Chapter 3
Ants of the Caatinga: Diversity, Biogeography, and Functional Responses to Anthropogenic Disturbance and Climate Change

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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

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)

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 | Code for sampling | | |
Ant species	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)

Table 3.1 (continued)

SUBFAMILY	Code for sampling		
Ant species	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	Code for sampling		
Ant species	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	Code for sampling		
Ant species	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)

a)

b)
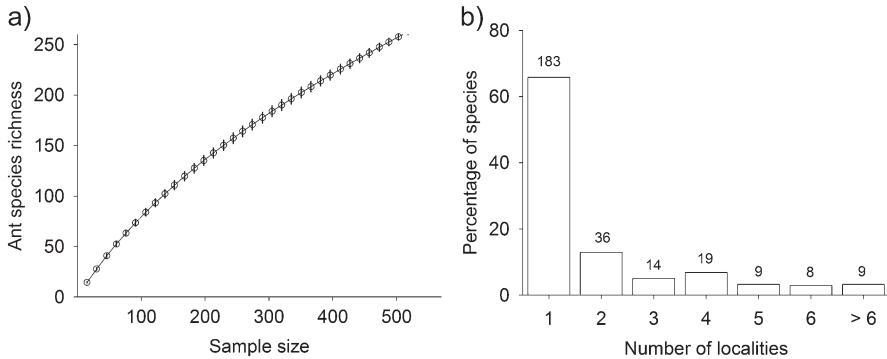
Fig. 3.1 (**a**) Ant species accumulation curve for 37 localities in the Caatinga, based on 571 species records. Vertical lines depict 95% confidence intervals. (**b**) Occurrence distribution of the 276 ant species across 37 localities in the Caatinga. Numbers above bars depict the number of species 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
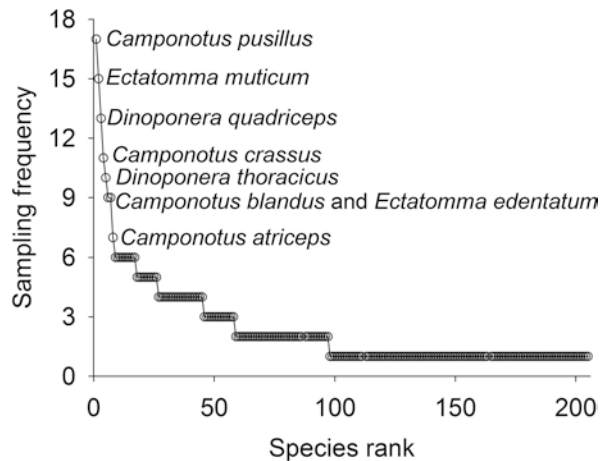
important disperser of myrmecochorous seeds in the Caatinga (Leal et al. 2014b, c). Another notable Caatinga endemic is the leaf-cutter *Atta opaciceps*. This is the most abundant leaf-cutting ant in Catimbau, and its colonies can consume more than 20% of leaf biomass in their foraging areas (Siqueira 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).
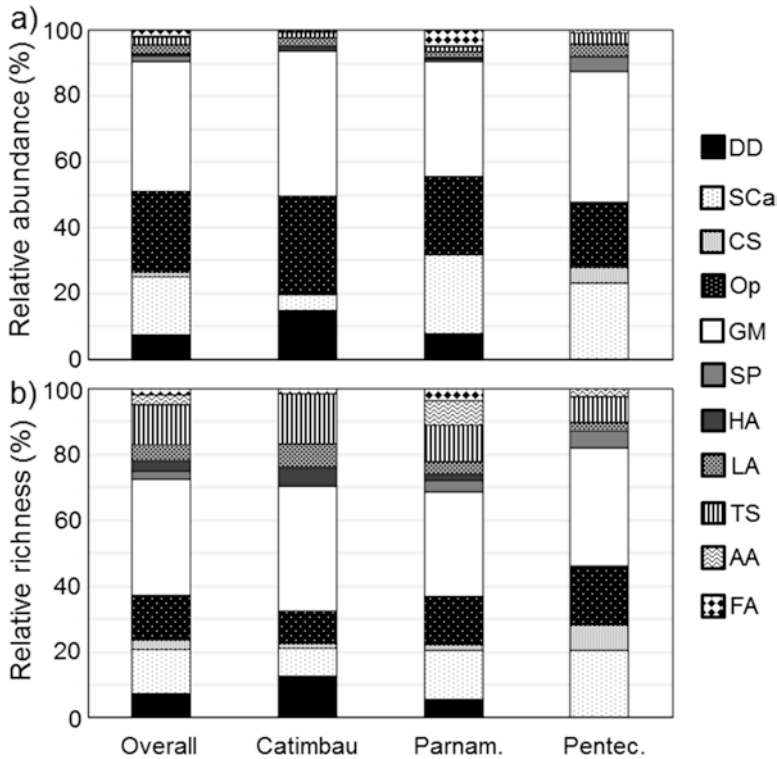
Fig. 3.3 Ant functional group composition (**a** relative abundance; and **b** relative species richness) at three Caatinga localities (Catimbau, Parnamirim [Parnam.], Pentecoste [Pentec.]), and considering the three localities together (Overall). The functional groups are: *AA* Army ants, *CS* Cryptic 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
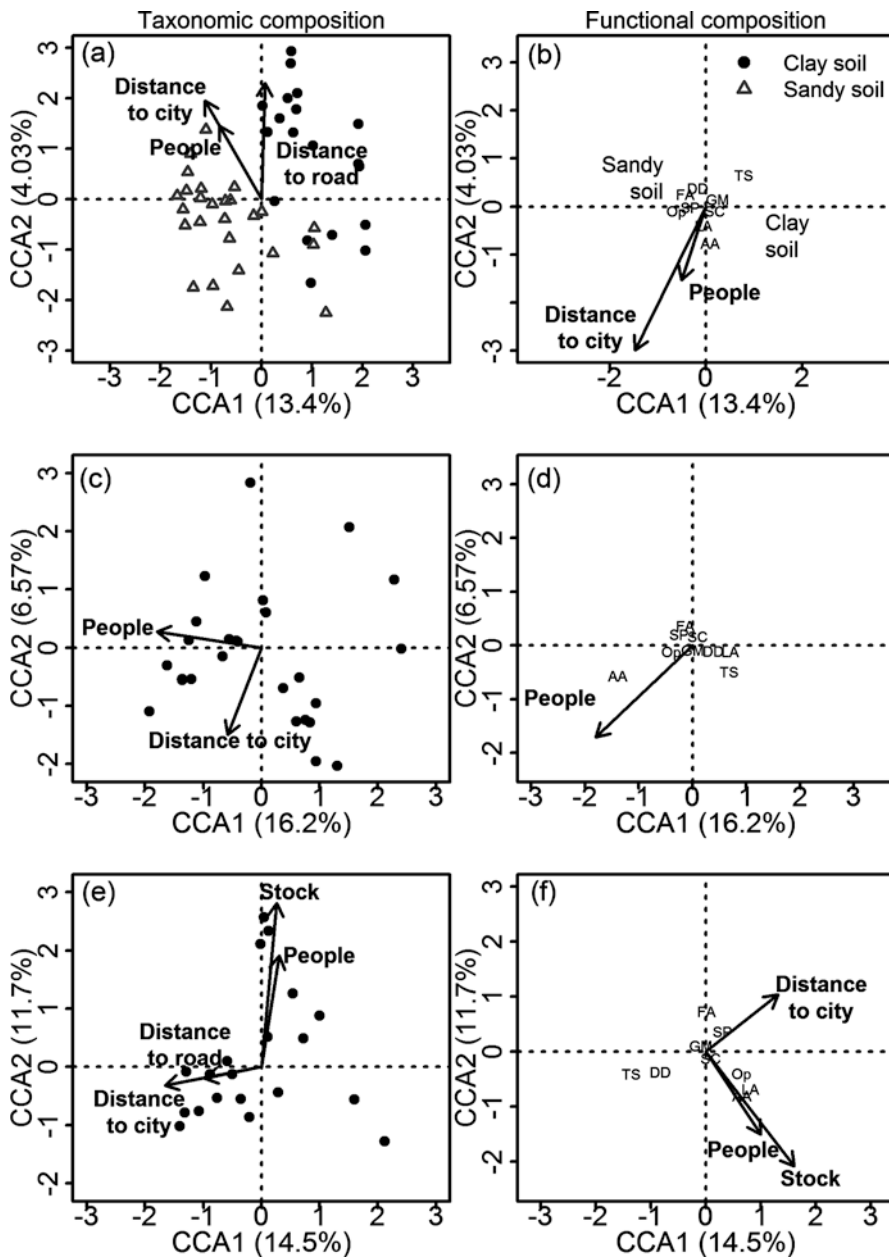
Fig. 3.4 Canonical correspondence analysis of 47 sites near Parnamirim based on taxonomic (**a**, **c**, **e**) and functional group (**b**, **d**, **f**) composition, with significant ($p < 0.05$ based on 10,000 aleatorizations) disturbance metrics shown as vectors. The different panels represent different soil types: (**a**, **b** both sand clay; **c**, **d** sand; **e**, **f** clay) (Adapted from Oliveira et al. 2017)
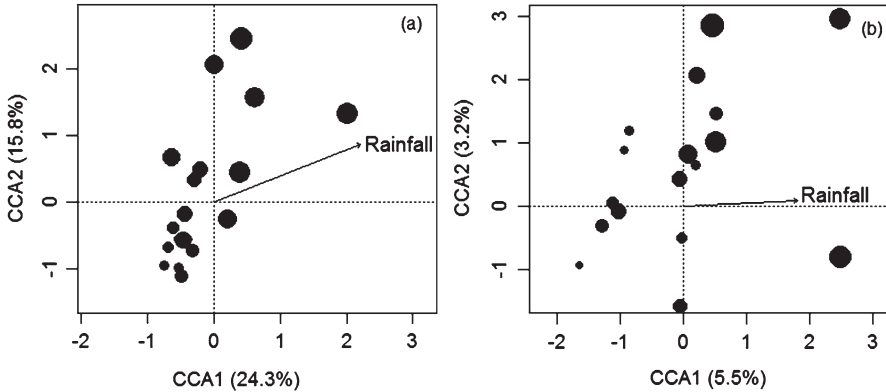
Fig. 3.5 Canonical correspondence analysis of 20 sites in Catimbau National Park based on taxonomic (**a**) and functional group (**b**) composition, with rainfall fitted as vectors. Circle size increases with increasing rainfall (Arcoverde et al. unpublished data)

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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