the aim of ascertaining their home range as well as the type of vegetation they use more during the daytime (5:00 am to 5:00 pm) when feeding. Our results suggest that goats have a range of about 100 ha on average (Fig. 14.2) and can roam as far as 2.6 km from their owner's house (Jamelli 2015). However, the more interesting finding was that these domestic goats prefer successional areas over natural vegetation. They use open areas and less dense vegetation in a proportion higher than available in the landscape. The opposite is true for areas with denser vegetation (more mature forest), which goats tend to avoid and use in a proportion smaller than is available in the landscape (Jamelli 2015).

Therefore, the results available to date do not support the idea that goats are a significant degrading force of the Caatinga as has been suggested for islands or other regions. In the Caatinga, it is likely that they mostly act as a barrier to forest regeneration as they have been shown to be closely associated with human settlements. Our models demonstrate that the two most important variables predicting goat presence/absence in Catimbau National Park are (1) distance to the owner house; and (2) the successional state of the vegetation. In brief, goats tend to be found in open, successional areas close to their owner's houses, mostly feeding on abandoned agricultural fields where pioneer species proliferate. Goats in the Caatinga do not go feral as in other regions around the world but are extensively managed and avoid areas of denser vegetation.

14.3.3 Invasive Species

Biological invasion is amongst the most important cause of species extinction around the world (Malhi et al. 2014). However, recent literature has shown that such a phenomenon is more severe on islands and lakes than in continental biotas (Head et al. 2015). The 'few winners versus many losers' paradigm has been updated to include the role of native winners among those proliferating species that may cause biotic homogenization (Tabarelli et al. 2012). In continental biotas, exotic species, although potentially playing an important role, do not seem to be as important as the proliferation of natural disturbance-adapted species (Lobo et al. 2011). The Caatinga vegetation must respond in the same way, and disturbance-adapted native species must therefore be proliferating in human-altered ecosystems (e.g., Euphorbiaceae species; Rito et al. 2017).

The emerging concept of 'novel ecosystems' (sensu Hobbs et al. 2013) has shed light on the potential role of exotic species on the functionality of human-dominated ecosystems (Hobbs et al. 2014). Therefore, exotic invasive species, if managed, can be as useful as their native counterparts and contribute significantly to the functioning of emerging novel/hybrid ecosystems (Head et al. 2015). The Caatinga has been used and inhabited for millenniums, more intensively during the last three centuries when several exotic tree species have been introduced (Almeida et al. 2015).

One of the most important tree species with huge invasive potential is the 'mesquite' (as it is known in Mexico) or 'algaroba' (the common name used in the Brazilian Caatinga), the *Prosopis juliflora* (Fabaceae). This species is estimated to now occupy 1,000,000 ha of the Caatinga, with reports of negative effects on native tree and shrub species (Andrade 2015). The available models for *P. juliflora* show, for example, that they are closely linked to human settlements and riversides in Ethiopia (Wakie et al. 2014). In the Caatinga, we have found that former agricultural lands very close to riversides that are now abandoned are prone to invasion by *P. juliflora* (Fig. 14.3). Therefore, it is reasonable to link the abandonment of agricultural lands to the invasion of *P. juliflora* and, thus, land use changes (this time freeing land for forest recovery) led to a novel ecosystem.

Fig. 14.3 Border of a natural lake in the Catimbau National Park in Caatinga, heavily invaded by *Prosopis juliflora* (green belt) after abandonment of an area once used as agricultural field. Note in the picture that this invasive species is close to the water and is not found on drier soils

The interesting thing about the *P. juliflora* invasion is that it can be good for the Caatinga's socio-ecosystem as a whole because the benefits of this invasive species can be much greater than the damage it may cause, or at least this is a reasonable hypothesis. First, *P. juliflora* seems to be a poor competitor in less disturbed areas of the Caatinga as it appears to occur mostly in currently abandoned areas previously used for agriculture. This species is often found in mono-dominant stands mainly along riversides and dry river beds heavily degraded by former agriculture. The competitive ability of *P. juliflora* can be more easily demonstrated when it suppresses the growth of some native Caatinga species (Nascimento et al. 2014). In Catimbau National Park, the populations of *P. juliflora* are almost exclusively found along drainage networks and very close to human settlements (Freitas 2015; Fig. 14.3). Distance to rivers and to human settlements accounted for 46% of the likelihood of presence/absence of *P. juliflora* in this protected area (Freitas 2015). We can, therefore, consider that this species has been used and managed by humans for decades and therefore serves many purposes that would otherwise be met by exploring native vegetation.

14.4 How Is the Caatinga Managed by Humans?

Given the scenario presented here, we can draw a picture to understand how human presence in the Caatinga ecosystem has led to a set of modifications to its original characteristics, not necessarily with massive deforestation, but driven by what we have defined earlier as ‘chronic anthropogenic disturbance’ (CAD). One main lesson is that one must consider that at least three primary sources of changes that are acting in synergism lead to such transformations: (1) use of timber and wood for several purposes, mainly firewood; (2) millions of free-ranging domestic goats; and (3) invasive species colonizing abandoned agricultural lands. With these three sources of CAD in mind, we can propose a model to understand what we find in the Caatinga ecosystem today (Fig. 14.4).

First, it is useful to answer the following question: are the human-modified caatingas becoming a novel or hybrid ecosystem? Depending on the scale analyzed, we

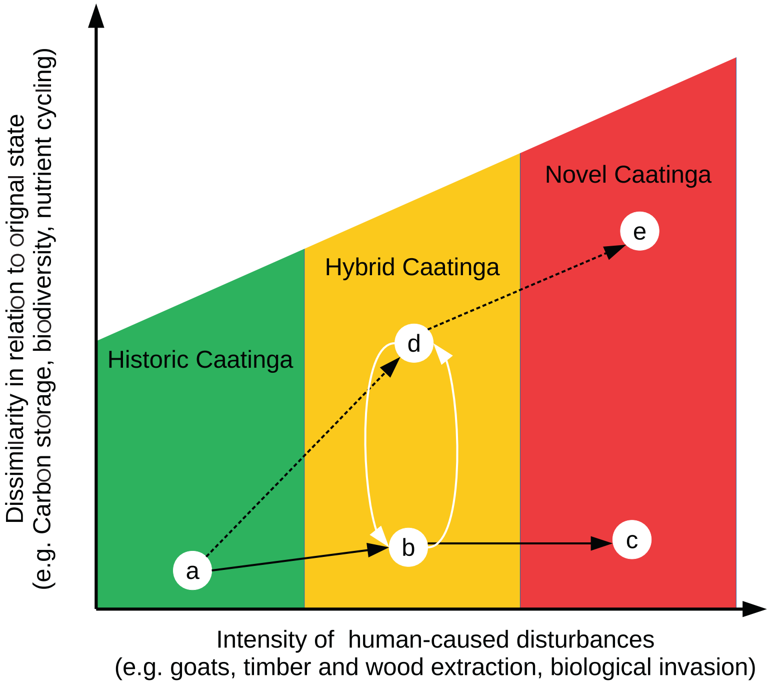

Fig. 14.4 Conceptual model of how chronic anthropogenic disturbance (x-axis) can be related to changes in both biotic and abiotic conditions (y-axis) of the Caatinga. Original ecosystem (green zone and circle ‘*a*’) can be modified following two paths depending on how local biota and abiotic conditions respond to disturbance. Well-managed Caatinga might follow the continuous arrows (states ‘*b*’ and ‘*c*’) preserving most of its original function and biotic/abiotic conditions. Shifts between states ‘*b*’ and ‘*d*’ probably take place when land rotation and restoration occurs. Otherwise, a degradation path can be followed if responses of the ecosystem lead to increasing dissimilarity due to overexploitation of the natural resources (Figure modified after Hallett et al. 2013)

may find both novel and hybrid scenarios. If we look at the millions of hectares of river banks once converted into agricultural fields and now abandoned and heavily invaded by *P. juliflora*, they can be considered to be a novel ecosystem (Hobbs et al. 2013). These areas have changed with regards to their biotic association (species assemblages) and diverge in function from that of pristine areas of caatingas (Hallett et al. 2013); they can, therefore, be considered as novel ecosystems. However, most of the region—which is not suitable for agricultural purposes—is somewhat conserved and resembles what was once (and still is) the most species-rich dry forest in the world, even with cumbersome and ancient timber extraction and grazing by millions of free-ranging goats, sheep, and cattle. These are the areas where CAD have been in action for centuries, probably changing the relative abundances of both plant and animal species and disrupting some ecological interactions but keeping the original physiognomy and largely its ecological function. These can be considered the hybrid ecosystems of the Caatinga region, conserving both biotic and functional resemblance in the original ecosystem.

Therefore, a more realistic picture can now be drawn of what the Caatinga we are talking about is. This SDTF is a very resilient ecosystem that has been able to deal with centuries of CAD but is currently threatened by large-scale deforestation and expansion of irrigated agriculture. Although acute disturbances are important in understanding the fate of an ecosystem, assessing the role of chronic disturbances is crucial for those biomes traditionally managed by humans long before the arrival of any agricultural frontiers. We cannot understand the biological organization of the Caatinga by searching only for landscape metrics measured by satellite images but must also look at the main socio-economic drivers of land-use change. These drivers will shape how people use natural resources and therefore the fate of the Caatinga.

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Chapter 15
Future Climate Change in the Caatinga

Roger Rodrigues Torres, David Montenegro Lapola,
and Nancy Laura Rios Gamarra

Abstract This chapter discusses the general aspects of climate variability and climate change in South America, with a special focus on Brazil's northeast region in which the Caatinga is located. It describes the main findings reported in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (IPCC AR5), and provides a brief review of the literature addressing climate change in northeast Brazil. In addition, simulations and projections of temperature and precipitation changes provided by 24 state-of-the art Earth System Models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) dataset that were analyzed in the IPCC AR5 are assessed. For scenarios of future projections, the near surface air temperature should increase by at least 1 °C for the Representative Concentration Pathways (RCP) 2.6 (low radiative forcing scenario) and by 4 °C for the RCP8.5 (high radiative forcing scenario) by the end of the twenty-first century. For the Caatinga, there is a considerable spread amongst rainfall change projections of ±1 mm day^{-1}, relative to 1961–1990, making it hard to identify any tendency in projected rainfall change. However, the RCP8.5 forcing scenario shows a slight rainfall reduction of about 0.3 mm day^{-1} by 2100. Among the most affected regions in Brazil, the Amazon and northeast regions appear to be large hotspots. For some modeling studies, projections of the future climate show a savannization of parts of the Amazon and desertification of the Caatinga region, with potential adverse impacts on biodiversity, supply and quality of water resources, carbon storage, and the provision of other ecosystem services.

Keywords Climate change • Northeast Brazil • Caatinga • Drought • Vulnerability • Impacts

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15.1 Introduction

Earth's climate shows variabilities in almost all time scales, from the annual to the multi-decadal scale. In some of these scales, climate variability is due to the intrinsically random nature of processes or due to numerous and complex causes (often unknown or poorly understood scientifically) that make it difficult to forecast (Giorgi 2005). Therefore, the use of climate information is frequently based on statistical analysis of historical series of observed climate variables (Barros et al. 2006).

Several decades ago, the use of climate information was based on the hypothesis that the climate was stationary, at least in the decadal scale, and thus future climatic conditions could be predicted only using a robust series of observed data in previous decades (Barros et al. 2006). However, this hypothesis of climate stationarity is no longer accepted by the scientific community given abundant evidence that human activities have contributed to a rapid change in known climatic patterns (IPCC 2007, 2013).

In this context, the term 'climate change' refers to a change in the state of the climate locally or globally, which can be identified (e.g., using statistical tests) by changes in the mean and/or the variability of its properties (e.g., rainfall, temperature, wind), and that persists for an extended period, typically decades or longer (Giorgi 2005; IPCC 2007). Climate change may be due to natural internal processes of the climate system[1] (e.g., the occurrence of El Niño/La Niña events in the seasonal to interannual time scale) or external forcings, or to persistent anthropogenic changes in the composition of the atmosphere or in land use (Glossary of Intergovernmental Panel on Climate Change Fourth Assessment Report [IPCC AR4] [IPCC 2007]).

Since its formation about 4.6 billion years ago, Earth's climate has undergone numerous changes due to the natural variability of the climate system. These natural changes occurred mainly as a result of the following external forcings:

- Changes in the structure and composition of the Earth's atmosphere during its formation
- Continental drift
- Variations in eccentricity, axial tilt, and precession of Earth's orbit (Milankovitch cycles)
- Volcanic eruptions, which cause the release of particles into the atmosphere (especially aerosols) that can be suspended for up to several months at higher levels of the atmosphere

These factors, which are cyclic in most cases, change the radiation balance in the climate system and cause large changes in the temperature of the planet (IPCC

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[1] The 'climate system' consists of five major components that interact with each other: the atmosphere, hydrosphere, cryosphere, lithosphere, and biosphere. The climate system changes over time because of the influence of its own internal dynamics and because of natural and anthropogenic external forcings.

2007). However, except for volcanic eruptions, these changes occur on a scale of thousands of years, which is too slow to be perceived in the lives of human beings. For this reason, the changes in climate that scientists have observed in recent decades (and which are included in the various reports of the Intergovernmental Panel on Climate Change [IPCC]) are more intense and faster than those observed for any known natural factor (IPCC 2007, 2013).

On the other hand, other external forcings that can also significantly contribute to a change in climate are those arising from human activities, such as changes in the composition of the atmosphere and land use changes,[2] which occur on time scales compatible with those abrupt changes observed in Earth's climate in recent decades (Meehl et al. 2007). These forcings are primarily responsible for the so-called 'greenhouse effect.' This term has been used since the nineteenth century to refer to a natural phenomenon associated with the property that some gases in the atmosphere (greenhouse gases [GHGs]) absorb and isotropically re-emit the long-wave radiation (specifically, thermal infrared radiation) emitted by Earth's surface (Meehl et al. 2007; IPCC 2007). Part of this radiation is directed back to the surface and lower levels of the atmosphere, resulting in a temperature rise of Earth's surface and the surrounding air.

GHGs are those gaseous constituents of the atmosphere, both natural and anthropogenic, that absorb and emit radiation at specific wavelengths within the spectrum of thermal infrared radiation emitted by the Earth's surface, the atmosphere itself, and by clouds. This property causes the greenhouse effect. Water vapor (H_2O), carbon dioxide (CO_2), nitrous oxide (N_2O), methane (CH_4), and ozone (O_3) are the primary GHGs in the Earth's atmosphere (Glossary of IPCC AR4, [IPCC 2007]).

However, the greenhouse effect is essential to Earth. Without it, life on Earth would not be possible, because without this, the mean temperature near the surface would be about −19 °C, in contrast to the +15 °C observed (IPCC 2007). Therefore, GHGs are critical to maintaining the planet being able to house all living beings. However, in recent decades, the greenhouse effect has taken on a negative connotation, being associated with climate change and global warming. This is due to the fact that with the intense and growing GHG emissions resulting from human activities, the greenhouse effect has intensified so that a larger amount of radiation is trapped in the lower layers of the atmosphere, and, hence, the temperature of the planet increases and some changes in Earth's climate occur.

Since the industrial revolution, the concentration of GHGs has increased remarkably in the atmosphere. For example, the concentration of CO_2 increased by over

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[2] 'Land use' refers to the total of arrangements, activities, and inputs undertaken in a certain land cover type (a set of human actions). The term 'land use' is also used in the sense of the social and economic purposes for which land is managed (e.g., grazing, timber extraction, and conservation). 'Land use change' refers to a change in the use or management of land by humans, which may lead to a change in land cover. Land cover and land use change may have an impact on the surface albedo, evapotranspiration, sources and sinks of greenhouse gases, or other properties of the climate system and may thus have a radiative forcing and/or other impacts on climate, locally or globally (Glossary of IPCC AR4 [IPCC 2007]).

35%, while the concentration of CH_4 increased by more than 2.5 times (IPCC 2007). The global increase in CO_2 concentration is mainly due to the use of fossil fuels and land use change, while the increase in CH_4 and N_2O concentrations is due primarily to agricultural and livestock practices (IPCC 2007).

The distinction between the effects caused by various external forcings and the natural variability of the climate system requires a careful comparison between the changes observed and those expected as a result of certain forcings. The studies that address this issue are known as 'detection and attribution of climate change' studies; they are based on thorough physical understanding of the mechanisms and feedbacks that govern the climate system and use a statistically complex and cautious treatment of the observed data (Hegerl et al. 2007; Stott et al. 2010).

Since the innumerous processes occurring in the climate system cannot be accurately reproduced in a laboratory experiment, scientists use numerical models known as climate models or Earth System Models (ESMs) to understand the possible responses and behaviors of this system when submitted to certain forcings, as well as to project the climate in the coming decades and centuries (Giorgi 2005). A climate model consists of a huge system of discretized differential equations of high complexity (transformed into a computer code containing thousands of command lines and subroutines) representing, among other things, the physical, chemical, and biological laws that govern the behavior of the climate system components (ocean, atmosphere, biosphere, etc.) and their interactions.

When the climate system is highly complex and has many processes that are still unknown or poorly understood by scientists (Giorgi 2005), climate models are approximate representations of this system. However, climate models are gradually evolving with the emergence of new scientific discoveries and new methods of analysis and measurement. This evolution can be observed, for example, through the five generations of climate models belonging to the Coupled Model Intercomparison Project [CMIP] (http://cmip-pcmdi.llnl.gov).

However, even though climate models are approximations of the climate system, the extent to which a model is able to reproduce the main features and the variability of the observed climate increases our confidence that this model can project future changes in climate (Torres and Marengo 2013, 2014). Moreover, despite the complexity involved in the simulation of the climate system, in large spatial scales and decadal and longer time scales it is expected that it will be possible to simulate the climate with reasonable reliability (Knutti 2008).

With the advancement of studies on climate change in recent years, the vast majority of climate scientists around the world take the fact that human activities are primarily responsible for observed climate changes for granted (IPCC 2007, 2012, 2013). Such changes are known as anthropogenic climate changes. The influence of humans in modifying both the composition of the atmosphere and the land surface of the continents during the last centuries has become so marked that some scientists have established a new geological era up to the present day known as 'Anthropocene', a term coined by the winner of the Nobel Prize in Chemistry in 1995, Paul Crutzen.

In order to better understand and try to project the climate in the coming decades, the World Meteorological Organization (WMO) and the United Nations Environment Programme (UNEP) established the IPCC in 1988. The IPCC consists of a group of hundreds of scientists from different countries around the world who meet periodically to discuss the latest research and discoveries about climate change. During these meetings, the scientists assess the current knowledge on climate change and prepare technical reports on possible impacts of climate change on humans and the planet's biodiversity in order to assist policy- and decision-makers in the design of adaptive and sustainable measures for countries.

According to the information contained in the IPCC Fifth Assessment Report (IPCC AR5) published in 2013, scientists conclude that the warming of the climate system is unequivocal, and many of the observed changes since the 1950s are unprecedented over decades to millennia. The atmosphere and ocean have warmed, the snow and ice have diminished, the sea level has risen, and the concentrations of GHGs have increased (IPCC 2013). Additionally, scientists conclude that it is very likely that emissions of anthropogenic GHGs affected the Earth's climate in the twentieth century and will continue to cause further warming and changes even more markedly in this century.

The global mean surface temperature over the last 100 years increased by approximately 0.7 °C, with most of that increase situated in the latter half of the twentieth century following the large increase in anthropogenic emissions during this period. According to climate projections for 2081–2100 relative to 1986–2005 contained in the IPCC AR5, the increase in global mean temperature is likely to be in the range of between 1 °C and 4 °C, accompanied by an increase of precipitation of around 2–6%. Moreover, these projections also indicate that most of these changes in temperature and precipitation around the world will be accompanied by more frequent extreme events such as heat waves, droughts, and heavy rains, which will cause numerous impacts on populations around the world (IPCC 2013).

Following the general context of climate change given already, Sect. 15.2 presents current climate simulations of near surface air temperature and rainfall over the Caatinga region produced by innumerous state-of-the-art ESMs. Climate simulations of precipitation and temperature are evaluated against observations to provide a measure of reliability of climate change projections and related uncertainties. Section 15.3 shows temperature and precipitation change projections covering the entire twenty-first century over the Caatinga region, as well as trends in climate extremes in the region. Finally, Sect. 15.4 presents some concluding remarks.

15.2 Present Climate Simulations Over the Caatinga Region by Earth System Models

As stated in the previous section, the current climate change projections are based exclusively on the use of climate models or ESMs, such as those belonging to the CMIP Phase 5 (CMIP5) dataset, the results of which are presented in this chapter (Table 15.1). Despite the continuous improvement of these models and the enormous growth in computing power in recent decades which enabled scientists to include numerous physical and dynamic processes and increased the spatial and temporal resolution with which they are set, the models are still being processed with spatial low resolution (of the order of hundreds of kilometers) and inadequate physical parameterizations (in part because of the difficulty of representation of some physical and dynamical processes in a low spatial scale, but also due to the

Table 15.1 List of models, approximate model horizontal resolutions, future (Representative Concentration Pathways [RCPs] 2.6, 4.5, 6.0, 8.5) and historical simulations, and number of runs in the Coupled Model Intercomparison Project Phase 5 (CMIP5) dataset used in this chapter

Models	Resolution (latitude/longitude)	Historical	RCP			
			2.6	4.5	6.0	8.5
FGOALS-g2	3.1° × 2.8 °	4	1	1	–	1
BCC-CSM1-1	2.8° × 2.8 °	3	1	1	1	1
CanESM2	2.8° × 2.8 °	5	5	5	–	5
MIROC-ESM	2.8° × 2.8 °	3	1	1	1	1
FIO-ESM	2.8° × 2.8 °	1	1	1	1	1
MIROC-ESM-CHEM	2.8° × 2.8 °	1	1	1	1	1
GFDL-CM3	2.0° × 2.5 °	5	1	1	1	1
GFDL-ESM2G	2.0° × 2.5 °	1	1	1	1	–
Giss-E2-R	2.0° × 2.5 °	5	1	5	1	1
GFDL-ESM2M	2.0° × 2.5 °	1	1	1	1	1
IPSL-CM5A-LR	1.9° × 3.8 °	4	1	3	1	3
NorESM1-M	1.9° × 2.5 °	3	1	1	1	1
CSIRO-Mk3-6-0	1.9° × 1.9 °	10	10	10	10	10
MPI-ESM-LR	1.9° × 1.9 °	3	3	3	–	3
INMCM4	1.5° × 2.0 °	1	–	1	–	1
CNRM-CM5	1,4° × 1,4 °	1	1	1	–	1
MIROC5	1.4° × 1.4 °	1	1	1	1	1
IPSL-CM5A-MR	1.3° × 2.5 °	1	1	1	–	1
HadGEM2-CC	1.3° × 1.9 °	1	–	1	–	1
HadGEM2-ES	1.3° × 1.9 °	4	1	1	1	4
ACCESS1.0	1.3° × 1.9 °	1	–	1	–	1
EC-EARTH	1.1° × 1.1 °	1	1	1	–	1
MRI-CGCM3	1.1° × 1.1 °	5	1	1	1	1
CCSM4	0.9° × 1.3 °	6	5	5	5	5

Models are ranked by their spatial resolution (as used in Torres and Marengo 2014) still inadequate knowledge of the processes involved such as cloud parameterization) (Giorgi 2005; Collins 2007; Räisänen 2007; Tebaldi and Knutti 2007; Annan and Hargreaves 2010; Knutti et al. 2010, 2013). Thus, the ESMs do not have a perfect representation of the current climate and do not allow for a refined spatial analysis of climate change projections, essential in studies of impact, adaptation, and vulnerability.

Therefore, given the above-mentioned problems, the first step to evaluating the climate projections in a certain region is to evaluate how climate models are representing at least the basic characteristics of the current climate in this region. Thus, this section assesses how climate models represent the climate of northeastern Brazil where the Caatinga is located.

Specifically, temperature and precipitation variables provided by 24 state-of-the art ESMs (representing nearly 450 runs, Table 15.1) from the CMIP5 dataset (Taylor et al. 2012) that were analyzed in the IPCC AR5 are assessed. The CMIP5 climate simulations and projections analyzed in this chapter were provided by the Program for Climate Model Diagnosis and Intercomparison (PCMDI; http://www-pcmdi.llnl.gov). Simulations for the twentieth century are compared against the observed surface air temperature and precipitation from the CRU TS 3.0 dataset (Mitchell and Jones 2005) produced by the University of East Anglia Climate Research Unit (UEA/CRU). Hereafter, the term 'simulation' refers to those numerical experiments with ESMs performed to observed climate periods (e.g., 1901–2000), and the term 'projection' refers to those experiments relating to future periods (e.g., 2020–2100) carried out by a given climate forcing. Moreover, changes refer to the difference between the mean values of the climate variables projected for the period 2071–2100 ('future climate') and simulated for 1961–1990 ('present-day' climate). Additionally, climate simulations and projections are evaluated at seasonal means as follows: austral summer (December to February [DJF]), fall (March to May [MAM]), winter (June to August [JJA]), and spring (September to November [SON]).

The CMIP5 climate projections are performed using the new generation of radiative forcing[3] scenarios called Representative Concentration Pathways (RCP) (Moss et al. 2010), and denominated as RCP 2.6, 4.5, 6.0, and 8.5, corresponding to an approximate radiative forcing by the end of the century of 2.6, 4.5, 6.0, and 8.5 Wm^{-2}, respectively, relative to pre-industrial conditions. With regard to the equivalent CO_2 concentrations, these RCPs correspond roughly to 490, 650, 850, and 1370 ppm, respectively, in 2100. Further details of the RCPs can be found, for example, in Moss et al. (2010) and van Vuuren et al. (2011).

Compared to the previous generation of climate models belonging to the CMIP Phase 3 (CMIP3) dataset, CMIP5 ESMs show slightly higher horizontal resolutions (approximately 1–3 ° of latitude/longitude) and also includes ESMs and experi-

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[3] Radiative forcing is the change in the net, downward minus upward, irradiance (expressed in W m^{-2}) at the tropopause (boundary between the troposphere and the stratosphere) due to a change in an external driver of climate change, such as, for example, a change in the concentration of carbon dioxide or the output of the Sun (Glossary of IPCC AR4 [IPCC 2007]).

ments that are more comprehensive (e.g., including carbon cycle or decadal climate predictability experiments), which allows scientists to explore a broader spectrum of scientific questions. Moreover, some of the main improvements in the CMIP5 ESMs are the addition of interactive ocean and land carbon cycles of varying degrees of complexity, and the more complete representation of radiative forcings due to, among other things, the inclusion of more comprehensive modelling of the indirect effect of aerosols and the use of time-evolving volcanic and solar forcing in most models (Taylor et al. 2012; Knutti and Sedlácek 2013; Sillmann et al. 2013a).

Northeast Brazil (NEB) has a total area of about 1.5 million km^2 and most of this region has a semiarid climate due to the prevailing rainfall regime (Torres and Ferreira 2011). However, while portions of the inland dry regions receive less than 600 mm of rainfall annually, the east coast receives around 2000 mm (Kousky and Chu 1978; Rao et al. 1993).

It is possible to identify different rainfall patterns in NEB. In the northern part of this region, the main rainy season occurs from March to April; in the south, the rainy season is observed from December to February; and on the east coast it occurs from May to July (Strang 1972; Rao et al. 1993). Moreover, there are regions with superimposed periods of maximum rainfall, such as the central and northeastern parts of the state of Bahia, where the maximum observed rainfall occurs from December to March, and the coastal part of Bahia, where the maximum occurs from December to May (Strang 1972; Kousky and Chu 1978). The spatial variability of annual rainfall is also high in NEB (Rao et al. 1993).

The maximum rainfall amount observed during the March–April period in northern NEB can be attributed to the latitudinal displacement of the intertropical convergence zone[4] (ITCZ), which reaches its southernmost position during these months (Hastenrath and Heller 1977). The observed maximum during November–December in the southern part of the region can be attributed to frontal systems that reach low latitudes and interact with convective activity from the Amazon Basin or from the northern coast of Brazil (Kousky 1979). Several attempts have been made to explain the rainfall maximum in autumn and winter along the east coast of NEB. Yamazaki and Rao (1977) emphasized the importance of westward-propagating cloud systems, as detected in satellite images over the Atlantic Ocean. Kousky (1979) showed that rainfall in eastern NEB is influenced by breeze circulations, mainly during the night. Kousky (1979) attributed the nocturnal maximum to the formation of a convergence zone between the land breeze and the background wind field. He also noted that the land breeze is strongest during autumn and winter, when the temperature contrast between land and sea is higher than normal. Studies such as Rao et al. (1993) indicate that the position and intensity of the South Atlantic subtropical high is an important mechanism for the low-level transport of water vapor toward NEB. Torres and Ferreira (2011) identified the occurrence of easterly wave distur-

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[4] The ITCZ (intertropical convergence zone) is the area encircling the Earth near the equator which represents the junction between the southeast and the northeast trades (of the Southern and Northern Hemispheres, respectively). The ITCZ appears as a band of clouds that circle the globe near the equator.

bances in the wind field, which propagated westward over the tropical South Atlantic Ocean during the austral autumn and winter. When these disturbances interact with local circulations, low-level convergence increases, causing strong rainfall on the eastern and northern NEB coasts.

Figure 15.1a–j shows the seasonal and annual precipitation observed and simulated over the Caatinga region from the average of all CMIP5 ESMs listed in Table 15.1 for the period 1961–1990. In general, the ensemble mean represents the observed climatological patterns of precipitation over the Caatinga well. However, some biases can be observed in some localities (Fig. 15.1k–o). For example, rainfall simulations show a wet bias (up to 4 mm day^{-1}) over the most of the region in austral summer and fall, but a very slight (<1 mm day^{-1}) wet or dry bias in austral winter and spring.

With respect to the simulation of the near surface air temperature, the average of the ensemble is very similar to the patterns observed (Fig. 15.2a–j) and the bias does

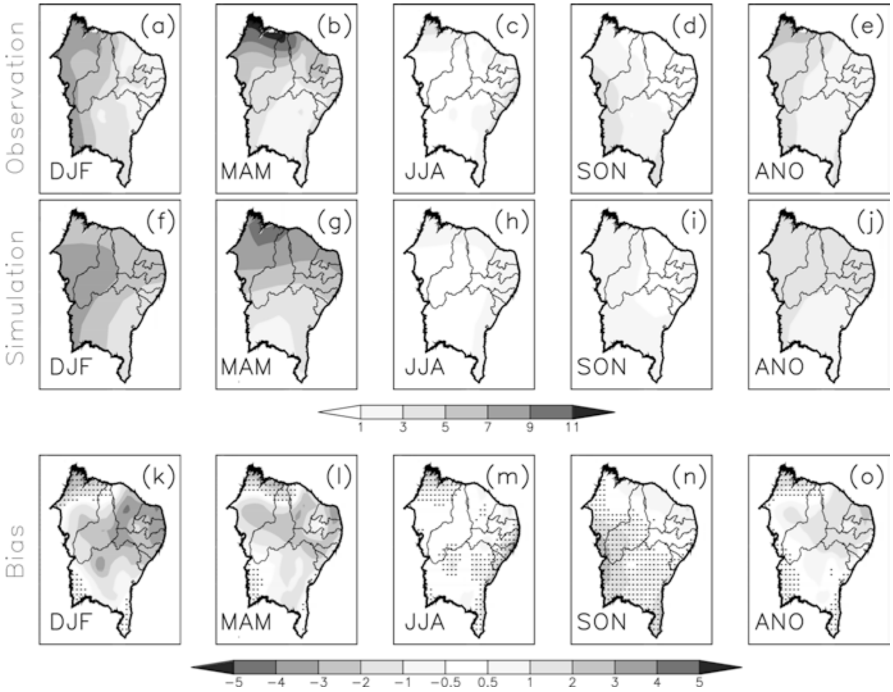

Fig. 15.1 Seasonal and annual mean precipitation from observations (**a**–**e**) and from the ensemble mean of climate models simulations (**f**–**j**) for northeast Brazil for the reference period 1961–1990. Bias (**k**–**o**) is defined as model minus observation. Dots indicate negative values. Climate simulations were obtained from the Coupled Model Intercomparison Project Phase 5 (CMIP5) models listed in Table 15.1, and observations from the Climate Research Unit dataset (CRU 3.0 dataset; Mitchell and Jones 2005). Results are shown for the austral summer, fall, winter and spring (December to February [DJF], March to May [MAM], June to August [JJA], and September to November [SON], respectively) and annual mean (ANO). Values are in mm day^{-1} (Adapted from Marengo et al. 2016)

not exceed 1 °C in most of the region (Fig. 15.2k–o). On the other hand, the ensemble mean shows a cold bias (1–3 °C) in some parts of the Caatinga region from austral summer to winter.

The annual cycles of rainfall and temperature for the present climate are reasonable well-simulated by the ensemble mean of the ESMs, although different performances can be noticed when evaluating the individual models (Fig.15.3). The timing of the February–April peak of the rainy season is well-depicted by the models (Fig. 15.3a), albeit with some models underestimating or overestimating the observed rainfall. The mean observed peak of the rainy season from CRU varies from 5 to 6 mm/day, while the ensemble models show 6–7 mm/day. With regard to temperature (Fig. 15.3b), the models tend to overestimate the amplitude of the annual cycle and underestimate temperatures during summer to spring (by <1 °C).

The aforementioned deficiencies in the simulation of climate conditions in the region (represented here by precipitation and temperature) may be related to numer-

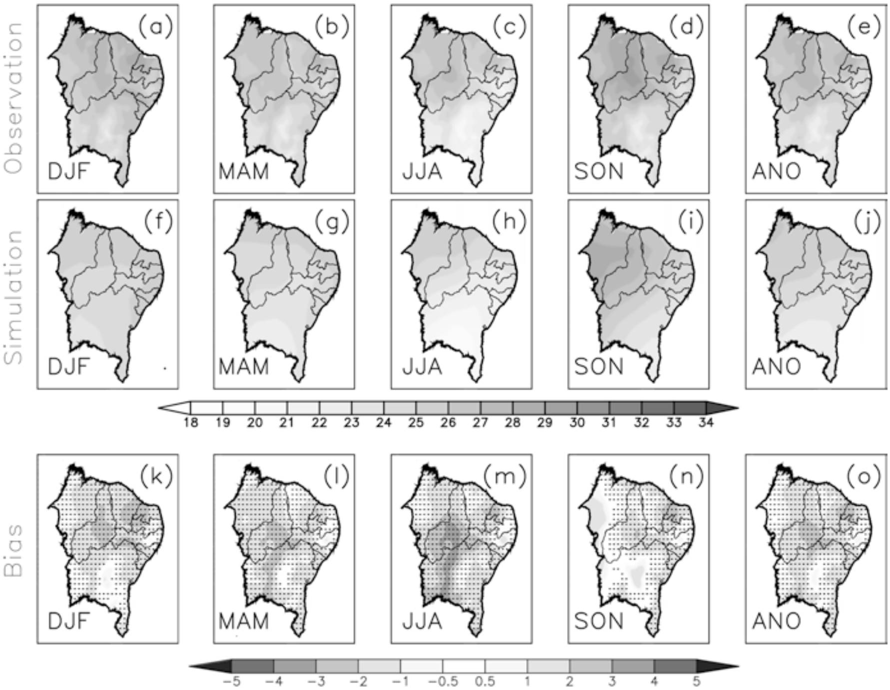

Fig. 15.2 Seasonal and annual near surface air temperature from observations (a–e) and from the ensemble mean of climate models simulations (f–j) for Northeast Brazil for the reference period 1961–1990. Bias (k–o) is defined as model minus observation. Dots indicate negative values. Climate simulations were obtained from the Coupled Model Intercomparison Project Phase 5 (CMIP5) models listed in Table 15.1, and observations from the Climate Research Unit dataset (CRU 3.0 dataset; Mitchell and Jones 2005). Results are shown for the austral summer, fall, winter and spring (December to February [DJF], March to May [MAM], June to August [JJA], and September to November [SON], respectively) and annual mean (ANO). Values are in degree symbol missing. kindly insert in superscript position °C (Adapted from Marengo et al. 2016)

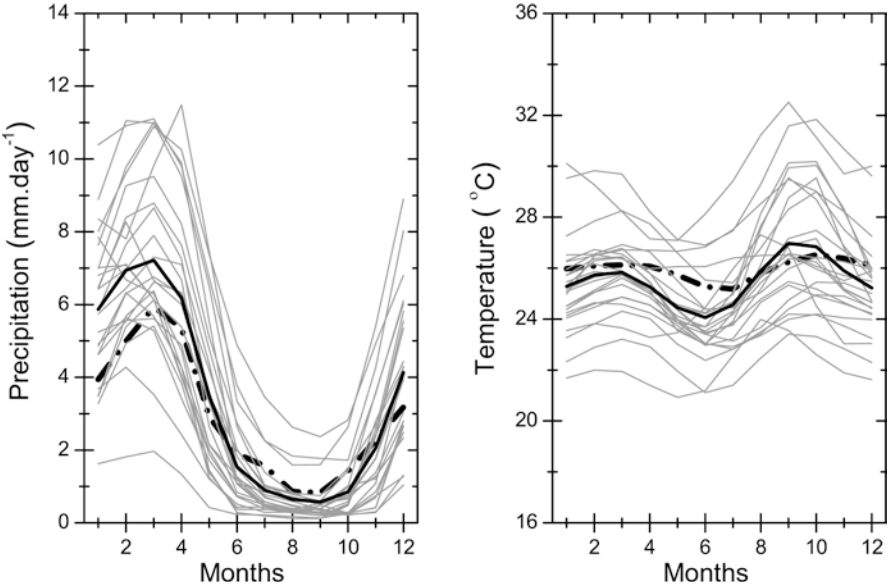

Fig. 15.3 Observed and simulated seasonal cycle of precipitation (left panel) and temperature (right panel) in the Caatinga region for the reference period 1961–1990. Climate simulations were obtained from the Coupled Model Intercomparison Project Phase 5 (CMIP5) models listed in Table 15.1, and observations from the Climate Research Unit dataset (CRU 3.0 dataset; Mitchell and Jones 2005). In each one of the panels the thick black lines represent the ensemble model mean, the thick dash dot lines represent observations, and individual models are shown using thin lines. Values for precipitation and temperature are in mm day^{-1} and °C, respectively

ous factors, among which can be highlighted: (i) horizontal resolution of ESMs is still rough and does not allow a more refined detail of the topography of the region; (ii) deficiencies in the cloud parameterization schemes; (iii) deficiencies of ESMs in properly representing the water vapor transport and moisture convergence over the region; and (iv) poor representation of biosphere–atmosphere interactions, soil moisture, and other processes in the planetary boundary layer. On the other hand, there is a large deficiency in the spatial and temporal coverage of observed data over South America, which must certainly influence the magnitude and location of the bias patterns, mainly for precipitation.

Therefore, despite the bias presented by the simulations of precipitation and temperature for the models analyzed, it can be concluded that the models could represent reasonably well the observed climatic conditions over the Caatinga region, given the complexity involved in these simulations. Therefore, these results give us good reliability for use in evaluating the projections of climate change presented in Sect. 15.3.

15.3 Climate Change Projections in South America

Several studies have identified South America as one of the regions in the world that may be deeply affected if current climate change projections are realized, especially in the tropical region of the continent (e.g., Baettig et al. 2007; IPCC 2007, 2013; Torres et al. 2012; Sillmann et al. 2013a, b; Torres and Marengo 2014). The region is vulnerable to current climate variability and extremes, mainly in the form of intense rain and floods or dry spells, and may be affected by more frequent extremes in a warmer climate (Marengo et al. 2010a, b; Rusticucci et al. 2010).

In particular, current climatic projections indicate that considerable changes may occur in the climate of Brazil during the twenty-first century (Torres and Marengo 2014; Magrin et al. 2014). Considering that in Brazil the production of food, commodities, and energy is highly dependent on climate and that a considerable part of the population is in a socially vulnerable situation (i.e., with overall low human development levels and/or living in risky areas), it is expected that climate change will likely have strong negative social impacts (Magrin et al. 2014; Darela-Filho et al. 2016). Examples of climate-driven high social and economic costs are evident in the severe drought of 2013–2015 that negatively affected water availability in large cities in southeast Brazil (Coutinho et al. 2015) and caused relentless suffering in NEB (Lindoso et al. 2014). However, while climate change mitigation has been on the agenda of the Brazilian Government for several years (IPEA 2011), effective long-term adaptation planning has lagged. This reinforces the importance of the discussion of this issue in Brazilian society so that adaptation measures for vulnerability reduction should be taken as soon as possible to avoid greater losses.

In recent years, numerous studies have examined the projections of climate change in South America, relying mainly on climate models from the CMIP3 and CMIP5 dataset (e.g., Boulanger et al. 2006, 2007; Vera et al. 2006; Vera and Silvestri 2009; Bombardi and Carvalho 2009; Seth et al. 2010; Junquas et al. 2012; IPCC 2007, 2013; Blázquez and Nuñez 2013; Joetzjer et al. 2013; Jones and Carvalho 2013; Torres and Marengo 2014). Several studies also analyzed the climate projections in the region using some downscaling methods in the results of ESMs (e.g., Nuñez et al. 2008; Urrutia and Vuille 2009; Boulanger et al. 2010; Marengo et al. 2009, 2010a, 2012; Bidegain et al. 2012; Chou et al. 2012). In general, the projections shown in those studies are in agreement with those shown in IPCC AR5 (IPCC 2013).

According to the results presented in IPCC AR5 (IPCC 2013), warming has been detected throughout South America (around 0.7 °C to 1 °C since the mid-1970s), as well as significant trends in precipitation. In addition, changes in climate variability and in extreme events have severely affected the region. Increases in temperature extremes have been identified in most of tropical and subtropical South America, while more frequent extreme rainfall in southeastern South America has favored the occurrence of landslides and flash floods (IPCC 2013).

Regarding climate projections, all studies mentioned in IPCC AR5 suggest increases in temperature and increases or decreases in precipitation for South

America by 2100. Projected warming varies from 1.7 °C (low radiative forcing scenario) to 6.7 °C (high radiative forcing scenario), where the magnitude of the major changes is located in the tropical portion of the South American continent. Rainfall changes for the region presents low confidence and varies geographically, most notably showing a reduction of 22% in NEB and an increase of 25% in southeastern South America. Additionally, projections show with medium confidence an increase in dry spells in tropical South America east of the Andes and in warm days and nights in most of this region by 2100.

Torres and Marengo (2014) identified possible hotspots of climate change in South America through an examination of the spatial pattern of the Regional Climate Change Index (RCCI) over the region by the end of twenty-first century (Fig. 15.4). The RCCI is a qualitative index that can synthesize a large number of climate model projections and is suitable for identifying those regions where climate change could be more pronounced in a warmer climate. This index is based on four variables representing climate change: change in temperature in a given specific region relative to the change in global mean temperature; change in average rainfall; and changes in the interannual variability of temperature and precipitation. All changes addressed in that study are related to projections for the period of 2071–2100 relative to 1961–1990. Torres and Marengo (2014) found that Southern Amazonia and the central-western region and western portion of Minas Gerais state in Brazil are persistent climate change hotspots through different forcing scenarios and ESMs belonging to CMIP3 and CMIP5 datasets. In general, as the scenarios vary from low- to high-level forcing, the area of high RCCI values increases and the magnitude intensifies from central-western and southeast Brazil to northwest South America. In general, the climatic hotspots identified in that study are characterized by an increase in the mean surface air temperature, mainly in the austral winter; by an increase of interannual temperature variability, predominantly in the austral summer; and by a change in the mean and interannual variability of precipitation during the austral winter. Although the Caatinga region is not identified as the most prominent hotspot in South America in that study, medium to high RCCI values can be noticed, mainly in the southern part of the region (Fig. 15.4).

15.4 Temperature and Precipitation Change Projections Over the Caatinga

The IPCC AR4 and AR5 (IPCC 2007, 2013) suggest that climate change is adversely affecting the ecosystems over the entire Earth. Projections of future climate using different global and regional climate models indicate that the distribution of the biomes around the world can be modified in the future due to increasing global warming, leading in general to increased aridity (Salazar et al. 2007; Lapola et al. 2009; Franchito et al. 2014). Expansion of subtropical desert and semi-desert zones

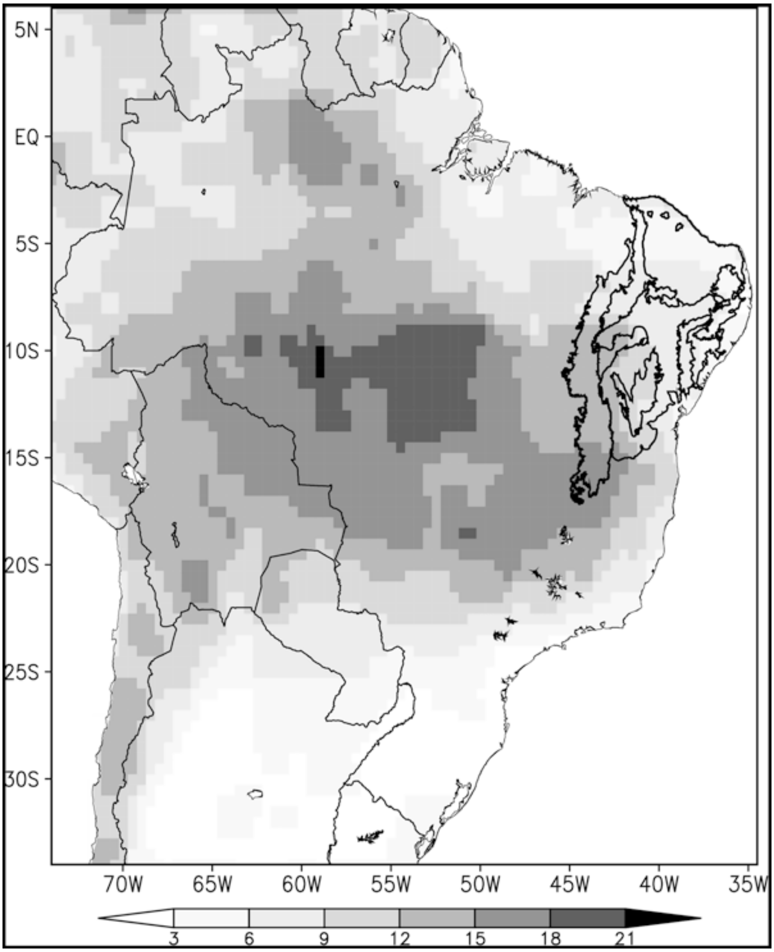

Fig. 15.4 Regional Climate Change Index (RCCI) for South America using climate projections of the Coupled Model Intercomparison Project Phase 5 (CMIP5, analyzed in the Intergovernmental Panel on Climate Change [IPCC] Fifth Assessment Report [IPCC AR5]) dataset by the end of the twenty-first century (2071–2100) under different Representative Concentration Pathways (RCPs). Darker colors indicate those areas where climate change may be more prominent. The Caatinga boundary is indicated by thick black lines. Values are dimensionless (Adapted from Torres and Marengo 2014)

and a reduction of the tropical rainforest and boreal forest can occur due to the increased GHGs concentration (IPCC 2007, 2013; Franchito et al. 2014).

The semiarid region of NEB is already vulnerable to the current interannual climate variability, and global and regional climate change projections indicate that the region will be deeply affected by a precipitation deficit and increased aridity in the next century, with negative consequences for the Caatinga (Salazar et al. 2007; Lapola et al. 2009; Franchito et al. 2014; Marengo and Bernasconi 2015; Vieira et al. 2015; Marengo et al. 2016). Rainfall variability, land degradation, and desertification are some of the factors that combined could make NEB one of the world's most vulnerable regions to climate change, with potential adverse impacts on the rich species diversity and water resources (IPCC 2012, 2014).

The time series of annual near surface air temperature and precipitation anomalies over the Caatinga region for the historical simulations and projections under the four RCPs from the CMIP5 models listed in Table 15.1 are shown in Fig. 15.5. Regarding to the historical simulations, it is possible to identify a temperature increase of about 0.8 °C from 1901 to 2000, but there is no apparent tendency of change in the mean annual rainfall. For scenarios of future projections, the near surface air temperature should increase by approximately 1.3 °C (0.5–1.9 °C) for the RCP2.6 (low radiative forcing scenario), and by 4.4 °C (2.7–6.2 °C) for the RCP8.5 (high radiative forcing scenario) by the end of the twenty-first century, relative to the reference period 1961–1990.

Regional precipitation changes depend on regional forcings and on how climate models simulate their local and remote effects (Marengo et al. 2016). Thus, this variable has a high degree of complexity in its simulation and future projections show a high degree of uncertainty. For the Caatinga region (Fig. 15.5), there is a considerable spread among rainfall change projections of ±1 mm day^{-1}, relative to 1961–1990, making it hard to identify any tendency in projected rainfall change. However, the RCP8.5 forcing scenario shows a slight rainfall reduction of about 0.3 mm day^{-1} by 2100 (Fig. 15.5).

Figures 15.6, 15.7, 15.8, and 15.9 evaluate the spatial distributions of the CMIP5-derived projections of temperature and precipitation changes over NEB by the late twenty-first century relative to the reference period 1961–1990. The ensemble mean of all CMIP5 ESMs project a temperature increase varying between 1 and 2 °C in the RCP 2.6 to above 5 °C for the RCP8.5, in which the warming is slightly more intense in austral winter and spring (Fig. 15.6). Furthermore, it is possible to observe a clear east–west gradient in the patterns of changes, in which the highest values lie more to the west of the region. Regarding projections of rainfall changes (Fig. 15.8), trends vary both spatially and seasonally. For the austral summer (DJF), the ensemble mean of all ESMs shows rainfall increases that vary from 0.5 mm day^{-1}(for the RCP2.6) to 1.0 mm day^{-1} (for the RCP8.5), in which the highest values are located in the north/northwest of the region. During the austral fall (MAM), the model ensemble shows a rainfall increase in the north and decrease in the south part of the region in the order of 0.5 mm day^{-1} for RCPs 2.6, 4.5, and 6.0, while for RCP8.5 the entire region shows a rainfall decrease of 0.5 mm day^{-1}. For the austral winter (JJA) and spring (SON), the model ensemble shows rainfall reductions between 0.1 and 1 mm day^{-1} for the entire region.

As an approximated indicator of temperature change uncertainty, the standard deviation for the different ESM projections used in this study is shown in Fig. 15.7 as a measure of ensemble spread. Temperature projections show larger spread over the western part of NEB; however, the standard deviation does not exceed 1 °C for almost the entire region. Regarding precipitation, the signal agreement from all

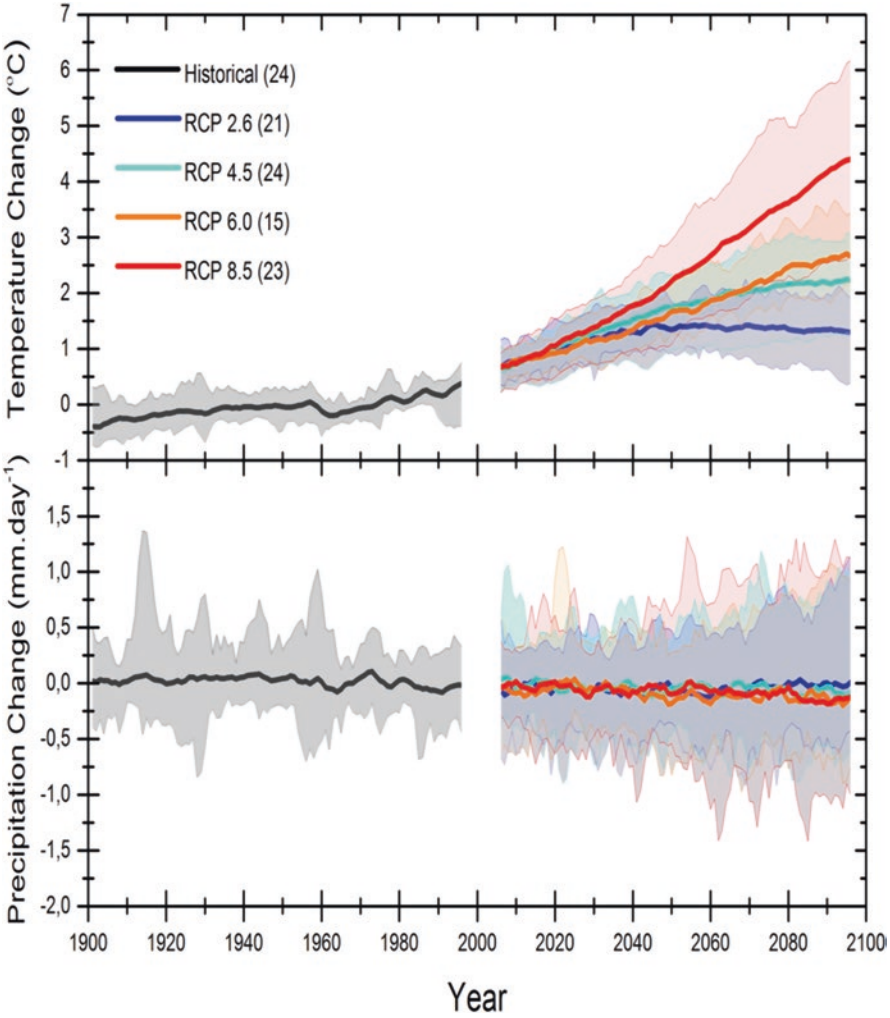

Fig. 15.5 Time series of temperature (upper panel) and precipitation (lower panel) anomalies over the Caatinga region for the historical simulations (left) and projections (right) under different Representative Concentration Pathways (RCPs) from the Coupled Model Intercomparison Project Phase 5 (CMIP5) models listed in Table 15.1. The number of models used in each group is shown in brackets. Anomalies are relative to the reference period 1961–1990. Shaded areas represent the dispersion among CMIP5 models. All time series have been smoothed using a 5-year moving average for better visualization. Values of precipitation and temperature are in mm day^{-1} and °C, respectively

models used in this study are employed as a measure of uncertainty (Fig. 15.9). In general, for all RCP scenarios, 60–80% of the models agree with rainfall increases in austral summer in the northern part of NEB, 60–80% agree with rainfall reductions in austral fall, and between 80% and 90% of the models show rainfall reduc-

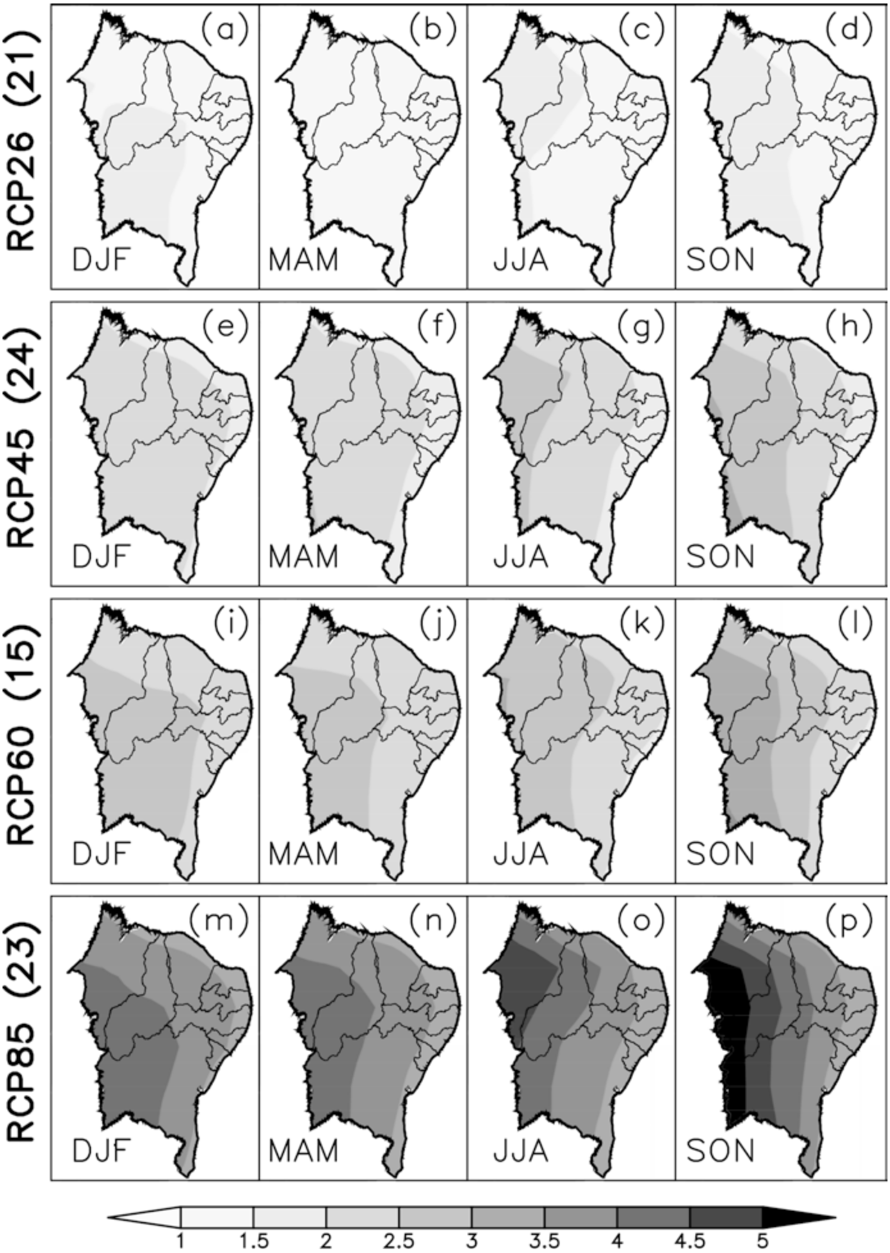

Fig. 15.6 Projections of near surface air temperature change (°C) for 2071–2100 relative to the reference period 1961–1990 under the four Representative Concentration Pathways (RCPs) scenarios over northeast Brazil. Results are shown for the austral summer, fall, winter, and spring seasons (December to February [DJF], March to May [MAM], June to August [JJA], and September to November [SON], respectively). The number of models used in each forcing scenario is shown in brackets

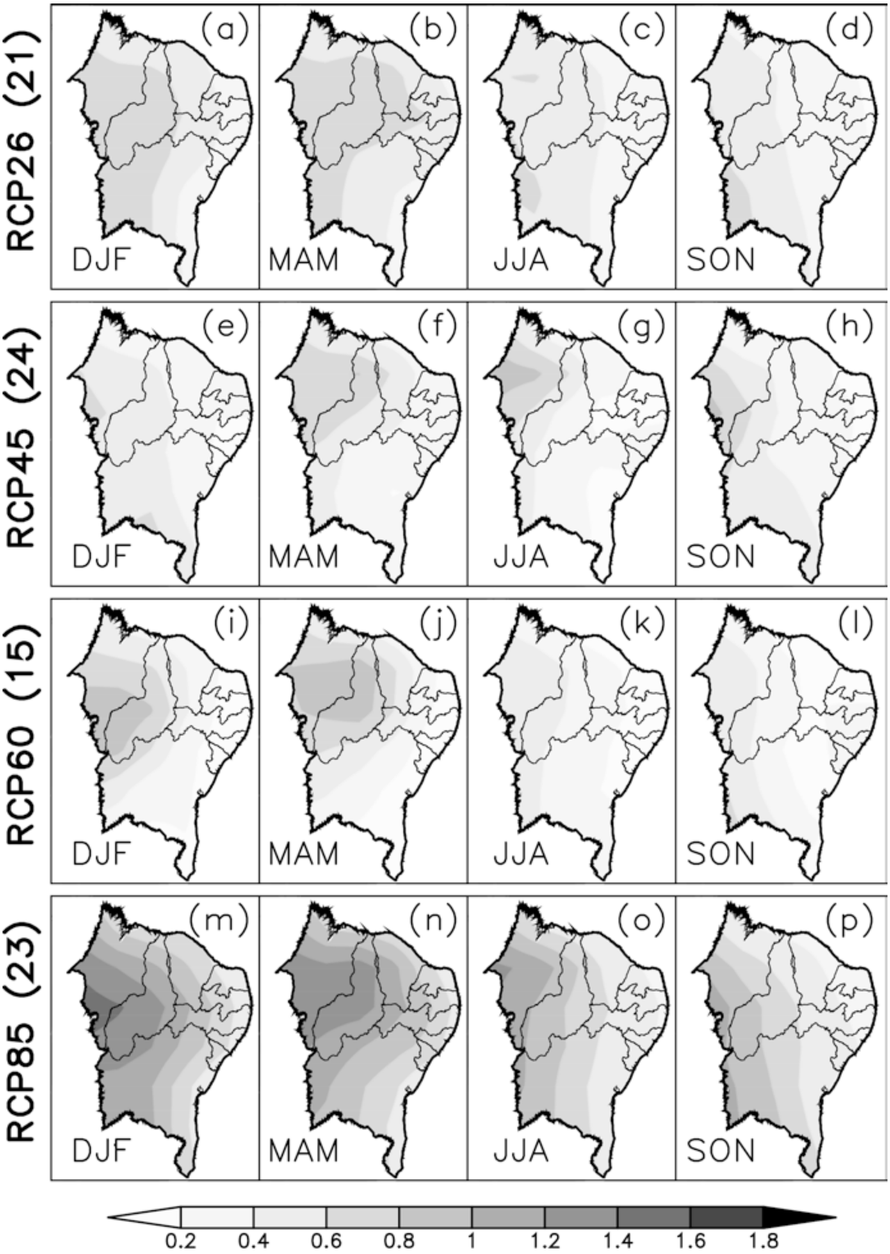

Fig. 15.7 Standard deviation (°C) among the different Earth System Models (ESMs) projections for the temperature change results shown in Fig. 15.6. Results are shown for the austral summer, fall, winter, and spring seasons (December to February [DJF], March to May [MAM], June to August [JJA], and September to November [SON], respectively). The number of models used in each forcing scenario is shown in brackets

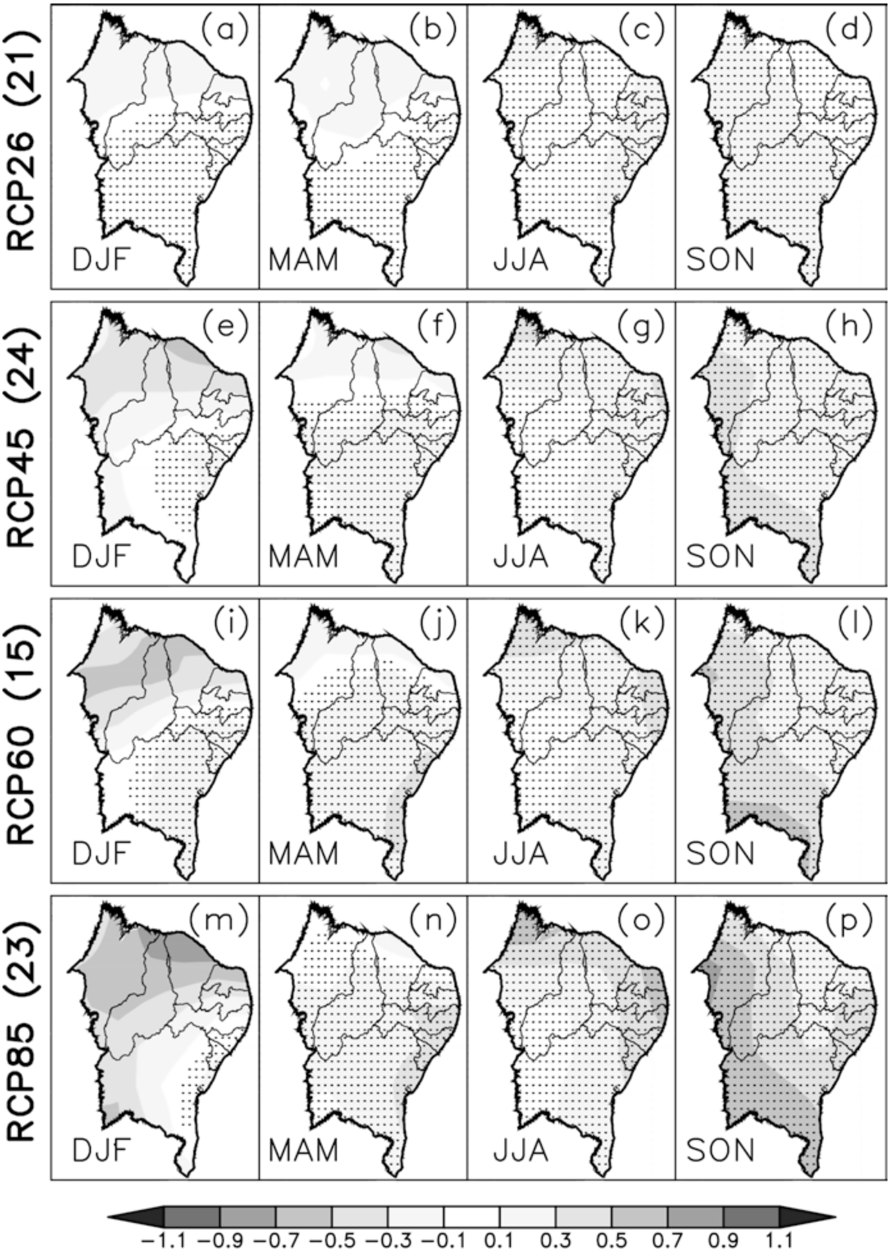

Fig. 15.8 Projections of precipitation change (mm day^{-1}) for 2071–2100 relative to the reference period 1961–1990 under the four Representative Concentration Pathways (RCPs) scenarios. Results are shown for the austral summer, fall, winter, and spring seasons (December to February [DJF], March to May [MAM], June to August [JJA], and September to November [SON], respectively). Dots indicate negative values. The number of models used in each forcing scenario is shown in brackets

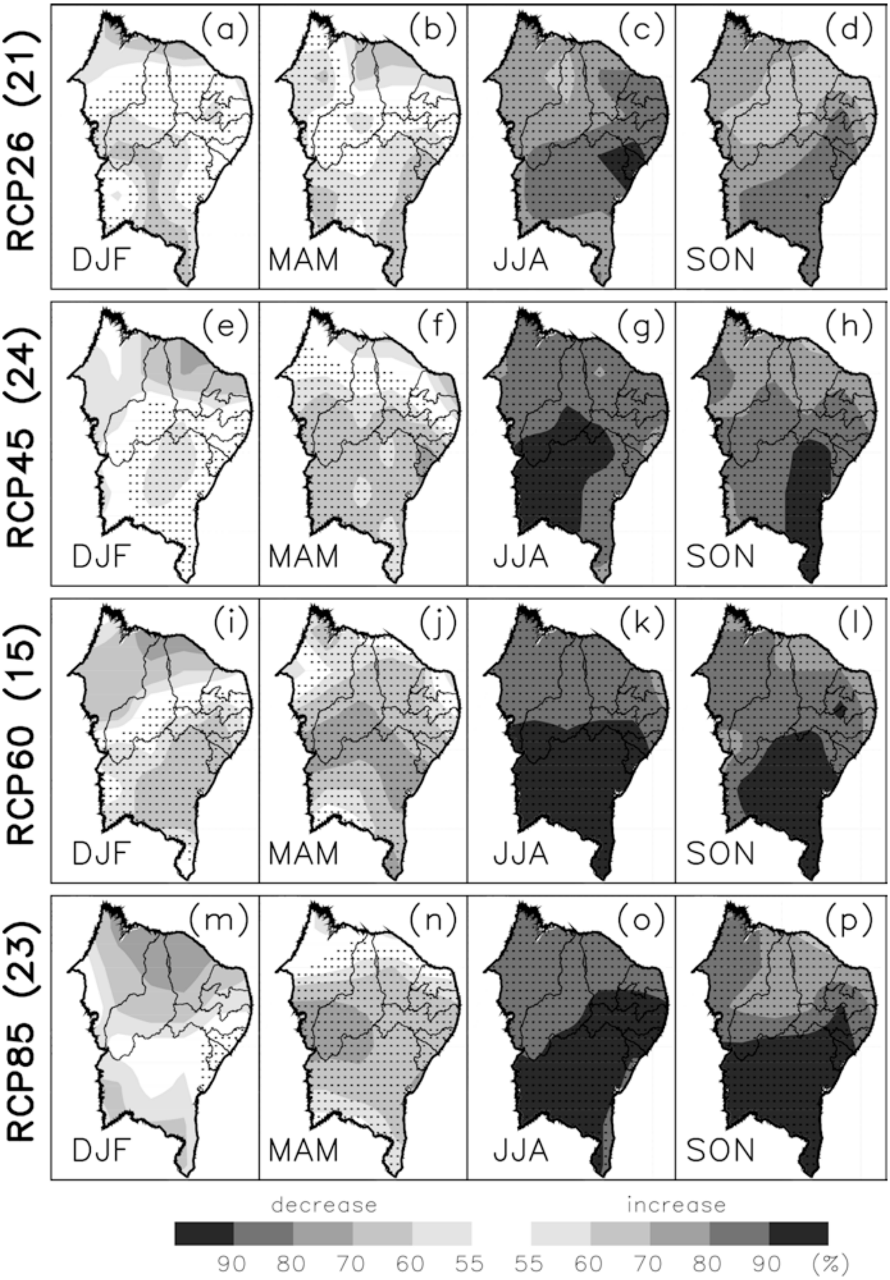

Fig. 15.9 Agreement (%) among the different Earth System Models (ESMs) for the signal of those projected precipitation change shown in Fig. 15.8. Results are shown for the austral summer, fall, winter, and spring seasons (December to February [DJF], March to May [MAM], June to August [JJA], and September to November [SON], respectively). Dots indicate negative values or decrease. The number of models used in each forcing scenario is shown in brackets

tions during austral winter and spring. Therefore, both Figs. 15.7 and 15.9 show that there is some degree of uncertainty in climate change projections for NEB, but with good reliability for rainfall decreases and temperature increases during the austral fall until austral spring.

15.5 Climate Extremes Trends Over the Caatinga

In addition to the changes discussed earlier in this chapter, the IPCC AR5 (IPCC 2013) also projects with medium to high confidence (based on the agreement among CMIP5 models and the consistency with other physical features of climate change) the following climatic stressors over NEB:

- Surface soils are projected to dry out;
- Both annual evapotranspiration and runoff are projected to decrease;
- Days and nights are projected to be warmer;
- More frequent intense rainfall episodes followed by dry and warm periods without rain; and
- Dry spells are projected to be longer with the possibility of droughts being triggered.

Figures 15.10 and 15.11 show some of the aforementioned climatic stressors through some climate extremes indexes computed with the CMIP5 dataset, namely: dry spells (depicted by the number of consecutive dry-days [CDD][5]), cold days (TX10p[6]) and cold nights (TN10p[7]), and warm days (TX90p[8]) and warm nights (TN90p[9]).

The CMIP5 ensemble mean projections of CDD change for three time slices (2011–2040, 2041–2070, and 2071–2100) and four RCPs, displayed as anomalies from the reference period 1961–1990, are shown in Fig. 15.10. Dry spells are projected to increase in all time slices and forcing scenarios from eight to more than 28 additional dry days, with the highest values located in the western portion of the northeast. Results generally indicate an intensification of the patterns of change with increasing radiative forcing. In this way, the largest CDD values (from 20 to more than 28 additional dry days) are observed during 2071–2100 for RCP 8.5.

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[5] Consecutive Dry Days (CDD): maximum number of consecutive days when precipitation is <1 mm.

[6] Cold Days (TX10p): percentage of time when daily maximum temperature is less than the 10th percentile.

[7] Cold Nights (TN10p): percentage of time when daily minimum temperature is less than the 10th percentile.

[8] Warm Days (TX90p): percentage of time when daily maximum temperature is greater than the 90th percentile.

[9] Warm Nights (TN90p): percentage of time when daily minimum temperature is greater than the 90th percentile.

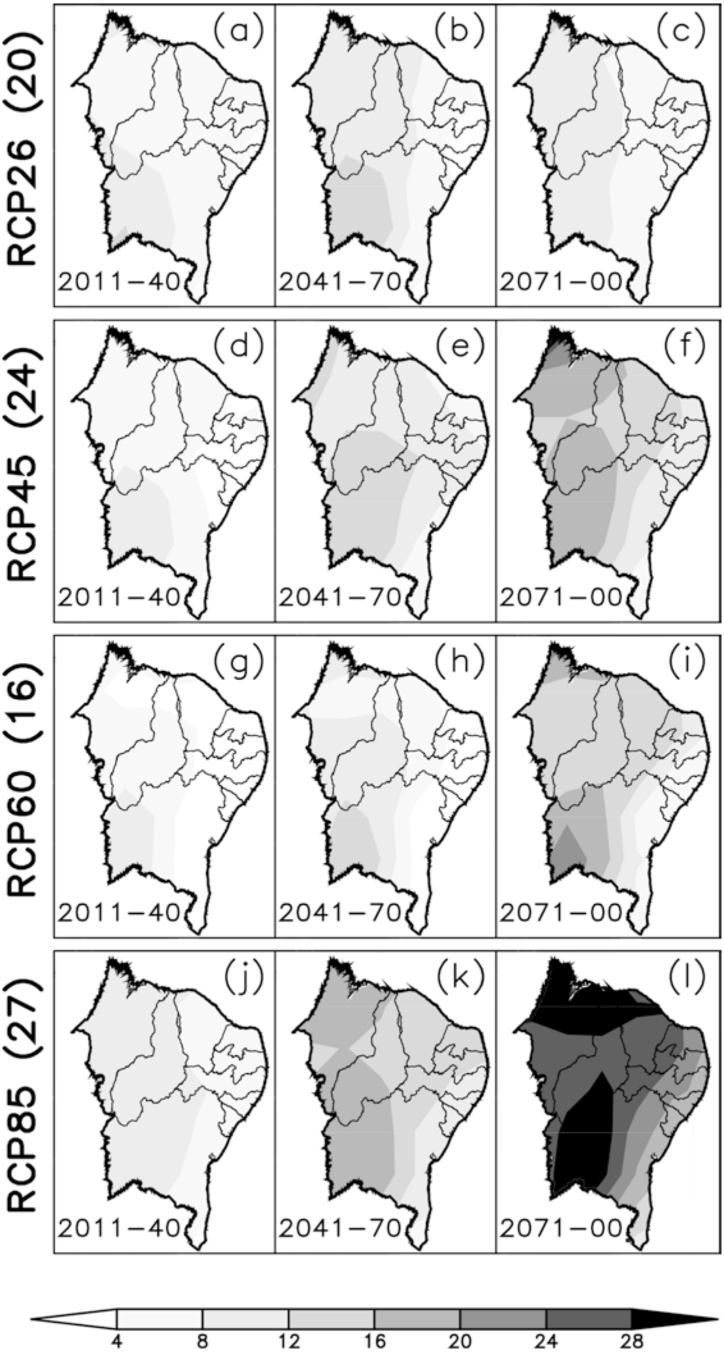

Fig. 15.10 Ensemble mean of consecutive dry days (CDD) changes projected for 2011–2040, 2041–2070, and 2071–2100 for the forcing scenarios Representative Concentration Pathway (RCP) 2.6 (**a**–**c**), RCP4.5 (**d**–**f**), RCP6.0 (**g**–**i**), and RCP8.5 (**j**–**l**), displayed as anomalies from the reference period 1961–1990. The number of models used in each forcing scenario is shown on the left (in brackets). Values are in days per year (Adapted from Marengo et al. 2016)

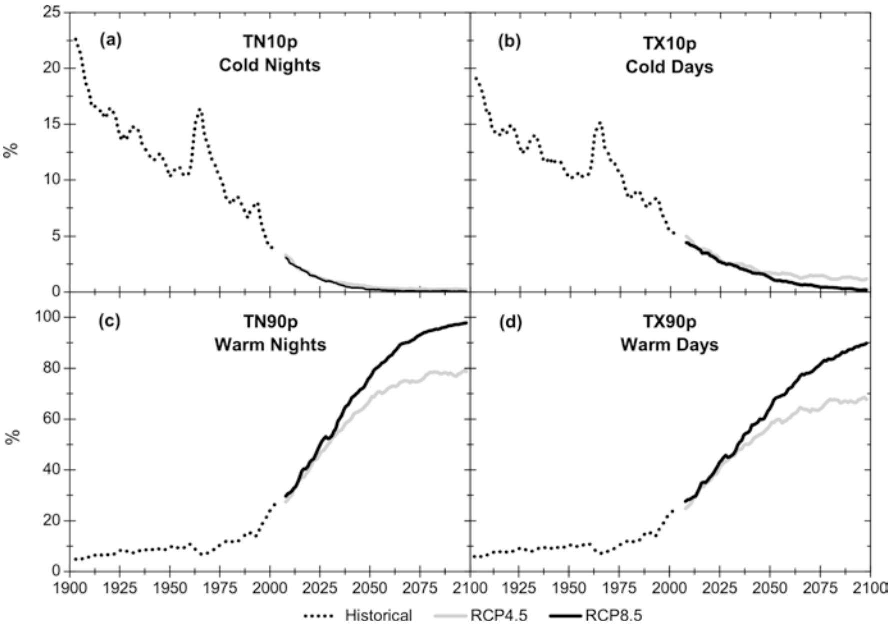

Fig. 15.11 Time series of the following extremes indexes over the Caatinga region: cold nights (TN10p), cold days (TX10p), warm nights (TN90p), and warm days (TX90p). Results represent the ensemble mean of all Earth System Models (ESMs) shown in Table 15.1. Dotted lines represent the ensemble mean for the historical period (1901–2005), and gray lines and black lines represent the ensemble mean for the forcing scenarios Representative Concentration Pathway (RCP) 4.5 and RCP8.5 (2006–2100), respectively. All time series have been smoothed using a 5-year moving average. Values are in percentage of events per year

In NEB, dry spells and drought events are part of the natural climate variability. These events have occurred in the past, are occurring in the present, and are likely to intensify in the future according to climate change projections (Marengo et al. 2016). Drought affects mainly vulnerable residents of the semiarid region, creating situations of water deficiency and risks to water, energy, and food security (Eakin et al. 2014). For example, the drought that intensified in 2012 and extended into 2015 is considered to be the most severe in recent decades and has had an impact on many districts in NEB, affecting almost nine million people (Marengo et al. 2013, 2016). Superimposing droughts upon pre-existing social–economic–political stresses place intense pressure on freshwater availability and quality in the region, and threaten its water, energy, and food security (e.g., Gutiérrez et al. 2014).

Regarding temperature extremes indices (Fig. 15.11), the ensemble mean of all CMIP5 ESMs shows a large tendency to decrease the number of cold nights and days and a relatively less pronounced tendency to increase the number of warm nights and days for the historical period (1901–2005), which have already been found in several observations studies in South America (e.g., IPCC 2007, 2012, 2013; Marengo et al. 2009; Rusticucci et al. 2010; Sillmann et al. 2013a, b). For the future projections (2006–2100), results generally indicate an intensification of the tendencies observed in the historical period and intensification with increasing radiative forcing. All these results are consistent with the expected changes due to increasing GHG emissions and consequently global warming.

15.6 Concluding Remarks

According to the latest reports of the IPCC, warming of the climate system is unequivocal, and many of the observed changes since the 1950s are unprecedented over decades to millennia. The largest contribution to these changes is attributed to the human influence in the climate system, mainly through the increase in the atmospheric concentration of CO_2 since the 1750s.

In Brazil, several studies based on global and regional climate projections indicate that important changes in the climate are still expected to happen in this century, with major social and economic impacts on food production, commodities, and energy, and also large impact on the region's biodiversity. The changes projected in the IPCC reports will certainly lead to a new set of risks and threats that can exacerbate existing risk situations in the country.

Among the most affected regions in Brazil, the Amazon and northeast regions appear to be large hotspots. For some modeling studies, projections of the future climate drive a savannization of parts of Amazon and desertification of the Caatinga region, with potential adverse impacts on biodiversity, supply and quality of water resources, carbon storage, and the provision of other ecosystem services. Therefore, despite the many uncertainties that remain in projections of climate change, the scientific knowledge available today is enough for decision-makers to implement mitigation and adaption measures to prevent dangerous climate change in the region.

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Part V
Solutions

Chapter 16
Sustainable Agricultural Uses in the Caatinga

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Abstract The productive use of the Caatinga vegetation, as native pasture, fallow in itinerant agriculture, and firewood production, has been the main reason why it still covers 40% of its original 1 million km^2. Producers could not find systems composed solely of planted species that were more profitable over long periods and large areas because of the low plant biomass production capacity due to low water availability. In the last decades, low productivity and high production costs, mainly labor, has rendered agriculture increasingly less competitive in relation to other Brazilian regions. Therefore, the area dedicated to agriculture has been decreasing and crops such as perennial cotton and sisal have almost disappeared. Since it has been predicted that plant-growing conditions will tend to become even harsher, with lower rainfall and higher potential evapotranspiration, a reversal of this trend is unlikely and corn and beans, the major crops, will be planted less. Conversely, livestock production may increase with the planting of African grasses. The balance of agriculture abandonment and pasture planting will determine how much Caatinga will be preserved. Firewood production may increase, mainly around large consumption centers, but the overall stock is enough to meet the demand. Efforts should be directed to improve productivity and land conditions in the portions that will be maintained under use. The current trends indicate that the area under native vegetation will not decrease from its present situation.

Keywords Crop • Livestock • Fuelwood • Land use • Vegetation • Biomass • Water and nutrient availability • Development history

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16.1 Introduction

The productive use of the Caatinga vegetation has been the main reason for its conservation. The Caatinga still covers about 40% of its original 1 million km^2 (Chap. 13) because its vegetation has been part of the three main rural production systems: livestock production, itinerant agriculture, and firewood production (Sampaio et al. 2009). This contrasts with other vegetation types in Brazil, such as Atlantic Forest and Cerrado, where the common uses of the land result in the complete substitution of the native vegetation by crops and planted pastures, which has led to the continual decrease in their original vegetation coverage (Scarano et al. 2012).

The maintenance of the Caatinga in the three main production systems has been due to economic considerations—producers could not find systems composed solely of planted species that were more profitable than those with Caatinga over long periods and large areas (Sampaio et al. 2009). This has been recognized since its initial European colonization, when most of the land was occupied with large unfenced livestock ranches and only more favorable areas, such as those covered with more luxuriant Caatinga or montane forests, were divided into smaller agricultural farms (Centro de Estudos de História Municipal 2012). Since then only a few planted systems have been successfully established over longer periods in some specific areas, and even fewer have boomed for periods over larger areas, mostly followed by an abrupt collapse when market demands changed or when they were out-competed by other regions (Furtado 1968; Sampaio and Sampaio 2002; Sampaio et al. 2009). The basic problem over most of the semiarid region of northeast Brazil, where Caatinga thrives, is the low average plant biomass production capacity per unit of land area which restricts profitability to a level above subsistence when one or a combination of three characteristics occurs: (1) products with a high price per biomass unit; (2) low costs of production per biomass unit; and (3) large production areas per unit labor (Souza 1979). These conditions have seldom been maintained over long periods and large areas in the region.

This chapter describes the main production limitations in the region, provides a brief account of the several attempts to establish productive systems in the region, and ends with a discussion of perspectives for future possibilities.

16.2 Description of the Caatinga Ecosystem and Its Limitations for Plant Growth

The basic difficulty of all production systems in the region has been the low average and highly variable biomass production that results from the harsh climatic conditions (see Chaps. 10, 15 for more details). The key factor is water availability to the plants in a semiarid area where annual potential evaporation is high, between 1500 and 2500 mm, and average annual rainfall is much lower, between 300 and 800 mm (Reddy 1983; Sampaio 1995). Rainfall is not only scarce but highly variable: (1)

from one year to the next, including severe drought periods that last 3–5 years every two to three decades; (2) in its distribution along the year, usually concentrated in 3–5 months, sometimes the total monthly amount occurring in a single rain event that lasts a few hours; and (3) in the beginning and end of the rainy season, which can be anticipated or postponed by up to 3 months from the most common pattern (Reddy 1983; Sampaio 1995). These rainfall characteristics have remained more or less constant over the past century, for which reliable data is available, and probably for several centuries, for which only sporadic descriptions exist, mainly of the severe drought periods (Sampaio 2007). Projections of future climate scenarios indicate that average annual rainfall may decrease and extreme events may be more frequent, together with an increase in average temperature and, consequently, in potential evapotranspiration (Marengo and Bernasconi 2015; Chap. 15). Therefore, plant-growing conditions will tend to become even harsher.

Water availability is not only limited by rainfall and evapotranspiration, it is also influenced by topography and soil retention capacity. Water flow to lower sites is proportional to the intensity of the rainfall event, the slope of the area, the permeability of the soil, and the openness of the vegetation coverage (Sampaio et al. 2009). Overall, water availability is lower in slopes and higher in valleys, where water can accumulate in natural or manmade reservoirs and flow in permanent or temporary rivers. Therefore, valleys contained the most luxuriant Caatinga, which has almost completely been substituted with crops and planted pasture, profiting from the better growing conditions (Sampaio et al. 2009).

Soil retention capacity depends on soil depth and soil texture. In general, valleys have deeper soils than slopes because eroded sediments accumulate in the lower parts (Sampaio et al. 2009). Slope soils become progressively shallower, mainly if their use accelerates erosion (Sampaio et al. 2003a). Higher water accumulation capacity reinforces the advantage of cultivation in the valleys. Soil texture depends basically on their geological formation. In the northeastern semiarid area, there are two main formations: slightly less than half of the territory is covered by deep sedimentary soils, mostly of sandy texture, and the other part by shallow soils, formed on residual deposits of the sedimentary layer or by weathering of the exposed Precambrian crystalline shield, mostly of heavier texture (Gariglio et al. 2010). The shallow soils accumulate little water and dry up after a few weeks without rain. The deep sandy soils retain little water within the superficial layers and most rainwater may percolate to depths beyond the reach of crop roots. Both soil types impose water limitations which contribute to reducing the area adequate for crops and planted pastures (Sampaio 2010).

Nutrient limitations add to this reduction. The sandy sedimentary soils have low nutrient stocks (Menezes et al. 2012). In all soil types, crops and pastures extract nutrients which are exported when the products are consumed elsewhere. In the slopes, nutrients are also transferred to the valleys by leaching and erosion of the superficial soil layer, which is the layer richest in nutrients accumulated by the deposition of plant litter that is part of the soil–plant cycling (Menezes et al. 2012). In agricultural areas throughout the world, the slow but continuous depletion of the nutrient stocks is usually replenished by fertilization, a costly process that has to be compensated by the price of the products. In the Brazilian northeast semiarid areas, little fertilization has been carried out during the last centuries (Sampaio et al. 2004). Therefore, nutrient limitations have gradually increased.

Caatinga plant species have millennium-old adaptations to the harsh environmental conditions. As usual under these conditions, survival is more important than high productivity. Most shrub and tree species are deciduous, quickly breaking the dormancy of the permanent wood structure and producing leaves of low energy costs during the few months of high water availability (Sampaio 2010). Most herb species have life cycles restricted to the rainy season (Freitas et al. 2012). Exceptions are the mainly succulent Cactaceae and Bromeliaceae, which have highly efficient water use but low photosynthetic rates (Menezes et al. 2005). Total annual biomass accumulation of all plants in a hectare, although highly variable depending on the rainy season, hardly ever reaches 10 Mg (Sampaio et al. 2009).

Most tropical tree and shrub crop species cannot withstand several dry months every year plus occasional droughts. Almost all of the few adapted deciduous or succulent crops have biomass productivities below those of Caatinga species. Annual crops with life cycles of less than 5 months may be viable but their productivities tend to be low when submitted to periods of water deficit along the cycle (Sampaio and Sampaio 2002). Since this is a common occurrence in the region, average productivities of annual crops along the years are low and annual variations are very high (Sampaio and Sampaio 2002).

16.3 Past and Present Productive Systems

Before the European arrival at the beginning of the sixteenth century, the native human population was very low in the semiarid area and concentrated where drinking water availability was higher (Kempton 1979). Population growth was limited by lack of construction of water reservoirs and transportation means. There was no livestock production and crops and fuelwood production were restricted to a few small plots. Lack of metal tools and the small number of domesticated plant species added to the difficulty of production. In spite of its scarcity, the indigenous population was still forced to migrate to the humid littoral area during drought years (Salvador 1975).

In the sixteenth century, Europeans established in the humid coastal area and only slowly penetrated the hinterlands. The occupation of most of the semiarid area was not completed until the beginning of the eighteenth century (Antonil 1817; Abreu 1982). Cattle raising was the economic force pushing this occupation and it is still the most important single use of the area (Sampaio et al. 2009). The animals were brought to an area and left to breed unrestrained by fences, in an extensive system that provided little care and was based on the fodder the animals could find in the native vegetation (Bruno 1967; Lins 1976). Herbs, shrub and tree leaves, and green twigs were consumed (Araújo Filho 1992). Goats and sheep were a small part of the livestock population, prevailing only where raising conditions were more difficult (Araújo Filho 1992; Sampaio et al. 2009). Occasionally, some of the cattle were gathered and moved, in marches lasting a few months, to the coastal areas, where they were slaughtered for immediate consumption or to produce jerked beef, which was exported to other regions in the country (Abreu 1982). Goats and sheep were consumed locally, only the hides being exported (Rocha 2013). All animals went undernourished in the dry season, losing weight that was replenished in the following rainy season. Along the generations, they adapted to these conditions by decreasing their body sizes, retarding maturation and spacing gestations (Sampaio et al. 2009). Production by unit land area was very low (5–10 kg of live weight per ha and year) and provided a comfortable but spare living standard only to those who owned large herds and usually also large properties, but not necessarily so since the animals roamed freely. This system gave no incentive to improve herds and to plant pasture and eventually would lead to overgrazing of many areas (Lins 1976; Sampaio et al. 2009). The overall effect on the Caatinga vegetation is not known but it is probable that more palatable herb species, especially grasses, were substituted with less palatable ones.

At the beginning of the European occupation, crops were mostly restricted to the small farms established in the more favorable areas. As the population increased, small fenced plots of maize, intercropped with beans or cowpea, and cassava spread to the large livestock ranches (Lins 1976). They were established to produce food, other than milk and meat, which was difficult to bring from other areas because transportation was a long and troublesome process, conducted on horse- and mule-back through a primitive and ill-conserved trail system, which was hardly improved until the beginning of the twentieth century (GTDN 1971). The plots were open to the cattle once harvested and moved to a different place after a few years, the area being left fallow for a few decades. Fuelwood was only necessary to attend the small local needs of cooking and producing cassava flour and baked clay goods and it was easily supplied by the opening of new crop plots in the itinerant agricultural system (Gariglio et al. 2010).

Until close to the end of the eighteenth century the production system remained the same, exploring a larger area due to the natural expansion of the domestic animal and human populations, which increased five to ten times across each century (Souza 1979). This expansion was seriously disturbed for the first time by the extremely severe drought of the seventh decade of the eighteenth century (the 1777 catastrophe) which killed a large proportion of the cattle population and also killed or forced a large part of the human population to abandon the area due to food shortage (Alves 1953; Pompeu Sobrinho 1958).The jerked beef industry closed for good. Without additional infrastructure improvement, the limit of human occupation during severe years had been reached.

In the nineteenth century, the industrial revolution in Europe and the opening of Brazilian ports to foreign trade led to a continuous increase in the cultivation of perennial cotton, also known as ‘arboreal cotton’ (Furtado 1968). This type of cotton occupied a niche in the market because of its long fiber, which was ideal to mix with the shorter annual cotton fiber in the textile industry (Campos 1991; Palacios 2004). It was the main commercial crop and spread to cover more than 2 million hectares, mostly on clayey, shallow soils (Palacios 2004). It was usually planted together with maize and beans (or cowpea) by landless laborers who kept or shared the grain with the landlord for 2–3 years until the trees were too big to intercrop (Andrade 1980; Palacios 2004). Productivity peaked between the fifth and tenth year but was very low (<300 kg ha^{-1}). Since the plots were open to cattle after harvest, the system was well-known as the cotton–subsistence–cattle triad. By the end of the twentieth century, changes in the industry and in the labor market and the introduction of boll weevil (an insect that feeds on cotton plants) reduced arboreal cotton planting to close to nothing (Campos 1991). It left behind severe erosion problems, especially in the slope areas.

Other crops flourished in special areas. The sub-humid areas (agreste) close to the coast produced grain to feed the growing populations of the state capitals, almost all seaports (Melo 1980). Although these agreste areas have a better rainfall distribution than the semiarid nucleus of the Caatinga, productivity has always been very low in normal years (about 700 and 300 kg ha^{-1} of maize and beans, respectively) and collapse in drought years (Sampaio 2007). In some valleys, blessed with a more humid microclimate, sugarcane was planted to produce hard sugar blocks (rapadura), which were mainly sold to the cotton areas to compose, together with cassava flour and dried meat, the diet of harvesters (Andrade 1980; Campos 1991). The severe drought period around 1877 repeated the tragedy of a century before, killing livestock and forcing migration of the human population (Alves 1953). Since this period, the semiarid area has been exporting people to other regions in the country and to the regional coastal area (Furtado 1968).

In the twentieth century, economic and social changes accelerated in Brazil and the semiarid area was engulfed in these changes, although it remained the region most resistant to implementing modifications (Souza 1979). Half a dozen railroads were built starting in the coastal capitals and penetrating the interior areas but were never connected into a regional system. Cars were introduced and roads were opened, and parts of them were eventually paved in the second half of the century. The roads connecting the northeast and southern regions allowed goods to be moved, integrating local into national markets. Some industries and mining operations were established with limited regional economic impact but some, such as the gypsum and iron industries, created a large demand for fuelwood, depleting their surrounding areas of Caatinga vegetation (Gariglio et al. 2010).

Thousands of small and dozens of large dams were constructed and large water stocks accumulated starting at the beginning of the twentieth century. These water stocks had limited use (Assunção and Livingstone 1993) until close to the end of the century when they were used to supply water to most of the urban centers in the area. Large state irrigation projects were implemented, mainly in the São Francisco River valley (Bahia and Pernambuco states), but also in the Açu (Rio Grande do Norte) and Jaguaribe (Ceará) River valleys. Many other small projects were also established in smaller basins. Most of the large projects were very successful and highly productive, but their expansion was limited by water availability and irrigation now covers only about 1% of the whole semiarid area (Sampaio et al. 1979;

Sampaio and Sampaio 2004). Most of the small projects ended up with salinization problems and many have been abandoned (Sampaio et al. 2009).

New crops and Indian cattle (breeds of *Bos taurus indicus*, also known as zebu cattle) were introduced and products extracted from the native vegetation gained international markets (Lins 1976; Sampaio et al. 2005). Indian cattle are more used to tropical conditions than the original European breeds but less so than the acclimated 'creole' cattle (Domingues 1961). On the other hand, they produce more meat and milk, provided fodder availability is improved. Most of the herds now are crossbreeds between Indian breeds and creole cattle. To improve fodder availability, *Prosopis*, prickly pear cactus, and African grasses (genera *Pennisetum*, *Cenchrus*, and *Andropogon*) were introduced (Menezes et al. 2005; Araújo Filho 1992; Oliveira et al. 2017). *Prosopis* was largely planted but also invaded valleys (Oliveira et al. 2017). It provided valuable feedstock but fell from use in disgrace because exclusive feeding on some occasions led to intoxication and death of ruminants (cattle, sheep, and goats). Prickly pear was largely planted in and around the Borborema region, where it became the basis of the diet of dairy cattle (Menezes et al. 2005). Although prickly pear has been severely hit by a cochineal pest, new resistant varieties will probably reoccupy the former planted areas. The grasses are being planted in larger scales, especially where rainfall distribution is somewhat better, in the eastern and southern portion of the semiarid region (Sampaio et al. 2009). Sisal was introduced from Mexico and spread for a few decades until production collapsed due to competition with synthetic fibers (Sampaio et al. 2005). Sorghum and pearl millet were introduced from Africa and are substituting maize or occupying drier niches but only slowly, despite their higher water deficit resistance, because people are not used to eating them, and their market prices are lower than that of maize (Santos et al. 2015). In addition, sorghum and pearl millet compete with low-cost maize produced in the Cerrado areas of Brazil.

Cashew nuts went from being a domestic delicacy to an export crop and, despite competition from other countries to which the plant was introduced from Brazil, it is still largely planted in sandy areas of the sedimentary basins and sub-humid coastal areas of the northern states in the region (Sampaio et al. 2003b). The high price per unit of product and the low costs of production of this adapted tree makes it the most profitable of the rain-fed perennial crops in the region. Carnauba wax and oiticica oil, both collected from native plant populations in the northern states, reached the international market but production has gradually decreased, especially that of oiticica oil (Sampaio et al. 2005). The main reason is competition with synthetic products but also declining plant populations and lack of cultivation efforts.

Throughout the last century, the increase in the use of fuelwood for cooking along with the multiplication of bakeries, pottery and tile kilns, and cassava flour-producing units, as well as larger localized wood-consuming mining industries led to a large demand for fuelwood (Gariglio et al. 2010). Therefore, the fuelwood obtained by clearing new areas for shifting cultivation was no longer sufficient. Around the larger consuming centers, Caatinga is vanishing, although on a regional scale the present stock is enough to supply the demand (Gariglio et al. 2010). No planted tree species has been found to produce a more economical return than native

Caatinga, including species that could be selected from the Caatinga flora itself. However, efforts to select and improve these native species have been insignificant, including those of species that produce oil, wax, or medicinal products.

The availability of water and transported food ended the human death toll brought by droughts but not impoverishment. Out of the semiarid region, in Cerrado areas, agricultural production multiplied several times, mainly beef and grains, turning the country into one of the largest food exporters in the world (Buainain et al. 2014). Rural workers conquered labor rights, mainly retirement salaries and minimum wage. However, the relative decrease in national prices and the ability to transport agricultural products from other regions, coupled with the low productivity and higher production costs, mainly labor, rendered agriculture in the semiarid northeastern region increasingly less competitive (Sampaio et al. 2003b). Poverty lingered on and today the area has the worst social and economic indices in the country (IBGE 2016). Most of the rural and part of the urban population lives on retirement funds, pensions, and governmental social programs, and from jobs maintained by federal money transferences to small municipalities (Gomes 2001).

16.4 Prospects for Future Sustainable Systems

16.4.1 Agriculture

Given the present environmental, economic, and social conditions, the prospects for agriculture in the semiarid region are quite bleak. The combination of low land and labor productivity and current agriculture product prices results in very low monetary returns per person, most frequently below the minimum wage. Therefore, a large part of the rural labor force lives in extremely poor conditions, alleviated by government welfare programs. Migration of more capable workers to other regions or to regional urban centers continues, slightly reduced in the last decade due to the expansion of public money transfers. As a consequence, the planted area is decreasing. This trend may continue or reverse depending on future conditions, which are evaluated in the following paragraphs, analyzing the components of production.

The prices of agricultural products remained relatively stable in the world in the last decades of the last millennium, increasing in the 2000s and reaching a maximum in 2011 and decreasing since then, with the possibility of additional decreases if oil prices stay low (World Bank 2016). The prices of agricultural commodities may increase again depending on oil prices and if demand outpaces production, a probable occurrence in developing countries where the population is still increasing at a fast rate (India and African countries) and/or a large part of the population is raising their standard of living (China, India, and most other developing countries). However, even if prices increase, it will be at a slow rate and it will probably take decades before they double, if this ever occurs. In Brazil, demand will not increase much given the current population growth and living standards and the country will continue to be a major exporter. Production and productivity have been steadily increasing outside the semiarid area and there is still room for further increases. The cost of labor has also steadily increased in Brazil. The stagnant, labor-intensive production in the semiarid area cannot currently compete with those of these other areas and will likely be less competitive in the future.

Most of the future climate scenarios foresee higher temperatures and lower and more erratic rainfall (Marengo and Bernasconi 2015; Chap. 15). Therefore, one may expect even lower land productivity. To increase labor productivity, with equal or lower land productivity, workers have to crop larger areas. This requires access to larger fields and higher mechanization. Property sizes vary substantially in the semiarid region but in more favorable sites most of them are too small to guarantee a minimum living income (Cardim and Guanziroli 2000; Guanziroli et al. 2014). In the whole semiarid region, two-thirds of the properties are less than 10 ha and half are less than 5 ha and only 5% are more than 100 ha (Guanziroli et al. 2014). With an average production of less than 12 bags of maize per ha and the current price of 40 Brazilian real (R$) per bag (in the retail market), this translates to a gross annual income per hectare of R$480, about half the official minimum wage for a single month. Beans and cowpea have similar income with average production of less than five bags per hectare and the current prices of R$120 and R$90 per bag, respectively. Considering that 10 ha would be cropped, the total gross annual income would be less than half that guaranteed by the minimum wage over 1 year. In fact, the yearly net income of the approximately 1.5 million small properties with minimum input use in the northeast region was only R$200 in 2006 (about R$360 correcting for inflation to 2016 values).

Increasing property sizes could provide higher income but it is a difficult task due to the government policy directed only at reducing the size of larger properties, the irregular legal situation of many of the small properties rendering it difficult to make an officially legalized sale, and the absence of an established and active market for rural lands. Although property aggregation is infrequent, the size available to work has been increasing when members of a family or neighbors migrate and leave their properties or share of the inherited property to those that remain. This is not acknowledged in the official statistics and its extent is unknown, but judging from the low proportion of family properties that are cropped by non-owners it must be relatively low.

Even 10 ha is too large an area to be cropped by a single worker with the prevalent tools (axe, hoe, and spade). Mechanization (tractor, planter, harvester) can multiply this size several times but has advanced very slowly in the semiarid region and more than half of all properties have no mechanization (Guanziroli et al. 2014). Few of these machines are made for small properties and the prices of the most common ones are too high for a single owner. Cooperatives could circumvent part of the problem but few of them work properly in the region and less than 2% of the properties are associated with a cooperative (Guanziroli et al. 2014). Cooperatives would help to solve the problem of sharing equipment within the short and irregular cropping period. In addition, large areas of sloppy topography and shallow rocky soils are not suitable for mechanization. Since they are the areas with lower nutrient and water availability they comprise most of the lands where agriculture is being discontinued and Caatinga vegetation is regenerating (Aide et al. 2013). It is unlikely that they will be cropped again on a regular basis. These slope areas are mainly cropped now where family members (sometimes women, minors, and older persons) have no alternative occupation and an extra income (frequently welfare programs and transferences from adults working elsewhere).

On the other hand, flatter areas, especially in the western sedimentary part of the region and in larger valleys of the eastern crystalline part, could profit from mechanization. In the valleys, the legal requirement to preserve riparian vegetation poses a conflict between use and preservation. This requirement has been largely ignored and their most luxuriant Caatinga vegetation has virtually disappeared (Sampaio 2010). It is likely that law enforcement will increase because of increased pressure from the majoritarian urban population, higher demands for ecological services, mainly water conserving practices, and improved methods of land use monitoring by government agencies. Revegetation of some of these more favorable areas, including the establishment of official reserves, presently too few and not representative (Chap. 17), will certainly be a pressing demand in the near future.

Despite this demand, many scattered more favorable areas where mechanization is possible will still be available for agriculture. They comprise between 5 and 10% of the whole semiarid area (Sampaio et al. 2009). In these areas agriculture can and should be improved and research has pointed to several ways of improving land and labor productivity and reducing land degradation (e.g., Sampaio et al. 2009; Furtado et al. 2014). Most of these single improved techniques provide only small gains, difficult to recognize within the large variation due to variable water availability, and few of them have been largely adopted in small farms. Combined and in the long run coupled with improved management skills, they could eventually double land and labor productivity. These techniques include erosion control (contour planting, zero tillage), fertilization (phosphorus and nitrogen applications), and improved nitrogen symbiotic fixation, integrated pest and disease control, improved varieties and species (sorghum substituting maize), and other practices. While they have been described in the extensive scientific literature and summarized in a few books (Sampaio et al. 2009), they have scarcely reached owners of small farms. If adopted, they would alleviate pressure in unsuitable areas where agriculture is leading to environmental degradation and reduced yields.

16.4.2 Livestock

Most of the semiarid area is not suitable for agriculture and has been used for livestock and fuelwood production. Likewise, in other countries, semiarid areas with high rainfall variabilities have also been preferentially used for livestock rather than for agriculture (Ellis and Galvin 1994). Fodder can be stocked for dry periods or brought from other areas and animals can withstand some weight loss, regained in the subsequent rainy season. In the case of more severe droughts they can be sold or moved to better areas. In dry areas, extensive livestock is the usual pattern, with low stocking rates and low labor intensity relative to agriculture. Economic return per unit of land in these extensive systems is also lower but per unit of labor may be equivalent if one person works a large area. It was estimated that the minimal area of a reasonably profitable ranch was 100 ha (Duarte 1999). Nowadays, this minimal area is larger because since that study was published salaries have increased more than the price of meat. Only 5% of the properties in the semiarid region are larger than 100 ha and they will probably continue to raise cattle. Productivity may increase with better management practices, including increased areas of planted pastures, adjustment of stocking rates, maintenance of fodder reserves to be used in the dry season and in drought years, genetic improvement of the herd, and control of zoonosis, such as foot and mouth disease and brucellosis (Souza 2007; Santos et al. 2012). The expansion of planted pastures may counteract part of the effect of crop area reduction in a way that means the area covered by Caatinga vegetation may not increase substantially above the actual 40% of the original coverage.

Intensive livestock systems require less land and will probably continue to thrive in small properties provided they have more labor and capital availability. Dairy, poultry, and, to a small extent, swine farm profitability depends on the relative prices of products and fodder. Since fodder has to be acquired outside the property, costs of production are higher than in other Brazilian regions but the lower transportation cost may balance the account. In addition, demand for fresh products (poultry, milk, eggs) favors local production.

16.4.3 Fuelwood and Other Caatinga Products

Fuelwood is a voluminous product and its fire is both difficult to start and to stop compared with other energy sources such as electricity, gas, and liquid fuels. Transforming it to charcoal or pellets reduces the volume but the improvement in burning characteristics is small. Therefore, it is preferentially used in combustions that last several hours and its traditional use as a domestic cooking fuel in the semiarid area has decreased continuously with the increased availability of these other sources (Gariglio et al. 2010). On the other hand, its industrial use has increased, especially in concentrated areas, such as the gypsum and iron-producing centers, due to its low price. Deforestation around these areas, backed by the national growing ecological concern about native vegetation disappearance, has led to approval of strict use regulations, which are erratically enforced in Caatinga areas (Gariglio et al. 2010). Therefore, most of the consumed fuelwood is obtained from illegal cutting of Caatinga plots. Legalization is an expensive process and requires establishment of a series of plots to be cut in consecutive years, returning to the same plot after the presumed period of vegetation recovery (about 10–15 years) (Gariglio et al. 2010). If regulations were strictly enforced, fuelwood prices would increase due to legalization costs and mainly because production would be discontinued in many properties. Subdividing small properties into a series of plots and cutting just one each year is economically unfeasible. The common practice is the eventual cutting of Caatinga to open a crop plot, although this has decreasing occurrence, or to cut it when it has enough wood and the property owner needs extra cash or is contacted by a dealer. Since wood cutting is spread over a multitude of small areas there are no central large charcoal- or pellet-producing units and most of the transformed fuelwood is turned into charcoal in small locally constructed and energy-inefficient furnaces.

The gross income of fuelwood production is relatively low. Adopting favorable values, 100 stereo, each one worth R$50, can be produced in 1 ha every 10 years. Therefore, the annual gross income is equivalent to R$500 ha^{-1} year^{-1}and a 10 ha property would have a gross income below the national minimum wage. Fifteen to 20 man days of labor (each day costing at least R$30) are required to cut 1 ha of Caatinga and this cost would have to be deducted from the gross income, as well as other expenses. Charcoal has a higher price but only a slightly higher return, considering that 4–7 tons of fuelwood are required to produce 1 ton of charcoal and carbonization demands extra labor.

The future use of Caatinga fuelwood depends on how regulation evolves and on the relative prices of energy sources. If regulation allows the eventual cutting of plots, supply is enough to cover the present and probably future regional demand (Gariglio et al. 2010) and fuelwood prices would increase at a rate similar to that of labor, the main cost input. Vegetation coverage around the centers of high consumption would eventually stabilize as cut plots grow enough wood to allow a new cut. However, this implies that the vegetation is maintained in a continuous state of regeneration, as already occurs in most of the Caatinga area (Singh 1998; Chap. 14), but with a short regrowing cycle. The spread of the producing area around these centers of consumption would depend on the relative costs of wood and of transportation. The eventual cutting of areas will continue, regulation or loose enforcement allowing. Part of the open areas may be planted to crops or, more likely, will be maintained as open by burning and animal pressure in order to be used as native pasture. In more favorable areas, pasture may be planted with exotic grass species.

It is expected that fossil fuel prices will increase while prices of other energy sources decrease. In fact, the decreases have occurred but fossil fuel prices have fluctuated considerably. They are still low enough to be the main energy source for transportation and industry and will probably remain so for many decades. Caatinga fuelwood energy will not be used for transportation in the short run and it is not expected that its industrial use will increase considerably in the semiarid area. Exportation to other areas, even neighboring ones, is limited by transportation costs, even in the form of charcoal.

Many other products may be obtained from the Caatinga besides fuelwood (Sampaio et al. 2005; Chap. 11) but they represent a very small proportion of rural income, far below that obtained from fuelwood. They have been, and still are, important in localized areas, but production of almost all of them have decreased in the last decades. The main products are carnauba wax, oiticica and licuri oil, *umbu* fruits, and fibers used in different handcrafts (Chap. 11). Except for carnauba and *umbu*, prospectives for higher production in the future are dim. Chemical and pharmaceutical substances are recognized as a promising field (Chap. 11) but currently are of minor importance, partly because of poor knowledge of their occurrence and lack of specialized production units. Even if their use is greatly improved, their market is limited and usually a few hundred hectares is enough to supply international demand. Production will probably be concentrated ia a few areas, domesticating and cultivatingthe native species that produce the demanded product. Most likely, the areas destined to these productions will represent a small fraction of the whole Caatinga area.

16.5 Prospects for Future Caatinga Coverage

About 40% of the original Caatinga area is still covered by Caatinga vegetation, most of it representing some stage of regeneration after being cut to produce fuelwood or after interruption of agricultural and pastoral activities (Chaps. 13 and 14). In recent decades, the low income provided by itinerant agriculture has led to a decrease in these activities, partly responsible for the increase in native vegetation coverage (Aide et al. 2013). This increase, coupled with a growing ecological concern and enforcement of legislation restricting hunting of native fauna, seems to be leading to a slow return of bird flocks and other animals, including large ones such as deer and wildcats. However, local information regarding this return of wildlife has not been confirmed by scientific reports. In the future, it is expected that the area dedicated to agriculture will continue to decrease, mainly in the semiarid portion over the Precambrian crystalline shield where soils are rocky and shallow preventing adoption of mechanized agriculture. The liberated land may return to native vegetation or may revert to native or planted pasture, depending on the size of properties and on the improvement of livestock production. Part of the new areas of native vegetation may eventually be cut to produce fuelwood, in a proportion that depends on future regulations and on the relative prices of energy sources. Predicting the proportions of pasture and fuelwood production in the future is highly speculative but the trend seems to point to a higher proportion left fallow. This means that hopefully most of Caatinga vegetation would not be under high risk of degradation, let alone disappearance, an exception among Brazilian large vegetation types. Efforts should be directed to improve productivity and land conditions in the portions that will continue to be used. There are several improved techniques and management practices that can be applied to both agriculture and livestock production, none of them leading to spectacular increases if used separately but able to double productivity if jointly used. Special attention should be given to pasture areas, which may occupy a larger proportion of the semiarid region and tend to be overgrazed and degraded even as far as desertification, as the native vegetation, even if the area is left unused, will take many decades to return to a condition similar to its primitive state.

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Chapter 17
Conservation Opportunities in the Caatinga

Carlos Roberto Fonseca, Marina Antongiovanni, Marcelo Matsumoto, Enrico Bernard, and Eduardo Martins Venticinque

Abstract This chapter describes a recent participatory effort coordinated by the Brazilian Government to update the Priority Areas for conservation, sustainable use, and shared benefits of the Caatinga biodiversity, which culminated in the determination of 282 Priority Areas as defined by the MMA Law 223 of 21 June 2016. This network, determined by systematic conservation planning techniques, specifies relevant areas for 691 conservation targets, including 350 red-listed plant species, 65 threatened birds, 31 mammals, 30 reptiles, 22 amphibians, and 126 fishes, besides additional special habitats (e.g., caves) and endangered ecosystems. A landscape connectivity analysis indicated the potential of each area for restoration programs. Furthermore, other potential conservation actions were proposed for each area, including the creation of Conservation Units of Integral Protection and Conservation Units of Sustainable Use. In fact, the analysis clearly identified 53 Priority Areas that are the best cost-effective proactive conservation opportunities in existence today. This chapter highlights that Brazil now has an updated systematic conservation plan for the Caatinga biome and a historically unique window of opportunity to protect its biodiversity for the centuries to come.

Keywords Biodiversity • Caatinga • Conservation Priority Areas • Habitat loss • Fragmentation • Restoration • Systematic conservation planning

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17.1 Introduction

Brazil is a megadiverse country, being home to at least 10% of the world's species (Mittermeier et al. 1997; Lewinsohn and Prado 2005). Since the 1992 Rio Earth Summit, the Brazilian government assumed the international commitment of conserving the biodiversity of all its biomes (CDB 2016), including the Caatinga drylands, which have officially lost approximately 40% of their original cover (but see Chap. 13) and contain a large number of threatened endemic species (Chaps. 2, 3, 4, 5, 6, 7, and 8). Since 1998 the Brazilian Ministry of the Environment (MMA) has been organizing participatory workshops to define Priority Areas for biodiversity conservation and management actions.

The first plan, established by MMA Law 126 of 27 May 2004 and decree 5092 of 24 May 2005, recognized 900 Priority Areas for conservation of Brazilian biodiversity. Some years later, the MMA adopted systematic conservation planning (SCP) (Margules and Pressey 2000) as a tool to define the Priority Areas for conservation, sustainable use, and shared benefits of the Brazilian biodiversity (see Box 17.1). In 2007, the MMA updated the previous resolution throughout the MMA Law 9 of 23 January 2007 and defined 1561 Priority Areas, in addition to the Conservation Units already established. For the Caatinga, 292 Priority Areas were proposed, including 72 Conservation Units.

Box 17.1: Glossary

Systematic Conservation Planning (SCP) – Objective method of determining a minimum set of Planning Units, which will be ultimately grouped into Priority Areas, that satisfy the conservation goals determined for all chosen conservation targets at the lowest possible cost.

Priority Areas (PA) – Areas of outstanding importance for conservation, sustainable use, and shared benefits of the biodiversity that are recognized officially by a Law from the Brazilian Ministry of Environment. Priority Areas drive future conservation actions, such as the creation of Conservation Units, management regimes, and support decisions on the occupancy of the territory by the private initiative. Normally, PAs are larger than UCs.

Planning Unit (PU) – The smaller spatial scale on which all information used on a Systematic Conservation Planning analysis should be presented. In the MMA analysis, 53031 watersheds of 1537.4 ha, on average, were used as Planning Units.

Conservation Units (UC) – Biodiversity protected areas. Conservation Units are created by the federal or by the state governments. Conservation Units do not include the Indigenous Lands that are recognized due to the original rights of indigenous people. In Brazil, the term Protected Areas encompasses both Conservation Units and Indigenous Lands.

Conservation Units of Sustainable Use (UC-US) – Conservation Units that promote the sustainable use of natural resources.

Conservation Units of Integral Protection (UC-PI) – Conservation Units whose main aim is biodiversity conservation, being more restricted in relation to human use.

In 2014, the Brazilian government launched the process of reviewing the Priority Areas. For the Caatinga, the justification for such an upgrade is clear since knowledge concerning the conservation targets and their distribution, although still restricted (Santos et al. 2011), has grown considerably in the past decade with the establishment of several new universities and research groups in the Brazilian northeast(MEC 2015). In addition, land use also suffered considerable changes due to the establishment of new agribusiness activities, roads, power lines, and other infrastructure projects, such as the transposition of the São Francisco River. Furthermore, spatial data, including vegetation cover and species records, has become freely available.

The aim of this chapter is to briefly describe the participatory process and main results of the second update of the Priority Areas for conservation, sustainable use, and shared benefits of the Caatinga biodiversity. This process culminated in the determination of 282 Priority Areas defined by the MMA Law 223 of 21 June 2016. We also discuss the limits of the actual Conservation Unit network of the Caatinga biome and the urgency for the implementation of conservation actions that profit from the windows of opportunity represented by the Priority Areas.

17.2 Participatory Systematic Conservation Planning

The Priority Areas for conservation, sustainable use, and shared benefits of the Caatinga biodiversity were defined through a participatory process, coordinated by EMV and CRF, which occurred along with a series of workshops that culminated in the final proposal that were the origin of the MMA Law 223 of 21 June 2016 (Fig. 17.1). All workshops were attended by representatives from the MMA and the Secretary of Environment from the ten Brazilian states that encompass the Caatinga, in addition to other state agencies (e.g., IBGE (Brazilian Institute of Geography and Statistics), IBAMA (Brazilian Istitute of Environment and Renewable Natural Resources), Chico Mendes Institute), universities, and non-governmental organizations (NGOs). A preliminary step, however, was to perform an online evaluation of the methods, results, and use of the products generated by the work done in 2007. In this process, adjustments in relation to the methodology were proposed, new products were designed, and a better understanding was achieved on how the information on Priority Areas is used by state and federal governmental agencies, NGOs, and the private sector.

The first face-to-face meeting, called a methodological workshop, was organized in Salvador (Bahia) with representatives from 16 institutions (44 people) with the aim of discussing and determining the methodology to be applied in the 2016 Priority Areas exercise. In this meeting, the theoretical basis of SCP was discussed and major methodological decisions were undertaken. An important decision was to use natural watersheds as Planning Units (PUs) (see Box 17.1) since (i) water is the most important limiting resource for the Caatinga biome; (ii) watersheds have natural boundaries that can structure ecological, biogeographic, and evolutionary

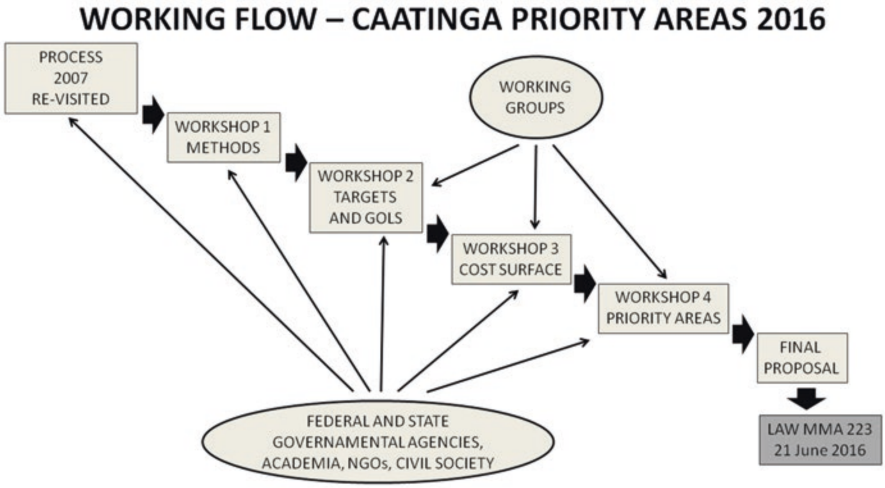

Fig. 17.1 Working flow of the prioritization process organized by the Ministry of Environment (MMA) that culminated in the establishment of 282 Priority Areas for conservation, sustainable use, and shared benefits of the Caatinga biodiversity according to Law MMA 223 of 21 June 2016

processes; and (iii) they have politic jurisdiction represented by the watershed committees. In the end, 53,031 watersheds of, on average, 1537.4 ha were used as PUs.

The second workshop, which was organized in Recife (Pernambuco) with representatives from 20 institutions (35 people), determined the conservation targets and their associated conservation goals. In fact, this meeting was the endpoint of a 6-month process that involved 99 researchers from 42 institutions organized in several virtual working groups (e.g., birds, mammals, reptiles, amphibians, plants, fishes). Each working group had a group of two to four coordinators and a variable number of collaborators that were responsible for defining a list of conservation targets, making explicit the criteria based on which they were proposed as targets (e.g., International Union for Conservation of Nature [IUCN] or Brazilian red-listed species, endangered ecosystem), and producing a map of their geographic distribution, sometimes using niche modeling techniques (Elith and Leathwick 2009). In the workshop, the coordinators of the working groups showed their proposal which received suggestions and amendments by the participants. Finally, several criteria were established to define the representation goal for each conservation target. For all species, the representation goal was established according the criteria proposed by Rodrigues et al. (2004). For species with an extent of occurrence lower than 1000 km^2 the representation goal was established as 100% and for those species occurring in more than 250,000 km^2 the goal was set as 10%. For species with an intermediate extent of occurrence the representation goal was established by the non-linear equation $Goal = -37.53 LogArea + 212.6$. For the remaining conservation targets, such as high, arboreal Caatinga remnants, caves, and special ecosystems (e.g., coastal dunes and mangroves) the criteria were defined democratically by the workshop members. A political agreement among the ten Brazilian states that possess Caatinga allowed the establishment of a 10% target in relation to their remaining natural vegetation, reaffirming their shared responsibility over the Caatinga biodiversity.

The third workshop, which also took place in Recife (Pernambuco) and involved 17 institutions (25 people), was designed to define a cost surface representing the relative cost, among PUs, of establishing conservation actions. The cost surface was created as the weighted mean of 21 spatially explicit primary variables representing social, economic, and environmental costs. For instance, population density was a key variable representing the social cost while the proximity to cities and paved roads, agribusiness, mining, and wood and oil extraction activities raised the economic costs. Environmental costs were associated with measures of habitat loss and fire incidence.

With the products of the previous workshop at hand, objective SCP techniques were applied to generate a preliminary proposal for Priority Areas (Margules and Pressey 2000). The simulation analysis was performed in MARXAN software (Game and Grantham 2008; Ball et al. 2009; http://marxan.net/) in such a way as to find sets of PUs able to satisfy the representation goals of all conservation targets while keeping the cost as low as possible. Although all PUs play a given role in conservation, SCP recognizes that some PUs will be more essential than others in the solution. In other words, PUs have different levels of irreplaceability. In fact, simulation analysis in MARXAN produces an irreplaceability surface showing areas more or less important for conservation. Also, MARXAN analysis identifies the set of PUs that constitutes the best solution (i.e., less costly). Based on such analysis, a preliminary proposal of the polygons of Priority Areas was established.

The final workshop, which was held in João Pessoa (Paraíba) and involved 22 institutions (46 people), had a primary aim of evaluating and proposing alterations to the preliminary proposal. Basically, deletions, additions, and changes in the limits of the polygons were proposed based on local knowledge, always respecting the representation goals of all conservation targets. At the end of this process, the Priority Areas were approved and classified in terms of their biological importance (i.e., degree of irreplaceability) and two criteria of urgency (i.e., habitat loss and desertification threat).

Also, each approved Priority Area had their potentiality evaluated in respect to potential conservation actions. For instance, some large Priority Areas with a high level of biological importance were indicated for the creation of new Conservation Units of Integral Protection. Others, depending on ongoing initiatives, were indicated for the creation of Conservation Units of Sustainable Use. Many Priority Areas were indicated for restoration projects considering their relevance to the functional connectivity of the biome (see Sect. 17.6) while others were suggested for special managing regimes (e.g., sustainable cattle ranching).

17.3 The Caatinga Conservation Targets

In total, 691 conservation targets were selected for the Caatinga biome (Table 17.1). Most of them were threatened plant species (S = 350) included in the *Red Book of the Brazilian Flora*, an updated publication produced in collaboration with around 200 taxonomists (Martinelli and Moraes 2013). In fact, 154 of the conservation targets were highly endemic (<1000 km^2) with representation goals of 100%, including many Asteraceae (24), Bromeliaceae (14), Cactaceae (9), Fabaceae (9), Xiridaceae (7), and Melastomataceae (6).

Interestingly, fishes were the taxon with the second highest number of conservation target species (S = 126) since the Caatinga biome contained a large number of highly endemic fishes distributed in several families, including Rivulidae (32), Loricariidae (15), Characidae (13), Trichomycteridae (8), and Heptapteridae (5). Such species were frequently restricted to a few PUs within the major watershed zones of the Caatinga biome. This group was included for the first time in the Caatinga prioritization process and benefited significantly from the decision to use watersheds as PUs.

Most of the 65 bird conservation targets had a less restricted distribution. In fact, 23 occurred in more than 250,000 km^2 with representation goals set as 10%. Several species, however, are considered critically endangered (*Antilophia bokermanni*—Pipridae, *Pyrrhura griseipectus*—Psittacidae) and endangered (e.g., *Formicivora grantsaui*—Thamnophilidae, *Scytalopus diamantinensis* and *Phylloscartes beckeri*—Rhinocryptidae, and *Lepidocolaptes wagleri* and *Xiphocolaptes falcirostris*—Dendrocolaptidae).Several sub-species were also selected as conservation targets (e.g., *Stigmatura napensis bahiae*—Tyrannidae and *Thectocercus acuticaudatus haemorrhous*—Psittacidae).

Table 17.1 Caatinga conservation targets and their distribution among the Brazilian states

Target type	AL	BA	CE	MA	MG	PB	PE	PI	RN	SE	Caatinga
Plants	28	307	44	6	21	39	58	31	18	12	350
Birds	48	65	58	28	49	57	62	56	49	40	65
Mammals	15	27	13	10	11	15	20	16	13	13	31
Reptiles	8	27	11	2	6	8	14	16	9	8	30
Amphibians	0	16	9	0	2	3	4	1	2	0	22
Fishes	10	72	31	19	21	10	20	31	10	16	126
Natural caves	1	4	3	1	1	1	2	2	3	1	18
Geodiversity	12	20	23	10	13	14	18	23	18	15	26
Coastal habitats	1	0	8	3	0	0	0	5	9	0	12
High Caatinga	1	1	1	1	1	1	1	1	1	1	1
State Caatinga	1	1	1	1	1	1	1	1	1	1	10
Total number	125	540	202	81	126	149	200	183	133	107	691

AL Alagoas, *BA* Bahia, *CE* Ceará, *MA* Maranhão, *MG* Minas Gerais, *PB* Paraíba, *PE* Pernambuco, *PI* Piauí, *RN* Rio Grande do Norte, *SE* Sergipe

Among the 31 mammal conservation targets, several species of primates are among the major concerns, since *Sapajus flavius*, *Callicebus barbarabrownae*, and *S. xanthosternos* are critically threatened, *Alouatta ululate* is threatened, and *Callithrix kuhlii* has a near threatened status according to the IUCN. Among the Carnivora, *Leopardus wiedii* and *Speothos venaticus* are classified as near threatened. *Lontra longicaudis* was virtually unknown in the Caatinga until recently and is classified as data deficient. The bristle-spined rat *Chaetomys subspinosus* (Rodentia) and the small marsupial *Monodelphis rubida* (Didelphimorphia) have also very limited geographic distributions. Other species have a widespread distribution, such as the Caatinga endemic *Kerodon rupestris*, but are threatened everywhere by hunting.

Among the 22 amphibian conservation targets, ten were highly endemic: *Siphonops annulatus* (Caecilidae), *Proceratophrys aridus*, *P. minuta*, *P. redacta* (Cycloramphidae), *Adelophryne maranguapensis* (Eleuterodactilydae), *Bokermannohyla diamantine*, *B. juiju*, *B. flavopictus*, *Corythomantis galeata* (Hylidae), and *Chthonerpeton arii* (Typhlonectidae).

Among the 30 reptiles conservation targets, the highly endemic species (<1000 km^2) were *Mesoclemmys perplexa* (Chelidae), *Gymnodactylus vanzolini* (Gekkonidae), *Acratosaura spinosa*, *Heterodactylus septentrionalis*, *Procellosaurinus tetradactylus*, *Scriptosaura catimbau* (Gymnophthalmidae), and *Tropidurus mucujensis* (Tropiduridae).

Besides the biological targets, some alternative habitats were included as conservation targets. An important target is the remnants of tall, arboreal Caatinga that have been recently mapped (Hansen et al. 2013). In order to partially contemplate alternative habitats that could be useful to small-sized organisms, such as arthropods, which were not considered explicitly as conservation targets, 26 topographic classes were included as conservation targets (e.g., inselbergs, dunes, coastal plains). Also, some ecosystems (e.g., mangroves) were selected as conservation targets. Furthermore, four classes of caves were defined according the basic lithology (i.e., granitoids, siliciclastics, carbonatics, and ferruginous) since this can determine a different endemic composition of troglophyles and troglobites (Silva et al. 2011).

17.4 The Caatinga Priority Areas

In the Caatinga biome, 282 Priority Areas for conservation were identified (Fig. 17.2). The Priority Areas varied considerably in relation to the number of conservation targets they possess; while some had five, a single Priority Area is home of 309 conservation targets (Fig. 17.2a). There is a noticeable latitudinal gradient from the northern areas that contains fewer conservation targets than southern areas which have hundreds of conservation targets.

An important landscape element defining such a pattern is the Diamantina Highlands. In fact, the Diamantina Highlands possess hundreds of endemic, red-listed plant species (Martinelli and Moraes 2013). Furthermore, several amphibian

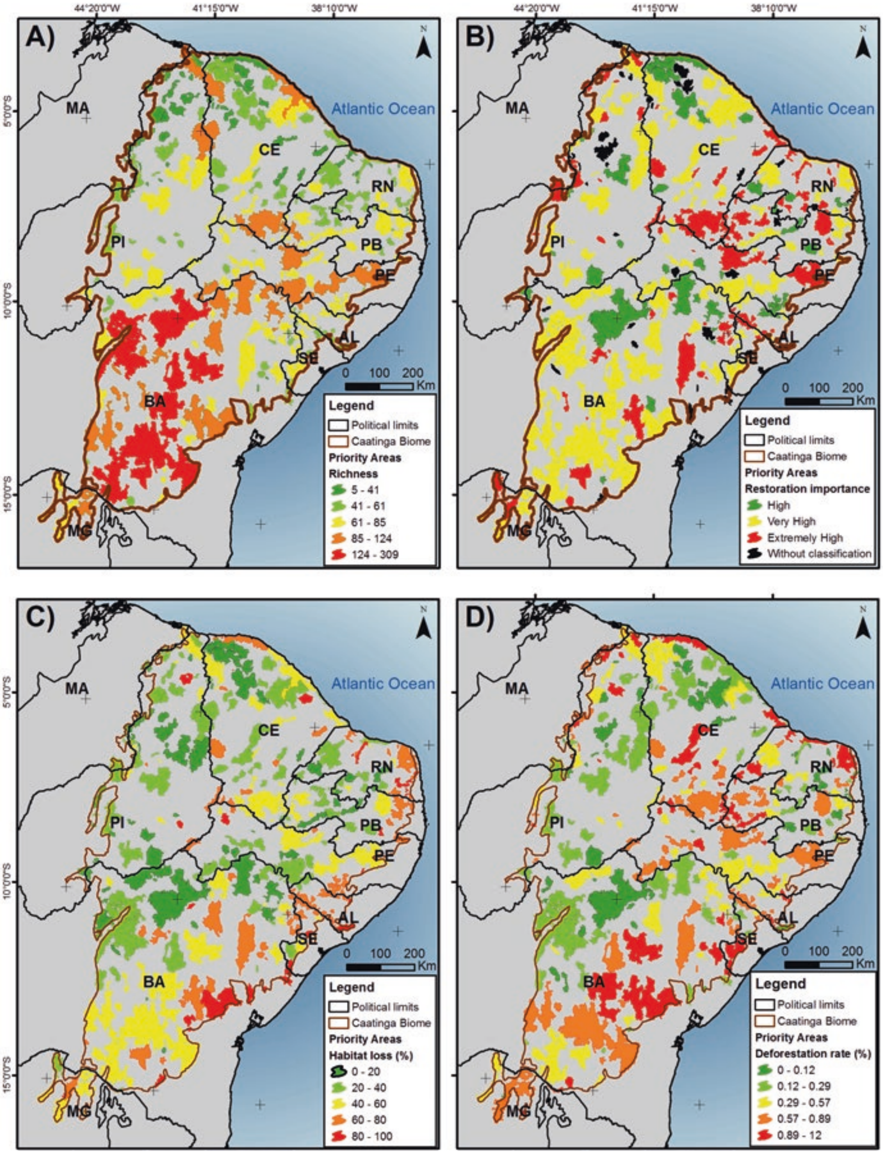

Fig. 17.2 Distribution of the 282 Priority Areas for conservation, sustainable use, and shared benefits of the Caatinga biodiversity according to Law MMA 223 of 21 June 2016. The Priority Areas are classified according to classes of (**a**) richness of conservation targets; (**b**) restoration importance based on landscape connectivity analysis; (**c**) habitat loss (%) until 2009; and (**d**) deforestation rate (%/year) between 2002 and 2009

Table 17.2 Distribution of the Caatinga Priority Areas among the Brazilian states

State	Priority Area (ha)	%	*N*	Caatinga area (ha)
Alagoas	381,599	29.4	16	1,299,387
Bahia	13,169,797	43.8	73	30,093,957
Ceará	5,378,831	36.1	55	14,890,874
Maranhão	334,621	89.2	13	374,960
Minas Gerais	801,580	72.3	10	1,109,334
Paraíba	1,446,198	28.2	32	5,137,097
Pernambuco	2,737,678	33.8	31	8,101,162
Piauí	4,172,145	26.4	52	15,810,964
Rio Grande do Norte	1,565,975	31.5	45	4,970,347
Sergipe	416,715	41.6	14	1,002,719
Total	30,405,138	36.7	282	82,790,802

species are restricted to this location, such as *Proceratophrys minuta* and *P. redacta* (Cycloramphidae), *Bokermannohyla diamantine*, *B. juiju*, *B. flavopictus*, *B. itapoty*, *B. oxente*, *Corythomantis galeata* (Hylidae), *Leptodactylus oreomantis* and *Rupirana cardosoi* (Leptodactylidae), and *Haddadus aramunha* (Craugastoridae).

The 282 Caatinga Priority Areas together covered 36.7% (30,405,138 ha) of the Caatinga territory (Table 17.2). The number of Priority Areas varied considerably among the Brazilian states, partially reflecting differences in the Caatinga coverage. For instance, the Bahia state had 73 Priority Areas distributed over 13,169,797 ha, corresponding to 43% of the total. However, 36% of the biome occurs in this state alone. In absolute terms, larger portions of Priority Areas are located in Bahia, Ceará, Piauí, and Pernambuco but this also is a direct function of the size of the biome within each state.

17.5 Habitat Loss and Deforestation Rates

The Caatinga biome officially had 54.5% of its original cover relatively intact in 2009 (but see Chap. 13). The situation, however, is clearly more worrying than this figure suggests since the whole biome has been explored for centuries and is affected by chronic anthropogenic disturbance (Ribeiro et al. 2015, 2016; Chap. 14).

Considering the 282 Priority Areas, mean habitat loss in 2009 was estimated to be 44.2% (Fig. 17.2c). Habitat loss, however, varied considerably among Priority Areas. Whereas some had already lost 99.6% of its cover, the loss in others was only 0.03%. The deforestation rate from 2002 to 2009 indicated that, on average, Priority Areas were losing 0.7% of their cover annually (Fig. 17.2d). Again, while some areas had undetected annual losses, others suffered a loss of 12% per year between 2002 and 2009.

17.6 Restoration for Caatinga Connectivity

Theoretical and empirical studies indicate that landscape connectivity is essential for the long-term maintenance of genetic diversity, animal and plant populations, community structure, and ecosystem processes and services (e.g., Taylor et al. 1993). A connectivity analysis based on graph theory (Antongiovanni 2017) that has been incorporated by the MMA for the definitions of the actions to be performed in the Priority Areas indicated that the connectivity of the Caatinga can be improved by restoration actions inside the Priority Areas. The analysis, which was based on watersheds of 8200 ha, determined the relative importance of restoration actions for all Priority Areas (Fig. 17.2b). Overall, 93 Priority Areas were considered to have an extremely high importance for the biome connectivity and deserve restoration effort. Also, 96 and 33 Priority Areas received a classification of very high and high, respectively, and 60 do not require any restoration effort.

17.7 A Scarce Conservation Unit Network

The National System of Conservation Units (SNUC) is a Brazilian law, created in 2000 to establish the criteria and norms for the creation, implementation, and management of Conservation Units (MMA Law 9985, 18 July 2000). Under this law, two basic types of Conservation Units are recognized: Conservation Units of Integral Protection and Conservation Units of Sustainable Use.

The main aim of Conservation Units of Integral Protection is biodiversity conservation, being more restricted in relation to human use. Among the different types of Conservation Units of Integral Protection, Biological Reserves are more restricted, while others are designed for scientific research (Ecological Station), to stimulate ecotourism (National Parks), to protect sites of singular beauty (Natural Monument), and to safeguard particular species or ecosystems (Wildlife Refuges). Only in the last two categories are private properties allowed to overlap with the Conservation Unit limits as long as there is no conflict of interest.

The main purpose of Conservation Units of Sustainable Use is to make biodiversity conservation and sustainable use of natural resources compatible. Among the Conservation Units of Sustainable Use, Areas of Environmental Protection (APA) are intended to be extensive and regulate private land use. In practice, this has been the most permissive Conservation Unit category of the whole SNUC system. Small private lands can also constitute Areas of Relevant Ecological Interest when they contribute to the protection of conservation targets of regional importance. Several Conservation Units of Sustainable Use, established in public lands, are designed to study and produce forestry products based on native species (National Forest), allow natural resource extraction activities by traditional populations (Reserve of Extractive Activities), facilitate studies on the management of animal populations of commercial use (Fauna Reserves), and embrace traditional populations that use

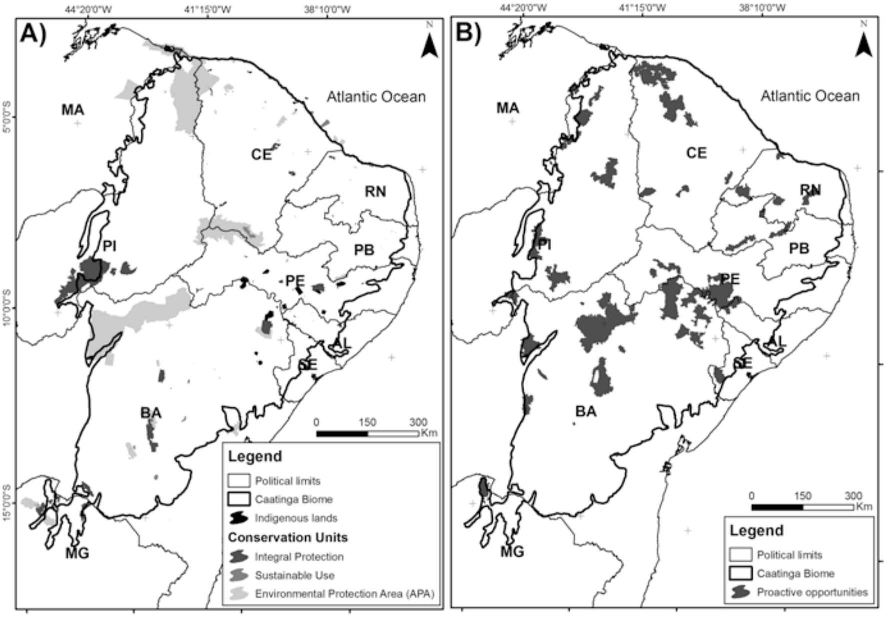

Fig. 17.3 Distribution of (**a**) the established Conservation Unit network in the Caatinga biome with the Conservation Units classified according the type of management category (see text) and (**b**) the 53 Priority Areas that are considered the best proactive conservation opportunities for the creation of new Conservation Units

local natural resources in a sustainable way (Reserve of Sustainable Development). Finally, there are private lands that receive a perpetuity title to be used exclusively for scientific studies and ecotourism (Private Reserve of Natural Heritage).

In the Caatinga, only 1.13% is currently protected by Conservation Units of Integral Protection (Fig. 17.3a). Additionally, 6.32% of the biome is protected in Conservation Units of Sustainable Use. However, 98.4% of the Conservation Units of Sustainable Use are APA, the most permissive of the SNUC categories (Fig. 17.3a).

17.8 Resource Limitations in the Established Conservation Units

The expansion of the areas under protection in the Caatinga is urgent and much needed (Fig. 17.3). However, like anywhere in the world, financial resources are essential for the effective management of Conservation Units (Bruner et al. 2001; Leverington et al. 2010; Geluda and Serrão 2014; Watson et al. 2014). Expanding the current Conservation Unit network in the Caatinga will certainly require further investments from the Brazilian Federal Government. A closer look at the available resources for the current federal Conservation Units in the region points to an already worrisome financial scenario. A recent analysis (Oliveira 2015; Oliveira and Bernard 2017) of the budget allocated by the Brazilian Government to 20 federal Conservation Units in the Caatinga between 2008 and 2014 indicated that, in spite of an apparent significant budget, the money available is unevenly and disproportionally spent in terms of both the size of the total area considered and the distribution of values among units. Resources varied from US$231,575 in 2008 to US$13,517,129 in 2011, totaling US$33,257,478 for the 7 years analyzed. However, land regularization in Serra das Confusões National Park in 2010 and 2011 alone consumed ~75% (US$24,873,718) of the whole budget for the entire period. Besides land regularization, the second largest expense in the Conservation Units in the Caatinga was ostensible property security (US$5,182,479), a third-party service, the focus of which is the protection of properties and goods (e.g., buildings, equipment, and cars—when existing), and not the biodiversity per se in the Conservation Units (Oliveira 2015; Oliveira and Bernard 2017). Ostensible property security consumed ~15.6% of the total budget, or ~61.8% of the remaining budget when land regularization is excluded.

The Conservation Units in the Caatinga are effectively receiving very few resources considering the area they cover (around 2.3 million hectares) and the environmental services they provide (Manhães et al. 2016). A comparison between the average amount spent in Conservation Units elsewhere and the budget allocated by the Brazilian Government for the federal Conservation Units in the Caatinga clearly points out how underfunded those sites are. Division of the whole budget spent in the 20 Conservation Units by the 7 years analyzed and by their total area results in an average cost of US$2.01/ha/year (Oliveira and Bernard 2017). Excluding land regularization costs spent in Serra das Confusões National Park, the total expenses averaged US$0.50/ha/year. This is approximately 12 times lower than the values specified by the own Brazilian MMA as necessary for the basic operation of a Conservation Unit in Brazil (MMA 2009), nearly 1.8 times lower than the average spent globally (James et al. 2001), up to six times lower than the average values spent in Latin American and African parks (Bruner et al. 2004; Green et al. 2012), and up to 86 times lower than values spent in protected areas in the European Union (López and Jiménez 2006).

Not coincidently, some of the federal protected areas in the Caatinga are acting as *paper parks*. According to the Cadastro Nacional de Unidades de Conservação (National Database of Conservation Units), of the 20 Conservation Units analyzed, 12 do not have a management council, 11 do not have a management plan, ten do not have basic infrastructure, and only seven are open to visitors (Oliveira and Bernard 2017). This situation violates the current legislation in several ways: since 1979 all Brazilian protected areas must have a management plan (Decreto 84,017/1979, Brasil 2000); a management council has been mandatory since 2000 (Brasil 2000); and the public visiting was one of the key objectives for the creation of several of the areas currently closed to tourists. Therefore, in order to maintain and expand the protected areas system in the Caatinga, an official commitment to secure funds from federal and state governments is mandatory.

17.9 Proactive Conservation Opportunities

Conservation strategies can be classified as proactive and reactive (Brooks et al. 2006). Proactive conservation strategies are those for which the moderate investment costs of open opportunities are covered sooner but with a stream of return benefit that will accumulate in the long run. Reactive strategies delay the investments in conservation actions for the future, but the total cost to be paid in the future rises steadily. As demonstrated by the spatial analysis here, there are still a number of great proactive conservation opportunities in the Caatinga (Fig. 17.2). Such areas are highly irreplaceable with many threatened species but are not substantially affected by habitat loss while recent measures of deforestation rates are still low. Many such areas are located in the north and northeast region of the Bahia state, but also in Ceará, Piauí, Rio Grande do Norte, and Paraíba. Therefore, the first step towards an effective proactive conservation strategy in the Caatinga is complete and updated—the localization of the main proactive opportunities based on their degree of habitat integrity, habitat connectivity, biological representativeness, geopolitics, and anthropogenic pressure.

The main mechanism for the proactive conservation strategy is, of course, the creation of new conservation areas. The 2016 MMA law indicated 150 Priority Areas for the creation of Conservation Units; however, a single Priority Area can be indicated for the creation of different Conservation Unit categories. In total, 79 Priority Areas were indicated for the creation of Conservation Units of Integral Protection, 54 for the creation of Conservation Units of Sustainable Use, and 45 with potential for the creation of Conservation Units of both types. Among the 150 Priority Areas indicated for the creation of Conservation Units, 53 were considered the best proactive opportunities due to their low level of habitat loss (mean = 17.3%) (Fig. 17.3b). From an economic viewpoint, the immediate creation of new Conservation Units in these Caatinga Priority Areas can be considered the best cost-effective action to be implemented.

The next step is to transform the recommendations that came out of this information-based planning phase into concrete actions, considering the growing pressure of several economic activities such as agriculture, cattle ranching, forestry, mining, and wind farms. Due to the recent economic crisis, the federal and state governments have now serious limitations to execute such conservation planning in the short run. We foresee, therefore, that new alliances with the productive sector can move such enterprises forwards. For instance, the wind power industry is growing substantially in the Caatinga. We envisage that the continuous expansion of the wind power industry in the biome should occur in parallel to the expansion of the Caatinga Conservation Unit network, via compensatory mechanisms to be openly discussed. Also, Caatinga conservation can profit immensely from the collaboration of international partners concerned with the world biodiversity. The Amazon, for instance, has profited substantially with collaborations from international NGOs (e.g., the World Wildlife Fund [WWF]) and financial institutions (e.g., World Bank, the German bank KfW). Independent of how the actions will take place, it is clear that Brazil now has an updated systematic conservation plan for the Caatinga biome and a historically unique window of opportunity to protect its biodiversity for the centuries to come.

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Chapter 18
Sustainable Development in the Caatinga

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Abstract Sustainable development can be defined as a development model that aims to achieve environmental conservation together with social inclusion and economic prosperity. It requires efficient management of two types of infrastructure: green and socio-economic. Over the last three decades, the Brazilian Government has been designing and implementing innovative policies that can foster sustainable development across the country, but it has failed to incorporate these policies into individualized local development plans. Most municipalities (56.3%) in the Caatinga present very low to low scores in green infrastructure and very low to low scores in socio-economic infrastructure, indicating that they are fragile societies. The fact that municipalities with high scores in socio-economic infrastructure have low scores in green infrastructure indicates that the conventional development model based on the depletion of natural resources is the dominant mindset across the region. Genuine sustainable development in the Caatinga requires the restoration of green infrastructure and improvement of the existing socio-economic infrastructure to increase the regional population's living standards.

Keywords Green infrastructure • Human development • Policies • Socio-economic infrastructure • Sustainability

18.1 Introduction

Conventional development models have focused almost exclusively on continuous economic growth (Todaro and Smith 2009). However, during the 1970s and 1980s, societies realized that economic growth by itself leads to environmental degradation and social inequalities, which, over the long term, can undermine global prosperity

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(Rao 2000). During the 1980s, the sustainable development model was proposed as an alternative (Costanza and Daly 1992). This model seeks to achieve environmental conservation together with social inclusion and economic prosperity (Sachs 2015).

The new concept was embraced by all: governments, civil society, and businesses. Everyone committed to changing their policies and practices and moving the world toward a more sustainable development path. Based on the discourses of key decision-makers, the conventional development model appeared to be left behind. Sustainable development had become the new international norm—the new standard by which countries should be measured.

Yet, over time, the translation from discourse to action remained a challenge, and genuine progress of implementing sustainable development has been spotty and segmented (Gupta and Vegelin 2016). It is fair to say that the global excitement about the concept of sustainable development has helped shape innovative national policies, drive international investments, foster a transformation in production and consumption systems, reduce global poverty, and alleviate some of the world's most pressing global health problems (Sachs 2015). However, natural ecosystems worldwide have never been so close to a collapse (Venter et al. 2015). Tropical forests and savannas continue to be transformed into agricultural fields (Foley et al. 2011; Food and Agriculture Organization of the United Nations [FAO] 2015), fisheries continue to be depleted (FAO 2011), and pollution continues to negatively affect all types of ecosystems, including the atmosphere, which has already undergone irreversible changes in terms of Earth's climate system (Intergovernmental Panel on Climate Change [IPCC] 2014). A recent evaluation of global progress towards better conservation and management of global ecosystems indicates that countries are failing miserably in their commitments to sustainable development and that long-term human prosperity is threatened as a result (Secretariat of the Convention on Biological Diversity 2014).

The United Nations (UN) has been promoting sustainable development as much as it can. Several meetings, treaties, and global initiatives, such as Agenda 21 (A21), the Millennium Development Goals, and, more recently, the Sustainable Development Goals, have been proposed and agreed upon (Langford 2016; Persson et al. 2016). However, a permanent flow of resources to accelerate the planet's transition to a more sustainable development path remains elusive. As a result, when facing social and economic crises, countries commonly revert to the same conventional development mindset that has allowed developed countries to accumulate their technology, health, and political power for decades. To date, sustainable development remains an unrealized promise.

Tropical dry forests and woodlands are among the most fragile and least studied terrestrial ecosystems (Dirzo et al. 2011). A harsh climate and nutrient-poor soil constrain the use of these ecosystems by human populations (Prado 2003). If not well-managed within their carrying capacity, they quickly become degraded. In just a few decades, such ecosystems can move from degradation to desertification (Hellden and Tottrup 2008; Sá and Angelotti 2009). Yet, human pressures on such regions do not end. Hoekstra et al. (2005) estimated that, at the global level, 45.8%

of tropical dry forests have been converted to other land uses, which supports the argument that they are one of the world's most endangered biomes (Janzen 1988; Dirzo et al. 2011).

The Caatinga in South America is the continent's largest tropical dry forest region (Prado 2003). Restricted to Brazil, the region has always been considered a national problem—one that is hard to tackle (Andrade 1998; Ab'Saber 1999). Unpredictable droughts, famine, long-distance migrations, deep inequality, depletion of natural resources, failed development plans, and a corrupt power system have limited human development across the region for centuries (Andrade 1998; Ab'Saber 1999). As a result, despite many attempts to rectify this by Brazilian society, the region has living standards below the national average (Chap. 1). Under such difficult circumstances, two basic questions should be asked. First, is it possible to envision a sustainable Caatinga? Second, what should the regional society do to shift its development path toward a more sustainable state? In this chapter, we address these two questions.

18.2 Sustainable Development and Infrastructure

We argue that, to move toward a sustainable development path, societies must manage their territories' infrastructures as efficiently as possible. Infrastructure is defined as all elements of interrelated systems that provide goods and services essential to enabling, sustaining, or enhancing societal living conditions (Fulmer 2009). Usually, when people talk about infrastructure, they are referring to socio-economic infrastructure, that is, the combination of all human-made assets, including human, political, and financial assets, required by social sectors (e.g., educational, health, cultural, and financial) and economic sectors (e.g., energy, water and sewage, and food and agriculture) to generate and distribute benefits, such as education, jobs, health, etc., across the social spectrum. The socio-economic infrastructure is imperative for sustainable development because it is the foundation on which complex economies can be built, human well-being indicators can be improved, and vulnerability to natural hazards can be reduced (Doyle and Havlick 2009; Sachs 2015).

However, natural ecosystems provide essential goods and services to human prosperity as well (Millennium Ecosystem Assessment 2005). Therefore, they should also be considered part of the infrastructure (Frischmann 2012). Silva and Wheeler (2017) reviewed the concept of ecosystems as infrastructure and found that the concept is not new but rather emerged in the 1980s in parallel to the discussion about sustainable development. Scientific literature has used different names, including ecological infrastructure, green infrastructure, natural infrastructure, and blue infrastructure, to describe the idea. Silva and Wheeler (2017) opted to use green infrastructure as a unifying concept because it was the most commonly used term in both scientific literature and political agreements. They also suggested a more inclusive concept by stating that green infrastructure is a network of natural, semi-natural, and restored areas that are designed and managed at different spatial scales that encompass all major types of ecosystems. Such a network aims to simultaneously conserve biodiversity, mitigate greenhouse gas emissions, enable societal adaptations to climate change, and deliver a wide range of other ecosystem services that human societies need to prosper.

Ultimately, green infrastructure is the mechanism by which societies manage their renewable natural capital in the same way that socio-economic infrastructure is the mechanism by which societies manage their social, human, and physical capitals (Benedict and McMaho 2006). Because the space within a society is finite, spatial trade-offs between green and socio-economic infrastructures will always exist. As a result, finding the right balance between these two types of infrastructure is a key characteristic of a sustainable society (Dias et al. 2016).

Collados and Duane (1999) envisioned a graphical model in which human quality of life is a function of both environmental services (provided by green infrastructure) and human-made services (provided by socio-economic infrastructure). Under this model, if societies are able to maintain both services above a certain level, they are in a sustainable state. Otherwise, they are in an unsustainable state. Over time, the quality and quantity of these services can change as a result of the society's decisions. If both types of services improve over time, the society is following a sustainable development path. If not, it is following an unsustainable development path. Collados and Duane (1999) found that only 14 of 51 possible development paths could be considered sustainable.

Sustainable development paths are not always progressive, meaning that societies can move over time from an unsustainable to a sustainable state and vice versa. Additionally, societies are not isolated but rather integrated through trade and other mechanisms so that interactions between societies can also influence their development paths. In the end, a society's development path is a result of how it uses its assets as well as how it interacts with other societies.

18.3 Sustainable Development in Brazil

From a policy perspective, national commitments to global agreements and initiatives, such as sustainable development, are considered 'outside–in policies' in which major elements are decided internationally but the concrete implementation of which is led by local governments. Local governments can react in different ways to global agreements, sometimes embracing them and sometimes rejecting them according to their sociopolitical contexts (Happaerts 2012). However, conflicts between national and local governments can be avoided if national governments proactively set policies that provide incentives for local governments to deliver portions of the country's commitments to global agreements (Wamsler et al. 2014). Therefore, an effective road map to sustainable development includes national governments setting transformative policies that are then integrated into local development plans.

According to the UN, empowering local societies is essential because people have a greater sense of responsibility when their local government and community organizations have the power to lead change (United Nations Conference on Environment and Development 1992). Moreover, development plans designed with broad public participation have higher legitimacy because they are based on citizen preferences and generate new information for decision-makers, thereby increasing the quality of the political decisions and boosting efficiency gains (Irvin and Stansbury 2005).

In the last three decades, Brazil has made a valiant effort to position itself as a global leader in sustainable development. First, Brazil hosted two major conferences on sustainable development—Rio 92 and Rio+20—and was a major supporter of A21, a non-binding coordinated global action plan that seeks to advance the sustainable development agenda at all different levels, from local to global. Second, between 1994 and 1997, Brazil's congress ratified the country's commitment to all three UN conventions created at Rio 92: the Convention on Biological Diversity, the UN Convention to Combat Desertification, and the UN Framework Convention on Climate Change. Third, a 1997 presidential decree created the Sustainable Development Policy Committee and National A21 (CPDS), which was coordinated by the Ministry of the Environment, has a membership equally representative of civil society and government, and whose major goal was to propose sustainable development strategies as well as to coordinate, design, and monitor the implementation of the Brazilian A21.

From 1999 to 2002, Brazil approved its A21 based on the input of approximately 40,000 people assembled during many consultation meetings (Brasil 2012). The final document was organized around five priority actions: (a) the economy of savings in the society of knowledge; (b) social inclusion for a solidarity society; (c) strategy for the urban and rural sustainability; (d) strategic natural resources—water, biodiversity, and forests; and (e) governability and ethics for the promotion of sustainability. Each priority action was composed of two to five objectives. In total, the Brazilian A21 has 21 objectives (Brasil 2002). Policies and plans were supposed to be enacted to support the objectives of the A21. These policies and plans, in turn, were thought to be integrated and mainstreamed into the local A21s (LA21s).

Brazil enacted important flagship policies for each one of its A21 objectives (Table 18.1). For instance, to ensure environmental conservation across the country, Brazil has approved a sound national environmental system (1981), a comprehensive national policy on biodiversity (2002), and a set of regulations for environmental conservation in both protected areas (2000) and private lands (2012). To guarantee social inclusion and development for all, the country's government established '*Bolsa Família*', a globally recognized social safety-net program (2003), as well as national policies for basic sanitation (2007) and education (2007). To shift current production systems, Brazil has adopted a national plan for sustainable production and consumption (2011), a national plan for low carbon emissions in agriculture (2010), and an energy conservation program (2012). Finally, to encourage high ethical standards and to ensure that government actions could be assessed by the population, the country's congress created a transparency portal on which all information

Table 18.1 Priority actions and objectives of Brazil's Agenda 21 and its respective flagship policies

Priority action and objectives	Flagship policies	Year
Priority action: the economy of savings in the society of knowledge		
Objective 1. Sustainable production and consumption to counteract the waste culture	National Plan for Sustainable Production and Consumption	2011
Objective 2. Eco-efficiency and social responsibility of companies	Sustainable Public Procurement Program	2012
	National Electricity Energy Conservation Program	1985
Objective 3. Recovery of the strategic planning, infrastructure, and regional integration	National Policy for Regional Development	2003
Objective 4. Renewable energy and biomass	National Program for the Production and Use of Biodiesel	2004
Objective 5. Information and knowledge for sustainable development	National Program of Environmental Education	1999
Priority action: social inclusion for solidarity in society		
Objective 6. Permanent education for work and life	National Plan for the Development of Education	2007
Objective 7. Promote health and prevent diseases by the democratization of the National Health System	Family Health Program	1991
Objective 8. Social inclusion and income distribution	'*Bolsa Família*' Program	2003
Objective 9. Universalization of environmental sanitation to protect the environment and health	National Policy of Basic Sanitation	2007
Priority action: strategy for urban and rural sustainability		
Objective 10. Management of the urban space and the metropolitan authority	National Plan for Urban Development	2006
Objective 11. Sustainable development of rural Brazil	Program for the Sustainable Development of Rural Territories	2003
Objective 12. Promote sustainable agriculture	National Policy for Technical Assistance and Rural Extension	2010
	New Forest Code	2012
	National Plan for Low Carbon Emissions in Agriculture	2010
Objective 13. Promote the local Agenda 21 and integrated and sustainable development	Agenda 21 Program	2001
Objective 14. Implement mass transportation and sustainable mobility	National Policy for Urban Mobility	2012
Priority action: strategic natural resources: water, biodiversity, and forests		
Objective 15. Preserve the quantity and improve the quality of the water in the hydrographic basins	National Policy of Water Resources	1997
Objective 16. Forestry policies, deforestation control, and biodiversity corridors	National System of Units of Conservation	2000

(continued)

Table 18.1 (continued)

Priority action and objectives	Flagship policies	Year
Priority action: governability and ethics for the promotion of sustainability		
Objective 17. Decentralization and the federative pact: partnerships, consortiums, and local power	The Municipality Participation Fund	1965
	The State Participation Fund	1965
Objective 18. State modernization: environmental management and economic mechanisms	National Environment System	1981
Objective 19. International relations and global governance for sustainable development	National Policy on Climate Change	2008
	National Policy on Biodiversity	2002
	National Policy to Fight Desertification and Mitigate the Effects of Drought	2015
Objective 20. Civic culture and new identities in the communication society	National Plan on Culture	2010
Objective 21. Pedagogy of sustainability: ethics and solidarity	Transparency Portal	2004

about the government's actions is publicly available (2004). Despite all the advances, the translation of these national-level sustainable development policies to LA21s has not been effective. In 2012, for instance, 82.3% of the 5565 Brazilian municipalities failed to implement their LA21s (Instituto Brasileiro de Geografia e Estatística [IBGE] 2013). This high rate of failure can be accredited to the fact that policy segmentation rather than policy integration was the norm in Brazil's quest for sustainable development, as most of the national-level flagship policies were implemented (if they even were implemented) independently, without any synergy with other related policies.

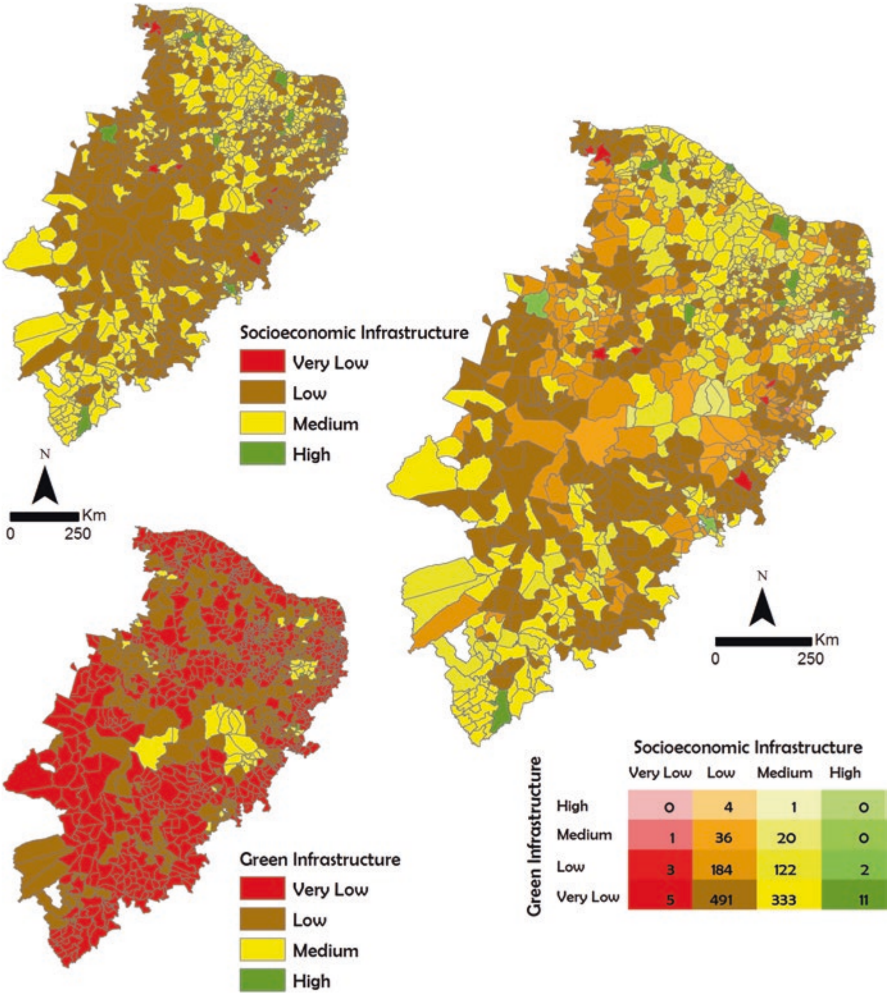
18.4 Sustainable Development in the Caatinga

The Caatinga has 1213 municipalities (Chap. 1), the smallest political units in Brazil. They have an autonomous government comprised of a mayor, directly elected by the people for a 4-year term, and a legislative body (Câmara dos Vereadores), also directly elected by the people. Municipalities have their own budgets and can set their own laws and regulations as long as they do not violate state and federal laws. In addition, they can set agreements with other adjacent municipalities to develop common initiatives. Municipalities are, in the end, places where actual development happens and where national-level policies and plans ultimately succeed or fail.

We used one indicator of green infrastructure and one indicator of socio-economic infrastructure to identify, for the first time, the present state of development for each one of these municipalities. As far as we know, nobody has attempted to investigate local development across the region by combining both types of infrastructure assets. The percentage of the area of the municipality that is still covered by natural ecosystems (see Chap. 13) was used as the indicator for green infrastructure. We assumed that the quantity and quality of the ecosystem services available for a local population is positively correlated with the area occupied by natural ecosystems. We classified the municipalities into four groups: very low (<20%), low (20–50%), medium (50–80%), and high (>80%) based on the area covered by natural ecosystems. As an indicator of socio-economic infrastructure, we used the municipal Human Development Index (HDI) from 2010. This index was calculated for all municipalities in Brazil by the United Nations Development Programme (UNDP), Instituto de Pesquisa Econômica e Aplicada (IPEA), and Fundação João Pinheiro (see www.atlasbrasil.org.br). We are aware that the HDI is not an indicator of the socio-economic infrastructure by itself; however, it measures income, health, and education, which are the most fundamental outcomes of a functional and reliable socio-economic infrastructure. Therefore, we assumed a positive relationship between the HDI and the socio-economic infrastructure. We classified the municipalities into four groups according to their HDI: very low (<0.49), low (0.50–0.59), medium (0.6–0.69), and high (>0.7). By combining the four categories of green infrastructure with the four categories of socio-economic infrastructure, we identified 16 categories, of which the one with the highest scores for both types of infrastructures represents the most sustainable state and the one with the lowest scores for both types of infrastructure represents the least sustainable state.

We found that most of the municipalities in the Caatinga have very low (840) and low (311) green infrastructure scores. Altogether, these municipalities cover an area of 993,302 km^2 and have a population of 18.7 million people. Municipalities with medium green infrastructure scores (57) cover an area of 61,999 km^2 and are home to 384,794 people. There are only five municipalities with a high green infrastructure. These municipalities are Fernando Pedroza in Rio Grande do Norte, Coxixola and Riacho de Santo Antônio in Paraíba, and Dois Riachos and Estrela de Alagoas in Alagoas. They have a total area of 984 km^2 and a population of 13,519. Regarding local socio-economic infrastructure, the municipalities of the Caatinga have very low (9) and low (715) scores. Municipalities with very low scores have an area of 6,296 km^2 and a population of 38,204 people, whereas those with low scores have an area of 615,730 km^2 and a population of 4.6 million people. A total of 476 municipalities earned medium scores and cover a total area of 417,498 km^2 with a population of 9.2 million people. Thirteen municipalities (Floriano in Piauí; Crato, Eusébio, Fortaleza, and Sobral in Ceará; Caicó, Mossoró, and Natal in Rio Grande do Norte; Campina Grande, Patos, and Várzea in Paraíba; Feira de Santana in Bahia; and Montes Claros in Minas Gerais) have high scores in socio-economic infrastructure. They cover an area of 16,762 km^2 and are home to 5.2 million people.

By combining green and socio-economic infrastructure scores, we found that most of the municipalities in the Caatinga are not even close to a sustainable state (Fig. 18.1). In fact, most of the municipalities (56.3%) present very low to low green infrastructures and very low to low socio-economic infrastructures (Table 18.2). Furthermore, no municipality has high scores in both types of infrastructure. The regional population lives mostly in municipalities with (a) medium socio-economic infrastructures and very low green infrastructures (18.2%); (b) low socio-economic



Green Infrastructure	Socioeconomic Infrastructure: Very Low	Low	Medium	High
High	0	4	1	0
Medium	1	36	20	0
Low	3	184	122	2
Very Low	5	491	333	11

Fig. 18.1 Distribution of the Caatinga's municipalities by categories of socio-economic infrastructure (top left), green infrastructure (bottom left), and by combining socio-economic infrastructure and green infrastructure (center right). The matrix represents the number of municipalities in each category of green infrastructure and socioeconomic infrastructure

infrastructures and very low green infrastructures (11.7%); and (c) high socio-economic infrastructures and very low green infrastructures (8.3%). Municipalities in the first and third categories have an urban population much greater than their rural population, while populations in municipalities of the second category are distributed evenly in both urban and rural settings (Table 18.2).

Table 18.2 Distribution of the Caatinga's municipalities by categories defined by combining socio-economic infrastructure and green infrastructure

Category[a]	*n*	Total area (km^2)	Total population (2010)	Total urban population (2010)	Total rural population (2010)
Very low–very low	5	4878	75,451	23,584	51,867
Very low–low	3	1245	41,020	11,483	29,537
Very low–medium	1	173	11,047	3137	7910
Low–very low	491	378,173	6,733,893	3,256,663	3,477,230
Low–low	184	192,227	2,435,396	1,118,290	1,317,106
Low–medium	36	44,516	556,000	249,084	306,916
Low–high	4	814	32,707	12,737	19,970
Medium–very low	333	259,369	10,371,913	7,211,878	3,160,035
Medium–low	122	140,648	2,758,530	1,849,392	909,138
Medium–medium	20	17,311	199,281	129,313	69,968
Medium–high	1	170	1771	782	989
High–very low	11	12,015	4,784,448	4,674,634	109,814
High–low	2	4748	614,332	560,605	53,727
Total	1213	1,056,287	28,615,789	19,101,582	9.514,207

[a] Categories are defined on the left by socio-economic infrastructure, using the Human Development Index as proxy, and on the right by the green infrastructure (i.e., socio-economic infrastructure–green infrastructure)

18.5 Looking Forward: Sustainable Development in the Caatinga

Our results show that all of the municipalities in the Caatinga are in an unsustainable state. The lack of municipalities with high scores in both types of infrastructure suggests that the conventional development mindset is still dominant across the region. Moreover, most of the municipalities with medium and high socio-economic infrastructures have very low and low green infrastructures, which reflects that local governments are unable to improve their social indicators while maintaining their natural ecosystems.

The municipalities of the Caatinga need to make an immense and complex effort to move toward a more sustainable path in the future. Though this is not a trivial task, the basic recommendation for most of them is simple and standard: municipalities must restore their green infrastructures to guarantee the continuous flows of ecosystem services as well as build socio-economic infrastructures that are socially inclusive, reliable, and can aggregate value to the goods and services produced locally. Because most of the municipalities in the region have depleted their natural resources without developing reliable socio-economic infrastructures, they do not have the means to transition toward more sustainable development paths. They are fragile municipalities and require substantial investments (both technical and financial) from governments, civil society, and businesses to make considerable progress in the path to sustainability.

From an environmental perspective, sustainable development in the Caatinga cannot be achieved without a large-scale regional program to restore its green infrastructure. Because the negative impacts of extreme climatic events on the region are predicted to increase over time (Marengo et al. 2016; Chap. 15), nature-based solutions seem to be the most feasible and socially inclusive way to increase the local population's ability to cope with future climate change (Scarano 2017). A program aimed at the restoration of the regional infrastructure requires the outright protection of the remaining natural vegetation as well as the selection of priority areas for restoration efforts (Possingham et al. 2015; Chap. 17). The conservation of the last patches of natural ecosystems is needed to ensure that the most important region's biodiversity sources are readily available to enable restoration efforts (Bullock et al. 2011). Selecting priority areas for restoration is important to maximize the production of ecosystem services while taking into consideration the impacts of global climatic changes on the region.

A green infrastructure restoration program should be executed locally and must produce both ecological and socio-economic benefits. Existing government-led programs, such as '*Bolsa Verde*' (http://www.mma.gov.br/desenvolvimento-rural/bolsa-verde), which provides payments for communities to protect or restore nature, can be used to motivate a broad engagement of the local population with ecological restoration efforts. In addition, the adoption of agroforestry systems using native plant species can help conservation efforts while generating an additional income source for local rural people.

Improving the socio-economic infrastructure in the Caatinga requires a well-coordinated program. To date, the benefits of this type of infrastructure have been captured mostly by the local oligarchies, which helped perpetuate the perverse levels of social inequality so well described in the literature on the region's human development (Andrade 1998; Ab'Saber 1999; Buainain and Garcia 2013a). During the 1980s, the population of the Caatinga shifted from predominantly rural to predominantly urban (Théry and Mello 2005; Ojima 2013). People moved to the major regional cities to search for better access to public services and employment opportunities. However, regional cities had not received enough investments to build the socio-economic infrastructure required to accommodate this intense migration. The mismatch between supply and demand for public services created unsustainable cities where living standards have remained below the national average (Table 18.3). Improving socio-economic infrastructure can foster new economic activities and enable endogenous local economic growth. This step is important because most of the Caatinga's municipalities rely on public services (including pensions) to stay economically viable (Table 18.3). In addition, local governments should improve

Table 18.3 Comparison between the Caatinga's municipalities andt all municipalities in Brazilin terms of Human Development Index, Fiscal Management Index, and % public services in the local Gross Domestic Product (GDP). Values are the mean and the standard deviation (in parentheses)

	Brazil	Caatinga
Number of municipalities[a]	5565	1213
Human Development Index (2010)[b]	0.66 (0.07)	0.59 (0.04)
Fiscal management index (2013)[c]	0.45 (0.14)	0.36 (0.13)
% Public services in the local GDP (2012)[a]	28.7 (14.7)	44.4 (12.1)

Sources:
[a] IBGE (https://sidra.ibge.gov.br)
[b] Atlas do Desenvolvimento Humano no Brasil (www.atlasbrasil.org.br)
[c] Índice Firjam de Gestão Fiscal (www.firjan.com.br/ifgf)

their capacity to manage their own budgets and do more with less. Right now, the quality of the management of the public budgets in the Caatinga's municipalities is below the country's average (Table 18.3).

A coherent plan to improve the socio-economic infrastructure in the Caatinga's municipalities should be designed and executed following a set of new practices. Instead of benefitting a few people, the plan should be socially inclusive. Instead of having large ecological impacts, the plan needs to focus on small areas and consume fewer natural resources. Instead of relying on archaic production systems, the plan needs to be technologically intensive and generate high-value products and services. Instead of being designed outside of the region, the plan should be co-created with the local population.

The restoration of the regional green infrastructure and the improvement of the socio-economic infrastructure must be developed together and be composed of a mix of policies that aim to produce high social–environmental benefits while reducing implementation costs. Because the local capacity to design such an innovative set of development policies is limited, municipalities in the Caatinga require policy entrepreneurs—that is, those who, working from outside the formal government, introduce, translate, and help implement new ideas into public practice (Roberts and King 1991). However, nothing can be achieved if local governments do not make efforts to improve their governance, which is defined by Andrews (2014) as "the existence of effective government organizations that have the authority and resources to unite political agents (across government, non-profit, business, and international arenas) as needed, when needed, and in the appropriate way, to solve problems that undermine the achievement of social objectives."

Our analyses demonstrated that the Caatinga should not be seen as a homogenous region from a development perspective and that environmental, social, and cultural differences should be taken into account when designing sound policies and plans. Despite the plethora of plans, programs, and initiatives led by all kinds of stakeholders in the last three decades (see list in Buainain and Garcia 2013b), unsustainable societies are still the norm across the region. Based on our analyses, there is no evidence that the current situation will change in the short or medium term. Therefore, only a radical shift in the way human development is understood by local governments will allow the region to move toward a more sustainable state in the future.

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Part VI
Conclusions

Chapter 19
The Future of the Caatinga

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Abstract The Caatinga is a socio-ecological system where the mutual interdependence of man and nature is outstanding. On one hand, ecological gradients maintain most of the large biodiversity and have been fundamental in shaping the modern regional cultural heritage. On the other hand, acute and chronic human disturbances together have led to a large-scale transformation of the Caatinga's ecosystems, thus reducing their capacity to provide critical ecosystem services to local communities. Future scenarios will possibly be worse due to climatic changes. The path toward sustainability and resilience in the Caatinga requires a major shift from the current ways in which local populations use and interact with natural ecosystems.

Keywords Biodiversity corridors • Desertification • Green infrastructure • Productive landscapes • Socio-ecological systems • Sustainability

19.1 Introduction

What lies ahead for the Caatinga and its people? What does the future look like? In this book, we assume that the desirable future is shaped by the 17 goals for sustainable development (see sustainabledevelopment.un.org) agreed upon by all the countries under the United Nations' umbrella. Most of these countries have also agreed upon common goals to combat climate change and desertification and to promote biodiversity conservation, through global conventions in which Brazil

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often played a protagonist role (Mittermeier et al. 2010; Scarano et al. 2012; Scarano 2017). Sustainability as a vision for the future of the Caatinga is, therefore, in agreement with global aspirations and with Brazilian official politics. However, in the Caatinga region, sustainability is yet to be achieved, from the household scale to the regional scale, as desertification and pervasive poverty exemplify. How do we get there? We believe this is both a scientific question and a policy-oriented question.

The preceding 18 chapters have provided some of the necessary scientific background to design a roadmap for a sustainable future in the Caatinga. They examined the Caatinga under different lenses and cast light on the complex network of historical and ecological processes that have shaped the relationships between ecosystems and people in one of the least studied ecological regions in the world. These chapters present modern syntheses about the current knowledge on the region's biodiversity and ecosystem services. Moreover, they describe the region's major environmental threats and identify some potential solutions for how local societies can conciliate environmental conservation and socio-economic prosperity for the first time since humans arrived in this region.

In this final chapter, we summarize the major findings of the preceding chapters to describe the current state of the Caatinga, we analyze the factors that can undermine the long-term resilience of this socio-ecological system, and, finally, we propose a roadmap for local society to move safely toward a more resilient and sustainable condition in the near future.

19.2 Caatinga's Socio-ecological System

The Caatinga is located between two of the world's largest and most species-rich tropical forests (Amazonia and Atlantic Forest) and the world's richest tropical savanna (Cerrado). In Brazil, the Caatinga has been compared with the adjacent ecological regions, and its biodiversity was considered as impoverished (Chap. 1). As a consequence, the region has received a lower priority for investments in biodiversity conservation and sustainable development than other Brazilian regions (Santos et al. 2011; Overbeck et al. 2015; Oliveira and Bernard 2017). However, such national-level comparisons are too simplistic because they compare ecological regions that are parts of different global biomes. As a result, they fail to highlight the global importance of each ecological region. If a global approach is used, then the Caatinga is one of the top global conservation priorities because it is the world's largest and most biodiverse region among the regions that compose the seasonally dry tropical forest biome. Moreover, the Caatinga emerges among the top six ecosystems with the largest intrinsic vulnerability to climate variability, which is largely explained by its critical water balance (Seddon et al. 2016).

The Caatinga is also home to 28.6 million people, of whom around 9.5 million live in small rural villages and who, despite all recent efforts by national governments, continue to survive from the simple extraction of resources from regional ecosystems (Chap. 1; Figs. 19.1 and 19.2). These ecosystems, in turn, have been

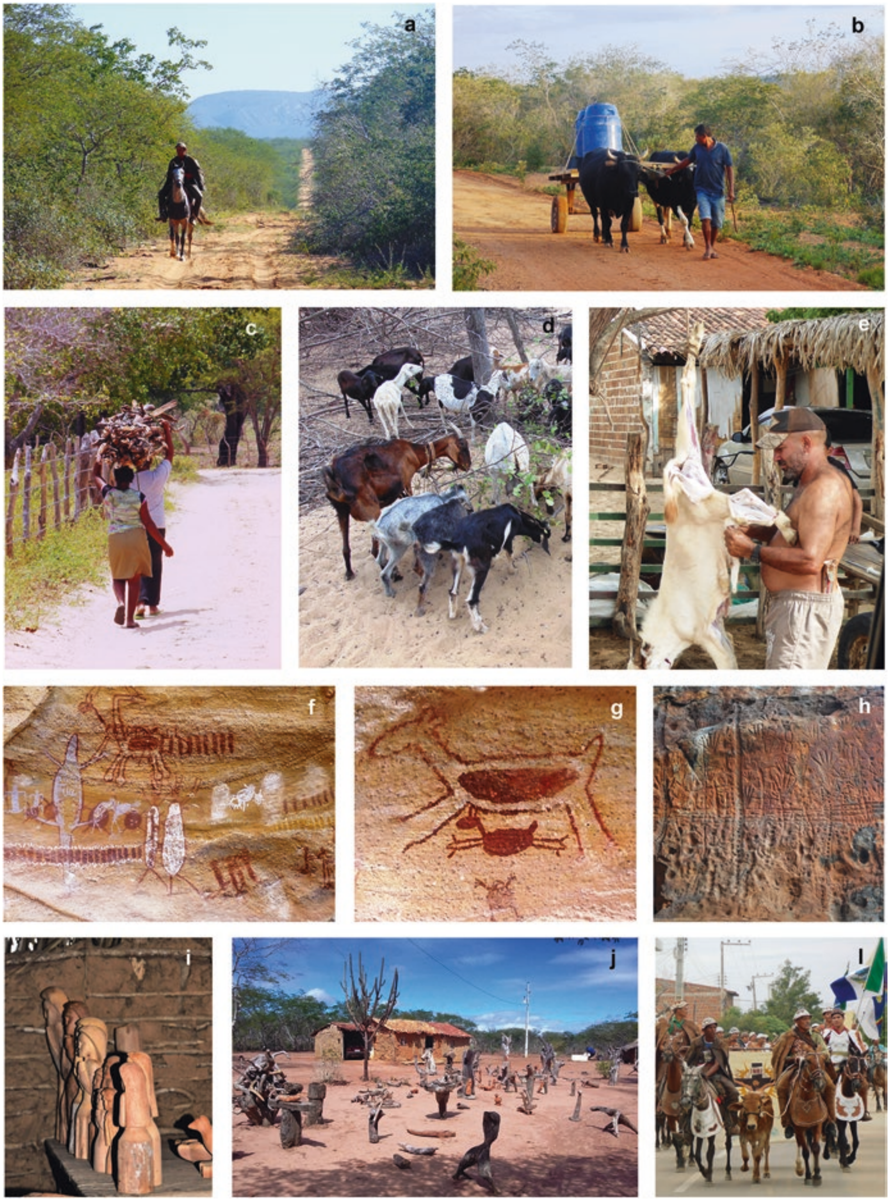

Fig. 19.1 The '*cultura sertaneja*' of the Caatinga: (**a**) a typical 'vaqueiro' (cowboy) with his leather clothes riding in the Caatinga; collection of water (**b**) and firewood (**c**) are daily routines of the rural population; goats are one of the major sources of savings (**d**) and animal protein (**e**); rock paintings in the Capivara National Park (**f** and **g**) and rock engravings in the Catimbau National Park (**h**) are evidence of ancient hunter-gatherer populations in the Caatinga; contemporary wood carving made mostly from *Commiphora leptophloeos* wood (**i** and **j**), and the traditional 'missa do vaqueiro', a catholic mass led by local cowboys (**h**). Image credits: (**a**, **b**, **c**, **d**, and **h**) Tatiane Menezes; (**e** and **i**) Rainer Wirth; (**f** and **h**) Inara Leal; (**g**) Felipe Melo; and (**j**) Fábio Scarano

Fig. 19.2 Key aspects of the Caatinga socio-ecological system: typical rural holdings in the Caatinga composed of patches of subsistence agriculture, livestock pasture, and caatinga vegetation (**a** and **b**); firewood and timber collection (**c**); typical fences known as '*cerca de faxina*' (**d**); a kiln used for charcoal production from native woody species (**e**); a stand of the invasive '*algaroba*' tree (*Prosopis juliflora*) (**f**); proliferation of the palm *Syagrus coronata* following slash and burn agriculture (**g**); highly degraded ecosystem following cattle pasture abandonment (**h**). Image credits: (**a**) Tatiane Menezes; (**b**) Kátia Rito; (**c**, **g**, and **h**) Rainer Wirth; (**d**, **e**, and **f**) Inara R. Leal

depleted over years by a combination of acute and chronic human disturbances and seem to have lost their capacity to provide the ecosystem services that both rural and urban populations require to prosper (Chaps. 10, 11, and 12). Unfortunately, social and environmental policies have been dissociated during the last decades, with social policies implemented without taking into account environmental conservation and environmental policies implemented without any concern for social problems. The decoupling of these two major policy agendas has been catastrophic. Currently, most of the region's municipalities have low stocks of both green and socio-economic infrastructures, which severely limits their paths toward a more sustainable and prosperous future (Chap. 18).

19.2.1 The Ecological System

The preceding chapters have demonstrated unequivocally that the Caatinga is a very heterogeneous region with highly diverse biota. The numbers are impressive. The region harbors an astounding diversity of native species: 3150 flowering plants (Chap. 2), 276 ants (Chap. 3), 386 fishes (Chap. 4), 98 amphibians (Chap. 5), 79 reptiles (Chap. 6), 548 birds (Chap. 7), and 183 mammals (Chap. 8). These numbers support the hypothesis that the Caatinga is one of the world's more diverse drylands. Yet, these numbers are far from being definitive. In all biological groups, new species have been discovered and described due to recent research efforts, and scientists have still never visited many places.

In the past, the Caatinga biota was thought to be composed mostly of widely distributed species with few being restricted to the region (see Chaps. 2, 3, 4, 5, 6, 7, and 8). However, all of the recent studies have rejected this conjecture. The number of endemic species among the biological groups in which there are sufficient data to make such calculations are quite astonishing, ranging from 6.0% in mammals (Chap. 8) to 52.9% in fishes (Chap. 3). The distribution of the endemic species within the Caatinga indicates that the region is not uniform from a biogeographic perspective, but composed of different biogeographic units, each one composed of a unique set of species (see Chaps. 2, 3, 4, 5, 6, 7, and 8). From a historical perspective, the Caatinga's biota has been assembled as a consequence of three biogeographic processes: species production, biotic exchange, and regional mass extinction (Chap. 7). The relative contribution of each one of these factors varies among biological groups. It seems that species production is more important in flowering plants, fishes, amphibians, and reptiles (Chaps. 2, 4, 5, and 6). In contrast, biotic exchange is more relevant in birds and mammals (Chaps. 7 and 8). The effects of the regional mass extinction still need investigation, but it has been very important in shaping the current regional mammal assemblage (Chap. 8). The estimated ages of the Caatinga's endemic species range from Early Holocene to Mid-Miocene (see Chaps. 2 and 7), indicating that species production has been continuous within the region. The Caatinga's endemic species are related to species that live in different

South American regions, indicating a complex network of biogeographic relationships for the region and a very fascinating paleoecological history.

Once thought to be relatively monotonous from a biodiversity perspective, the Caatinga emerges from recent studies as very heterogeneous. Although dominated by different types of dry forests and woodlands that cover the region's extensive peneplains, the presence of enclaves of tropical humid forests, savannas, and rupestrian grasslands contributes to sustaining a significantly high number of species across the region. For instance, among birds, almost 60% of the species require forests (a habitat that covers less than 15% of the region) for their life cycles (Chap. 7). The region's environmental heterogeneity shapes the distribution of the species, forming environmental gradients found nowhere else. These gradients are also fundamental in providing mesic refuges during the long dry season for several species that are able to move between habitats within landscapes and between landscapes within the region (Chap. 7). Ecological gradients enable the evolution and the maintenance of complex and unique types of plant–animal interactions, such as myrmecochory, herbivory mediated by the presence of extra-floral nectaries, and pollination by trap-line hummingbirds (Chap. 9).

19.2.2 The Human System Connected to the Ecological System

The environmental gradients that once covered the Caatinga have also been critical in driving the evolution and development of multiple human cultures and ethnic groups in the last 25,000 years (Chap. 12). Beginning with Amerindian societies that used to move along the ecological gradients tracking mesic spots as a strategy to cope with the long and unpredictable droughts, the regional society was enlarged and modified by the arrival of Europeans and Africans in the sixteenth century. Such a fusion resulted in a distinguishable rural culture, the '*cultura sertaneja*' (backland culture), adapted to and shaped by the Caatinga's semiarid conditions (see Chap. 12, Fig. 19.1).

Since earlier times, the '*sertanejo*' culture has been deeply connected to the engagement of rural populations into small-scale agriculture (i.e., slash-and-burn agriculture) and cattle ranching by adopting the Caatinga dry forest as a native pasture (Chap. 16, Figs. 19.1 and 19.2). In addition to food, native vegetation represents a key resource for livelihood, from the nutrients for crops to the animals and plant species used in handicraft and religious rituals (Chaps. 11 and 12, Figs. 19.1 and 19.2). Vegetation is also commercially exploited for firewood or charcoal, which represent an extra source of income at the household level, while it meets industrial and urban energetic demands for a cheap source of energy (Chaps. 11 and 14). An outstanding number of Caatinga flora and fauna species have been recognized as useful for local communities, from firewood for domestic cooking to food security; that is, plant-based resources used during prolonged droughts (Chap. 11).

Such an intense connection between people and nature via multiple services provided by the ecosystems and mediated by a semiarid climate has converted the

Caatinga into a unique biocultural environment. Both the '*sertanejo*' and the '*sertão*' (backland) are topics of some of Brazil's most acclaimed masterpieces of literature, poetry, and music, as well as well-established traditions in craftworks, such as carving, pottery, and leatherwear. As highlighted in Chap. 12, the Caatinga environment persists "as a source of cultural inspiration and development, recreation, knowledge, and spiritual significance for both local inhabitants and the many visitors that are drawn to this biologically and culturally unique region" (see also Siqueira Filho 2012).

19.3 Threats and Trends

The Caatinga's ecosystems have long been exposed to human disturbances (Coimbra-Filho and Câmara 1996), but their large-scale transformation began with the aggressive expansion of Portuguese colonization around 1600 (Chap. 13). Three groups of disturbances are recognized in the Caatinga. The first group includes acute disturbances connected to large-scale and fast transformation of the native ecosystems into anthropogenic ecosystems (Chap. 13). The second group is composed of chronic disturbances associated with traditional farming devoted to subsistence agriculture (smallholder farming and extensive livestock production; Ribeiro et al. 2015; Chap. 14). The third group is the disturbances caused by the introductions of an ever-growing number of exotic species (Nascimento et al. 2014; Almeida et al. 2015). Chronic disturbances were the dominant factor in the Caatinga's degradation for centuries, but acute disturbances took their place with the expansion of roads and monocultures in the region after the 1950s. The impact of exotic species still needs to be assessed (but see Nascimento et al. 2014).

The low-income rural population is the major driver of the chronic disturbances, while the rich urban population is the major driver of the acute disturbances. Across the region, rural people have small land parcels that are used mostly for slash-and-burn agriculture and livestock (Fig. 19.2). This small-holding agriculture model is, in turn, highly dependent on resources from native vegetation, such as soil nutrients (local farmers rarely have access to fertilizers), native plants as forage for livestock, firewood for cooking, and timber for farm infrastructure (Fig. 19.2). This extractive and low-input farming process is not sustainable because it degrades the environment and does not generate enough income for rural populations due to low agricultural productivity. Since the agriculture productivity cannot be improved due to water scarcity (Chap. 10), poor soils (Chap. 16), and inappropriate technology (Chap. 16), local farmers are usually captured in a permanent poverty trap. In contrast, in the cities, immense social pressures force governments to increase investments in the social infrastructure required to promote economic development and deliver better public services (Chap. 18). The governments' responses have always been in the form of large, multi-billion-dollar physical infrastructure projects, which, in turn, foster disturbances that are still more acute. Infrastructural measures alone may face setbacks related to long-term viability, effectiveness, or environmental soundness, such as in the case of river transposition to avoid drought, as some believe to be the case with the transposition of the São Francisco River (Lemos et al. 2016). In general, the combination of acute and chronic disturbances over time and space has negatively affected most of the ecosystems in the Caatinga. Currently, 94% of the region has moderate to high desertification risk (Vieira et al. 2015).

From a landscape to a regional spatial level, most of the Caatinga can be described as a mosaic consisting of (a) patches devoted to slash-and-burn agriculture and pastures; (b) second-growth vegetation covering a gradient of regeneration ages but exposed to the exploitation of vegetation resources; (c) degraded and frequently desertified spots; and (d) rare and small old-growth forest patches (Chaps. 13, 14, and 16). Soil degradation, nutrient exportation, reduced plant recruitment, and other processes associated with chronic disturbances (including slash-and-burn agriculture) can continuously reduce ecosystem productivity and drive former forest patches toward shrub vegetation or even desertified spots (Fig. 19.3), as anecdotally mentioned in the literature (see Sampaio et al. 2005). Desertification (as an alternative stable state), low-competitive agriculture, reduced-income farmers, and historical events of human migration (particularly during years of severe drought) represent unquestionable evidence that such a socio-ecological system based on the extraction of natural resources and large-scale ecosystem degradation due to physical infrastructure development is biologically, economically, and socially unsustainable.

In the rural Caatinga, human poverty and land degradation are intimately related, fostering land abandonment and desertification. This relationship can be described

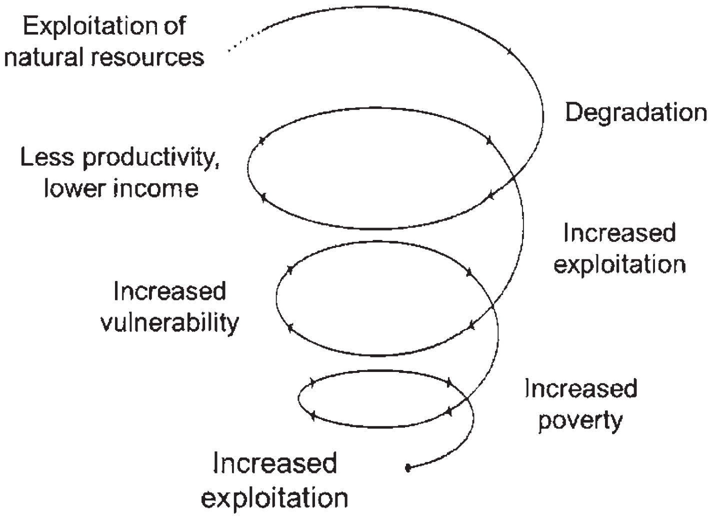

Fig. 19.3 A hypothetical model for ecosystem response as exposed to human disturbances during long periods. Continuous events of biomass removal by humans can drive ecosystem toward stable alternative states, such as the transformation of forest patches into desertified spots in the Caatinga region

as a socio-ecological vortex in which the exploitation of natural resources (including nutrients via crop production and cattle raising) reduces ecosystem productivity, farm income, and the capacity to adopt appropriated technologies, leading to a new exploitation round to compensate for reduced productivity. Over time, this process can accelerate ecosystem degradation, the collapse of farming activities, and the increase of poverty (Fig. 19.4). This working hypothesis contrasts with the perspective that the current land-sharing system adopted by rural farmers across the Caatinga is able to maintain biodiversity and ecosystem services while fostering human prosperity. Of course, modern agriculture systems can be implemented in selected water-rich sectors of the region, such as the tropical fruit and grape/wine production via irrigation along the Sao Francisco River, but this economic activity is still territorially unexpressive, and the appropriate water-management skills required to avoid desertification due to soil salinization are lacking.

Climate change is expected to dramatically increase population vulnerability to food scarcity and water shortage in the Caatinga. The potential reduction in average annual rainfall (Chap. 15) and an increase in the frequency of extreme events, such as prolonged drought, may (1) reduce farming productivity; (2) cause frequent crop failure; and (3) increase production costs without effective adaptation measures. Considering the current financial and technological constraints, these trends, either isolated or collectively, are likely to represent additional pressure on the already scarce native ecosystems. Indeed, when climate change was analyzed in interaction with habitat loss and fragmentation, Segan et al. (2016) designated the Caatinga as a priority biome to restore.

During recent decades, many strategies have been proposed and implemented to mitigate the negative effects of droughts, water scarcity, and low agricultural productivity on human prosperity. These strategies include (1) exploiting native drought-resistant species as fodder; (2) replacing beef cattle farming by goat farming; and (3) using native seeds/fruits and bushmeat as a complementary source of food intake. However, these strategies represent typical maladaptation (i.e., unsustainable adaptive strategies) because they lead to a loss of biodiversity and ecosystem services (Brown 2011). We acknowledge the existence of several local initiatives

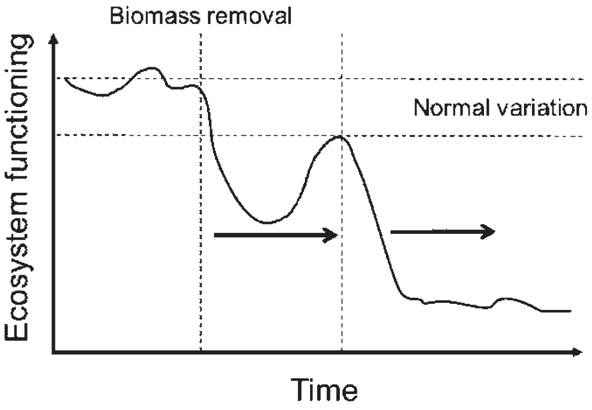

Fig. 19.4 Potential causal relationships connecting the exploitation of natural resources, habitat degradation, shifts in ecosystem productivity, and human poverty in rural societies depending on the resources of native vegetation to proper livelihood. Such feedback looping can be recognized as ecosystem downgrading or a socio-ecological vortex

(mostly run by non-governmental organizations [NGOs]) devoted to the development and communication of more sustainable and climatically adapted farming systems, but these systems have not been scaled up to the point that they improve the resilience of the regional population to changes in climate.

19.4 A Roadmap for Sustainability

Here we assume that biodiversity persistence, the provision of key ecological services, and human well-being represent worthwhile, interconnected, and inseparable final goals (Díaz et al. 2015). This assumption inevitably leads to the concept of sustainability.

The scientific framework to address the question of how to achieve sustainability in the Caatinga is provided by the so-called sustainability science, in which the core research agenda simultaneously requires transdisciplinary scientific rigor (Lang et al. 2012) to result in measurable societal impacts (Bettencourt and Kaur 2011). Thus, sustainability science is by definition policy driven. In practical terms, sustainability implies integrating conflictive perspectives, particular goals, political agendas posed by different disciplines related to humans, and natural sciences. In fact, it sees human and natural systems as actually integrated socio-ecological systems (Pant et al. 2015). Since sustainable development is an operationally complex and long-term goal, for which many potential intermediate steps and routes can be envisioned, we are sure that there is no 'silver bullet' for the Caatinga. However, we argue that an effective road map should have clear targets associated with the conservation and restoration of ecosystems for biodiversity conservation and ecosystem service provision. Without these targets, sustainable development is conceptually incomplete and economic growth and social development are not feasible.

Since biodiversity, ecological services, economic activities, rural development, and climate change are completely inter-dependent in the Caatinga region, a sustainable transition from extractive to productive farming and from degraded landscapes to biodiversity-friendly landscapes must be ecosystem based. Accordingly, a central concept or a structuring goal to achieve a sustainable and resilient Caatinga (from biodiversity to a socio-economy) is that of green infrastructure; that is, a network of natural, semi-natural, and restored areas that are designed and managed at different spatial scales that encompass all of the major types of ecosystems. Such a network aims to simultaneously conserve biodiversity, mitigate greenhouse gas emissions, enable societal adaptations to climate change, and deliver a wide range of other ecosystem services that human societies need to prosper (Silva and Wheeler 2017). Plenty of arguments support why green infrastructure represents an irreplaceable component of any conservation or sustainability plan in the tropical region (Chap. 18). It is worth mentioning that local persistence in terms of biodiversity relies on ecological processes that operate at multiple spatial scales, from a local to a regional level. In human-modified landscapes, it is mandatory that protected areas remain physically connected by vegetation corridors or patches through which species can disperse. Changes in local patterns of rainfall distribution (i.e., climate change) add an additional reason to guarantee species movement/migration at larger spatial scales than protected areas or private landholdings. However, biodiversity is unlikely to achieve long-term persistence in the case that the rural population remains heavily dependent on vegetation resources and continues to promote habitat degradation in private landholdings. High demands for vegetation-related resources will inevitably (1) increase the pressure on protected area resources, maintain private landholdings as a sink for native biodiversity, and operate as a source area for invasive species, such as the mesquite tree or 'algorabeira' (*Prosopsis juliflora*); and (2) reduce the matrix permeability and biological flux. In synthesis, a well-designed and comprehensible green infrastructure represents a non-negotiable requirement for the biological dimension of sustainability.

Green infrastructure alone is not going to lead to sustainable development—an efficient socio-economic infrastructure is also required (Chap. 18). Therefore, tailor-made territorial interventions combining both green and socio-economic infrastructures are the best way to ensure biodiversity conservation, the provision of ecosystem services, climate adaptation, and economic prosperity (Chap. 18). The lack of adequate green and socio-economic infrastructures reinforces the Caatinga's current and future fragility (Chap. 18). The integration of the two types of infrastructure in time and space can create opportunities that will move the rural population away from the current extractive practices. New production models or farming types for the Caatinga should respect the region's carrying capacity and not lead to resource depletion or exhaustion. This shift could result in (1) higher rates of high-quality vegetation cover; (2) the natural rehabilitation of degraded lands; and (3) the appropriate provision of ecological services at multiple spatial scales, such as soil rehabilitation, watershed protection, aquifer recharge, nutrient capture and storage, climatic buffering and evapotranspiration control, and the storage of forest products for coping with environmental hazards (food security). These services offered by the Caatinga native vegetation are assets to the local populations and represent a necessary condition for a transition from extractive farming to a more intense, productive, and profitable farming economy, from a local to a regional level. Such productive farming should not only be able to alleviate poverty and improve food security but also support social prosperity and reduce vulnerability to climate change, while protecting the environmental safeguards associate with Caatinga biodiversity.

In synthesis, 'business as usual' (i.e., extractive farming) will keep transforming the natural landscapes of the Caatinga into environmentally degraded, resource-impoverished, economically fragile, and socially questionable human-modified landscapes, with desertification as one of the possible alternative stable states. This process started as soon as the first Europeans settled in the region around the sixteenth century and has continued as the norm until now. Ecological and social degradation across the region is still on course and tends to be scaled up by climate changes and their cascading effects on rural productivity. We argue that the results of the scientific information presented in this book provide enough reasons to think that a transition to a sustainable and resilient Caatinga is still possible.

We propose ten fundamental targets that should be pursued by the region's society in its pathway toward a more sustainable and resilient Caatinga:

1. Expand the regional protected area system by creating new protected areas to protect 100% of all the remaining natural ecosystems and all areas classified as conservation priorities by scientists (Chap. 17);
2. Reconnect all protected areas by restoring native vegetation along all major rivers;
3. Achieve zero species loss by developing and implementing integrated conservation plans for all endemic and threatened species;
4. Expand cash transfer programs that seek to achieve poverty reduction and environmental conservation simultaneously;
5. Provide land tenure to all small land owners and implement a regional monitoring system of land-use change at the property level for the entire region;
6. Promote the adoption of more productive farming systems based on intensive, modern, and innovative technologies across the entire region;
7. Move away from extractive industries that lead to ecosystem degradation towards economic activities that are based on goods and services with high aggregated value and low socio-ecological risks, such as cultural industries;
8. Shift 100% of the regional energy matrix, moving away from firewood and charcoal and from deforestation to alternative sources, such as wind and solar energy;
9. Significantly increase the socio-economic infrastructure of all urban centers across the region, with special emphasis on educational, health, and economic infrastructure; and
10. Increase the capacity of local governments to design and implement local sustainable development plans aligned with major national policies and Brazil's commitments to global conventions.

We hope that the major lessons described in this book can promote deep reflections about the challenges associated with achieving sustainable development in the Caatinga as well as in all other seasonally tropical dry forests.

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Index

J.M.C. da Silva et al. (eds.), *Caatinga*,
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