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Lower ant Diversity on Earth Mounds in a Semi-Arid Ecosystem: Natural Variation or a Sign of Degradation?

KS Carvalho[1], MAF Carneiro[2], IC Nascimento[1], AK Saha[3], EM Bruna[4]

1 - Universidade Estadual do Sudoeste da Bahia (UESB), Departamento de Ciências Biológicas, Jequié-BA, Brazil

2 - Universidade Estadual do Sudoeste da Bahia (UESB), Departamento de Ciências Naturais, Programa de Pós-Graduação em Genética, Biodiversidade e Conservação, Vitória da Conquista-BA, Brazil

3- MacArthur Agro-ecological Research Center, Archbold Biological Station, Lake Placid-FL, EUA

4 - University of Florida (UF), Department of Wild life Ecology and Conservation, Gainesville-FL, EUA

Corresponding author
Karine Santana Carvalho.
UESB, Departamento de Ciências Biológicas
Av. José Moreira Sobrinho, S/N
CEP: 45206-190, Jequiezinho
Jequié-BA, Brasil
E-Mail: ksczool@yahoo.com.br

Abstract

Natural earth mounds in many ecosystems harbor higher biodiversity than surroundings because they provide greater habitat heterogeneity. However, in the semi-arid Caatinga ecosystem of NE Brazil, natural mounds have much less vegetation and leaf litter with lower biodiversity as compared to the surrounding lowlands. The following hypotheses were tested: (i) low vegetation cover on the mounds results from highly compacted and leached soils as compared to adjacent lowlands and (ii) low vegetation cover reduce ant populations and diversity because of limited foraging and nesting resources. This study was carried out in four mound fields. At each mound field, 30 sampling were taken using pitfall traps. The high resistance of the mound soil to root penetration and low soil pH were the main reason for the difference in ant diversity between mound and adjacent lowlands. Adjacent lowlands were found to have twice as many ant individuals as the mounds along with higher ant species richness and diversity. These results suggest that environmental degradation in the Caatinga led to deforestation and thus compaction and leaching of soil mounds.

Introduction

Biodiversity is typically distributed heterogenously among habitats; therefore, understanding the spatial aspect of biodiversity underpins ecosystem conservation and management (Ricklefs, 2004). Arid and semi-arid ecosystems often possess spatial heterogeneity in habitat over a scale of several meters to more than 100 m (Berg, 2012). Life in such regions is often restricted to patches of vegetation that are surrounded by more in hospitable rock and dry soil. Such vegetation tussocks are found to be biodiversity hotspots when compared to the surrounding landscape (Housman et al., 2007). Vegetation and litter act as physical barriers to soil temperature fluctuations and surface erosion while providing greater soil moisture content during the dry season as compared to the surrounding areas (Sayer, 2006). Studies in African savannas have shown that active termite mounds in the otherwise relatively flat homogeneous landscapes increased nitrogen availability by supporting nitrogen-fixing plant species, resulting in significantly higher nutrient concentrations than those resulting from droppings of herbivorous ungulates (Fox-Dobbs et al., 2010). Similarly, semi-arid environments in Asia possess high spatial variability in soil nutrient and vegetation properties, where organic matter and nutrients were shown to contribute to the islands of fertility phenomenon (Chen et al., 2006), what is also registered for desert ecosystems (Ganer & Steinberg, 1989).

On the other hand, there are also local biodiversity 'coldspots' (Kareiva & Marvier, 2003) - a situation contrary to the 'islands of fertility' concept, whereby certain features deter colonization by flora and fauna due to various reasons such as lack of moisture and nutrients (sandy soils) or allelopathy

by a plant species. In the Caatinga ecosystem that is one of the largest continuous area of seasonal dry tropical and thorn-scrub forest in north-eastern Brazil (Pennington et al., 2009), we have observed naturally occurring earth mounds that have much lower vegetation cover and plant diversity than the surrounding lowlands. Lower vegetation cover and diversity could in turn severely limit habitat for invertebrate fauna, including ants that play an important role in nutrient cycling in an ecosystem (Vasconcelos et al., 2008). Several studies have suggested that ant species diversity rises with the increase in environmental structural complexity (Jeanne, 1979; Benson & Harada, 1988; Corrêa et al., 2006; Pacheco et al., 2009) by offering a wider range of sites for nesting, feeding and various ecological interactions favouring ant activities (Benson & Harada, 1988; Ribas et al., 2003).

The Caatinga is a semi-arid ecosystem in northeastern Brazil that is characterized by high plant species diversity and endemism (Ribeiro et al., 2015) in response to low rainfall and soil heterogeneity. The intensity of year-round solar radiation and high soil temperatures causes rapid breakdown and decomposition of organic matter (Pacchioni et al., 2014). In general, soils in the Caatinga are shallow and rich in minerals but poor in residual organic matter (eg. Andrade-Lima 1977, Eiten, 1983). The low prevalence of vegetation and organic matter is even more pronounced on elevated mounds as compared to the surrounding lowlands. Naturally occurring mound fields occupy large areas in the Caatinga (Antunes et al., 2012), with a density of about 35 mounds/ha (Funch, 2015). These mounds are extremely hard sun-baked elevated structures about 1-3 m high with regular spacing that do not touch or overlap (Funch, 2015) thus indicating a scale-dependent feedback among them (Rietkerk & Van de Koppel, 2008). The mounds are piles of soil or a type of micro relief in landscapes associated with poor drainage conditions (Resende et al., 2002). Their origin remains controversial (Renard et al., 2012) with two competing hypotheses (Silva et al., 2010) – a termite mound origin versus differential erosion over time. The termite mound hypothesis suggests successful colonization by successive generations of termites that thereby increases the diameter and height of these structures, which are further acted upon by earthworms and ants (Resende et al., 2002). The differential erosion hypothesis focuses on geomorphology and suggests that mounds are reliefs resulting from differential erosive action (Oliveira-Filho, 1992a, b; Midgley, 2010), with the softer lithography eroded away. Regardless of their origin, the presence of mounds can change the dynamics of environmental functioning since spatial structures are important in regulating interactions between communities and ecosystem processes (Rietkerk & Van de Koppel, 2008).

The greater solar exposure and lower vegetation cover on Caatinga mounds as compared to the surrounding xeric-forested lowlands can alter: 1) the microclimate 2) the chemical and physical properties of soil and 3) the distribution of organisms that live and/or forage on mounds.

This study aims to measure ant diversity along with soil properties and vegetation cover on mounds and surrounding lowlands, in order to verify whether the mounds are indeed relatively impoverished in species abundance. Results will then provide a basis for further investigations, whether the low diversity is a natural feature or is it reflective of ongoing anthropogenic change involving removal of vegetation and consequent soil alteration. In this context, the following hypotheses were tested: (i) mounds with low vegetation cover have more compacted and leached soils than the surrounding lowlands and (ii) this negatively affects the distribution and diversity of ant species due to the shortage of resources for foraging or nesting, as compared to the surrounding matrix.

Material and Methods

Study area

The study was conducted in four mound fields, i.e. fields with numerous regularly spaced mounds. Two of the mound fields had white soil (quartz-rich podzols) while the two others had red soil (latossols with a high concentration of iron and aluminium oxides). The mound fields on white soil exhibited a diverse thorny plant community with predominance of cacti. The mound fields on red soil had a relatively homogeneous vegetation cover composed of both trees and shrubs. The mound fields were separated from each other by a minimum of 1 km and were located near the protected area of the Floresta Nacional (FLONA) Contendas do Sincorá, Bahia, Brazil (13^{0}55'14.4"S; 041^{0}06'54.9" W).

The climatic classification of the region, according to Koppen, is semi-arid with scarce and irregular rainfall, concentrated in the summer. The average annual rainfall is 596 mm. Most of the National Forest and buffer zone is inserted in Argissolos classification (eutrophic red-yellow podzolic), being small part, formed by Latosols (IBAMA & MMA, 2006).

Sampling design

At each moundfield, 30 sampling points were taken 20 m apart from each other along a transect. Each mound was randomly chosen while sampling transect on the adjacent lowland was chosen in a random direction. In order to test whether the mounds locally affect the distribution of richness and diversity of ant species, collections were carried out from October to December 2014 (rainy season) at each sample point using pitfall traps. The traps were kept active for 48 hours in the field. At each sample point using (Bestelmeyer et al., 2000). In total, 120 mound samples (30 samples per mound) and 120 adjacent ground samples were collected. Collected ants were identified following the classification proposed by Bolton (2016) and witness individuals were deposited in the Collection from Zoology of the Universidade Estadual do Sudoeste da Bahia and in the entomological collection from the Myrmecology Laboratory from the Comissão Executiva

de Pesquisa da Lavoura Cacaueira (CEPEC/CEPLAC), in Itabuna, Bahia.

Three soil penetration resistance measurements were made with a penetrometer (Solotest 2.10) in order to test whether the soil of the mounds is more compressed or compacted as compared to the surrounding soil. Penetration tests were carried out on ten mounds randomly chosen and similarly, three measurements each at ten points on the adjacent lowland in each field. Soil samples were also collected from each mound and adjacent lowland and sent to Soil Laboratory of the Universidade Estadual do Sudoeste da Bahia (UESB) for chemical analysis of macronutrients and organic matter. Height and width measures were taken and calculated by using the cone area to infer the surface area of mounds.

Data analysis

Analysis of variance was performed (two-way ANOVA) using Systat 12.0 (2007) in order to test whether the soil compaction and nutrient availability (abiotic variables) and the abundance, richness and diversity of ant species (ecological descriptors) differed between mounds and adjacent lowlands by using (1) site: mound or lowland; and (2) mound field: white and red soil, as sources of variation in the model.

The diversity of ant species between sites (mound and lowland) was compared using the Shannon-Wiener Index (using Estimates 9.1.0; Colwell, 2006) since species richness data alone cannot express the dominance of species in a community. For the calculation of this Index, the relative frequency of each species in a given sample was used instead of the abundance of individuals. This is used due to worker ant recruitment for foraging, displayed by the majority of ants, which can be more or less efficient in a species and therefore it may under- or overestimate the values. The composition of ant species between mound and adjacent lowland and among mounds fields was compared with the values of Jaccard similarity index (Systat,2007).

A Principal Components Analysis (PCA) was performed to visualize correlations of abiotic factors in mounds fields. Then, in order to know how these factors relate to ecological descriptors (abundance, richness and diversity) a Pearson correlation analysis was performed using Past 3.0 (2016).

Results

Structure of mounds and physicochemical characteristics of the soil in the mounds fields

The density of mounds was approximately 9 per 100m². On average, the surface area ranged from 27 to approximately 39m² while height ranged from 1.4 ± 0.4 to 1.8 ± 0.3 m. The volume of a mound ranged from 14.6 to 38.3 m³. Out of the 40 mounds sampled, (20 in the mound fields on white soil and 20 in the mound field on red soil) had 50-75% vegetation cover while the others had much lower cover ranging from less than 50% to almost none (Table 1).

Table 1. Structure of mounds in mounds fields from Caatinga ecosystem, northeastern Brazil.

	Surface area (m²)	Height (m)	Volume (m³)	Vegetation cover (%)
Mound field rs 1	27.01±7.3	1.51±0.3	14.8±6.6	0-50 (57%)
Mound field rs 2	34.7±10.3	1.6±0.4	32.1±16.1	26-50 (79%)
Mound field ws 1	29.9±11.1	1.40±0.4	38.3±31.7	0-50 (80%)
Mound field ws 2	38.8±9.6	1.81±0.3	35.2±18.1	0-25 (80%)

rs = red soil;
ws = white soil

The penetrometer tests found that the soil on mounds was more compact or dense as compared to the soil on adjacent lowlands (F = 3.90; df = 1; p<0.049; n = 240; Table. 2). On average, the pressure (in kg / m³ of soil) necessary for penetration on the mounds was 29.2 ± 3.0 units, whereas the adjacent lowlands required much less - 1.67 ± 2.56. White soils offered significantly higher resistance to penetration as compared to red soils (F = 120,518; df = 1; p≤0.001; n = 240). There was no interaction between the two factors.

Interestingly, soil organic matter did not differ between mound and adjacent lowland but the mounds had a more acidic pH (5.30 ± 0.7) than the adjacent lowland (6.24 ± 0.82; F = 15,145; df = 1; p ≤ 0.001; n = 40; Table. 2). Soil pH varied significantly with soil color (F = 8.62, df = 1; p ≤ 0.006; n = 40) with white soil being less acidic than red soil. The interaction between the factors was not significant.

Aside from calcium (Ca^{2+}) and magnesium (Mg^{2+}) ions, macronutrients did not differ between mounds and adjacent lowland in any of the studied fields. The Ca content of the mounds was 2.98 ± 1.16 cmol / dm³ and 1.82 ± 0.64 cmol / dm³ in the adjacent lowland (F = 36.739; df = 1; p≤0.001; n = 40; Table 2). Mg presented 1.29 ± 0.4 cmol / dm³ in mounds and 0.98 ± 0.28 cmol / dm³in the adjacent lowland (F = 8.984; df = 1; p≤0.006; n = 40; Table 2). There appeared to be an effect of soil type on the Ca content (F = 18.496, df = 1; p≤0.001; n = 40) and the Mg content (F = 4.654; df = 1; p≤0.038; n = 40). White soil presented higher concentration of both macronutrients as compared to red soil. Similarly, phosphorus (P) and potassium (K) concentration were different accordint to soil color (P: F = 7.921; df = 1; p≤0.008; K: F = 6.369, df = 1; p≤0.016 n = 40), being the highest in white soil mounds fields.

Abundance, Richness, diversity and composition of ants assembly or community in the mound fields.

We identified 30 ant species belonging to 16 genera and six subfamilies living in mounds fields Caatinga (Table 3). Overall, the average number of ant individuals in pitfall traps on adjacent lowlands (14.5 ± 20.7) was twice higher than those on the mounds (7.7 ± 9.4; F = 13.2; df = 1; p≤0.001; n = 240). Ant abundance also varied significantly with soil colour (F = 14.1; df = 1; p≤0.001; n = 240). Mound fields having white soil were found to have the highest abundance

Table 2. Physicochemical characteristics of the soil in the mounds fields from Caatinga ecosystem, northeastern Brazil.

Mound field	Site	Pressure for penetration (kg / m3 of soil)	pH	Macronutrients	
				Ca2+	Mg2+
red soil	mound	0.28±1.63	5.2±0.7	2.12±0.70	1.16±0.44
	adjacent lowland	0.22±0.12	5.7±0.6	1.32±0.41	0.88±0.29
white soil	mound	4.09±3.21	5.5±0.6	3.84±0.85	1.42±0.33
	adjacent lowland	2.97±2.98	6.7±0.7	2.32±0.39	1.08±0.23
Statistical difference					
mounds vs. adjacent lowland		p≤ 0.049	p≤ 0.001	p≤ 0.001	p≤ 0.006
red soil vc white soil		p≤ 0.001	p≤ 0.006	p≤ 0.001	p≤ 0.038

of ants. The interaction between the site (mound or adjacent lowland) and the soil color (white or red one) was statistically significant (F = 6.13, df = 1; p≤0.014; n = 240).

The richness of ant species was also higher in the adjacent lowlands (3.6 ± 1.8) than on the mounds (2.6 ± 1.9; F = 17.9; df = 1; p≤0.001; n = 240). There was a significant effect of soil colour on the species richness (F = 31.4; df = 1; p≤0.001; n = 240) and the interaction between these factors (F = 6.87, df = 1; p≤0.009; n = 240). The highest species richness was found in the mound fields of white soil.

Ants species diversity was higher in the adjacent lowland (F = 27.4, df = 1; p≤0.001; n = 240) than on the mounds and higher in white soil fields (F = 58.6, df = 1, p≤0.001; n = 240) than in the red soil fields. The interaction between the sources of variation (mound/lowland and soil color) was significant (F = 10.5; df = 1; p≤0.001; n = 240).

There was significant difference in the composition of ant species between mound and adjacent lowland. The Jaccard index found a species overlap of 58% between the mounds and adjacent lowlands on white soils, and a lower ovelap (39%)

between the two habitats on red soils. The species with the highest frequency of occurrence in samples and more frequent in the adjacent lowland were *Dinoponera quadriceps*, *Pheidole radoszkowskii* and *Ectotomma muticum* (Table 3). The specie *Camponotus blandus* was relatively common in both places (mound and adjacent lowland; Table 3)

Interactions between mounds, mounds fields and ant communities

The axis 1 (PC1) of the Principal Components Analysis (PCA) revealed two distinct groupings between soil types (white soil and red soil) which are influenced positively by macronutrient content (calcium and phosphorus). Axis 2 (PC2) separated mound and adjacent lowland which are positively correlated with soil resistance and negatively correlated with pH (Fig 1).

The Pearson correlation matrix found that there is a significant linear relationship between the diversity of ant species and the component 2 of the PCA (Table 4).
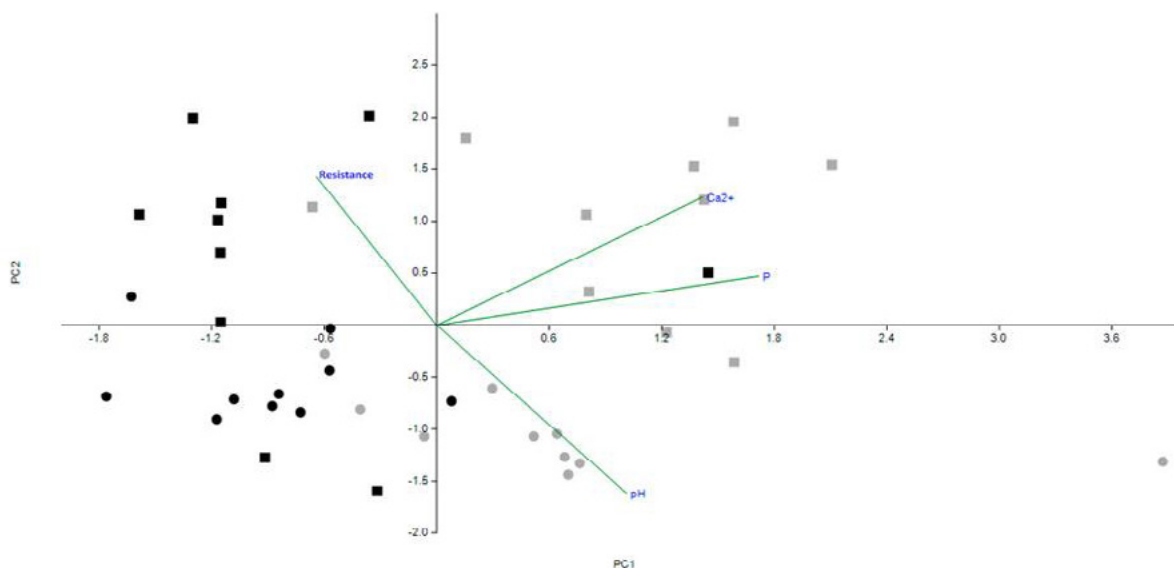
Fig 1. Main component analysis of macronutrients (Ca2+, P), pH and soil resistance to root penetration. (Colours: black = red soil, grey = white soil; Square = mound; Circle = adjacent lowland).

Table 3. Frequency of occurrence (%) of ant species in mounds fields (2 fields in red soil and 2 fields in white soil) from Caatinga ecosystem, northeastern Brazil. (AL = adjacent lowland; M = mound).

Subfamily/Species	Red soil fields		White soil fields	
	AL	M	AL	M
Dolichoderinae				
Dorymyrmex brunneus Forel, 1908	6.7	6.7	26.7	-
Dorymyrmex sp.3	-	-	-	10
Dorymyrmex thoraxicus Gallardo, 1916	-	-	3.3	-
Forelius brasiliensis (Forel, 1908)	1.7	1.7	20	11.7
Forelius maranhaoensis Cuezzo, 2000	-	-	-	10
Linepithema neotropicum Wild, 2007	-	-	18.3	10
Ectatomminae				
Ectatoma suzanae Almeida Filho, 1986	16.7	11.7	-	-
Ectatomma muticum Mayr, 1870	10	13.3	43.3	15
Gnamptogenys acuminata (Emery, 1896)	3.3	-	-	-
Gnamptogenys moelleri (Forel, 1912)	5	-	-	-
Formicinae				
Camponotus blandus(Smith 1858)	31.7	33.3	23.3	43.3
Camponotus meloticus (Emery, 1894)	-	-	11.7	-
Camponotus novogranadensis Mayr, 1870	-	-	-	3.3
Campotonotus (M*yrmephaenus*) sp. 1	-	-	-	1.7
Myrmicinae				
Atta sexdens rubropilosa Forel, 1908	6.7	-	13.3	-
Cephalotes pusillus (Klug, 1824)	3.3	1.7	-	1
Crematogaster erecta Mayr, 1866	-	1.7	-	-
Crematogaster distans Mayr, 1870	3.3	11.7	-	1
Nesomyrmex itinerans (Kempf, 1959)	-	-	-	1.7
Pheidole radoszkowskii Mayr, 1884	8.3	13.3	53.3	41.7
Pheidole sp.7	-	3.3	-	-
Pheidole gp. Tristis sp.18	1.7	-	-	-
Pogonomyrmex naegelii Emery, 1878	-	-	1	-
Solenopsis globularia (Smith, 1858)	13.3	8.3	36.7	20
Solenopsis sp.2	3.3	-	1.7	8.3
Solenopsis sp.5	-	-	1.7	-
Ponerinae				
Dinoponera quadriceps Kempf, 1971	56.7	35	26.7	6.7
Platythyrea pilosula (Smith, 1858)	-	-	-	1.7
Pseudomyrmecinae				
Pseudomyrmex termitarius (Smith, 1855)	-	-	5	13.3
Pseudomyrmex gracilis (Fabricius, 1804)	3.3	-	-	-

Table 4. Pearson correlation matrix among abundance, richness and diversity of species of ants and the values of the two axes of a Principal Components Analysis (PCA).The numbers represent the r values of linear correlation between variables. The P values indicate the level of significance of the correlation (P <0.05).

	Correlation			P < 0.05	
	Abundance	Richness	Diversity	PC 1	PC 2
Abundance		0.048	0.007	0.076	0.061
Richness	0.315		0.008	0.464	0.368
Diversity	0.420	0.414		0.104	0.004
PC 1	0.284	0.119	0.261		0.911
PC 2	-0.299	-0.146	-0.451	-0.018	

Discussion

The results of this study show that mounds have highly compacted soils, lower vegetation cover and locally reduced population and diversity of ant species as compared to the adjacent lowland. Ant diversity is otherwise quite high in the Caatinga ecosystem. This study shows that the mounds in the Caatinga are definitely spots of lower ant abundance and diversity - a finding contrary to the usual biodiversity hotspots on elevated mounds and tussocks in dry ecosystems (Housman et al., 2007; Berg, 2012).

Apart from calcium and magnesium, there was no difference in the concentration of other macronutrients between mounds and adjacent lowlands within a mound field. The similarity in nutrients across mounds and adjacent lowlands suggests that nutrient limitation is not the main reason for low vegetation cover on mounds, thus supporting the idea that the mounds' inhospitability to life (compacted soil) may have resulted from anthropogenic removal of vegetation. Removal of natural vegetation can lead to the erosion and hardening of soils through increased exposure to natural elements. Further investigation can look into whether this low species diversity status and low life-support capacity of mounds has always been naturally so (because of the origin of the mounds), or is that an outcome of the ongoing degradation in the region.

Ant population size, diversity and spatial landform type (mounds and adjacent lowlands)

As expected, the population size and species diversity of ant species were lower on mounds compared to the adjacent lowland. The relatively lower population size and species diversity is likely related to the greater soil compaction and lower pH of soils on mounds, both factors that discourage the establishment of vegetation and nesting sites of ants. This was seen to be true in both white and red soils. The greater physical compaction of soils on mounds implies much higher resistance to penetration by roots, thereby acting as a deterrent to plant establishment (e.g., Kozlowski, 1999). The smooth surface on mounds discourages the retention of seeds. Seed germination

would also be discouraged by the relatively inhospitable conditions prevailing on mounds –much higher exposure to strong sunlight that increases soil temperature and decreases soil moisture. In comparison the adjacent lowlands have higher vegetation cover by shrubs and occasional trees that shade the soil against drying out by solar radiation and wind as well as reduce diurnal soil temperature variations (e.g. Sayer, 2006). The vegetation cover also generates a litter layer that conserves moisture and adds to spatial heterogeneity of habitats, thereby supporting larger and more diverse populations of ants as noted by Carvalho et al. (2012) in areas of Caatinga.

Some ants which are strongly associated with vegetation, as the species of the genus *Camponotus* (Brandão et al. 2009), were virtually absent in the red soil mound fields. The exception was *Camponotus blandus*, present at a high frequency (> 20% of samples) in the field mounds and at both sites (mounds and adjacent lowlands). The nests of *C. blandus* are found in the soil, in preexisting cavities under rocks or termite mounds (Gallego-Ropero & Feitosa, 2014), and it is considered a predatory specie, especially of termites (Mendonça & Resende, 1996; Gallego-Ropero & Feitosa, 2014). The occurrence of *C. blandus* homogeneously may indicate that it is nesting on these structures and/or making predation on termite inside the mounds. Although we have not conducted systematic collection of other arthropods, termite galleries were observed in murudus.

Higher soil acidity (lower pH) poses constraints for soil biota thereby lowering the ecological functions of soil biota in creating favorable conditions for plant establishment and growth, from soil organic matter decomposition, nutrient availability and mycorrhizal networks (Whitford, 1996). Soil biota composition has been seen to be very sensitive to soil degradation and restoration in the Caatinga (Araújo et al., 2014). However, contrary to our first hypothesis, the mounds were not more leached than the adjacent lowlands since they have higher calcium (Ca) and magnesium (Mg) content. This result is initially surprising, considering that the acidic soils usually have low base concentrations (especially Ca and Mg despite the high presence of these elements in parent material). Termite nests and tunnels were evident upon excavation of mounds.

In fact, termites act as ecosystem engineers (Jones et al., 1994), through their transportation of soil nutrients both vertically and horizontally (Sileshi et al., 2010). According Lobry de Bruyn and Conacher (1990), termites can increase carbon and nutrient levels. The extent of the increases depends on the type of mound construction and the degree to which organic material is incorporated. More studies are needed to understand the role of termites in increased levels of calcium and magnesium in mounds of Caatinga.

In addition to the soil that influences vegetation, the physical structure of mounds should also be considered. In this study, the average surface area of a mound ranged from 27 - 39 m², a considerable area in terms of energy required by an ant to climb and travel in search for resources, especially

if the mound has little or no resources like living or dead organic matter. In ants, as well as other animals, the ecological success depends on the ability to maximize success foraging and quantidade of energy invested (Stephens & Krebs, 1971). The total volume of soil (15-38 m³) can also be a physical barrier to hypogaeic species (underground foragers), due to the absence of roots and microorganisms associated with them, among other features. Perhaps other factors not measured in this study, such as the areal extent of bare soil patches and links between plant and ant species compositions could also explain the differences found in the abundance and ant species richness between mounds and adjacent lowlands.

Ant diversity and soil types – influence of vegetation and nutrients

Mound fields with white soil had a greater abundance of individuals and richness of ant species as compared to mound fields with red soil. This was true for both mounds and the surrounding matrix in each soil type. The red soil fields have relatively homogeneous shrub vegetation and therefore possess less microclimatic and microhabitat variation as compared to fields with white soil types. Mound fields of white soil have a much higher diversity of vegetation, including high levels of endemism, more diversified rupestrian vegetation, with the presence of rocky outcrops, and the predominance of cacti. Thus, the highest abundance, richness and diversity of ant species in white soil fields are probably related to their more complex vegetation structure. Further studies would be needed to understand this relationship in greater detail. However, it is known that climate, microclimate and particularly microhabitat explain variations in biodiversity in a mesoscale ranged from few kilometers to few hundred kilometers (Hutchings et al., 2003). In addition, insect abundance in the Caatinga was also found to be much higher during and just after the brief rainy season largely spurred on by higher vegetation productivity and food/nutrient availability during that time of the year (Vasconcelos et al., 2010).

Mound fields with white soil had significantly higher values of calcium, magnesium and phosphorus than mound fields with red soil. This study did not look at the differences in vegetation composition in mound fields between the two soil types; however the higher availability of nutrients on white soils could also leads to greater availability of niches that promote higher species diversity and endemism for which the Caatinga is well known.

Low diversity on mounds - natural or anthropogenic?

The Caatinga is a unique ecosystem, where the combination of water stress and soil nutrient variability has resulted in high floral and faunal species diversity, particularly remarkable for plants, birds and fish- for instance, over 1,200 species of vascular plants occur here, with 30% of them being endemic to the region (Leal et al., 2003). Over fifty percent of habitat has been altered due to agriculture

development or cattle grazing (Smithsonian information sheet) while only around 1% of the region is protected under National Parks (TNC & Associação Caatinga, 2004). Unplanned agricultural expansion can accelerate soil erosion, lead to fires and seriously threaten the structure of Caatinga plant communities (Mamede & Araujo, 2008). Funch (2015) mentions cattle grazing as a common activity in mound fields in the Caatinga and that in recent decades the clearing of the fields has revealed mounds that were originally hidden by low (≤4 m) but very dense vegetation. Funch (2015) describes the mounds as places normally covered by vegetation, penetrated by roots and limited erosion by wind and rain - an opposite description to the mounds in this study which were seen to be bare spots on the landscape.

Probably the contrasting finding in our study reflects the degree of degradation of the areas selected for study, which has witnessed human influence over recent decades, by removal of vegetation from mounds that has led to exposure-related soil hardening, with attendant deterrence for vegetation recolonization. In fact, according to the sociocultural survey of the region described in the management plan of the FLONA, the history of the region shows fields for the planting of various products such as beans, corn, cotton and especially cassava from the slavery period in northeastern Brazil (XVIII century). The region also has other more drastic uses such as logging for railroad construction and asphalt (fences), magnesium mining and coal mining until about September 1999, when the FLONA was created (IBAMA & MMA, 2006).

If that is the case, then mounds can be considered as sentinels indicating the ongoing degradation of the Caatinga biome. A recent study by Ribeiro et al. (2015) showed that chronic anthropogenic disturbance caused by the high population density and livestock, among others, are driving the vegetation of Caatinga towards species impoverishment.

This is the first investigation to our knowledge of the (negative) effects of spatial heterogeneity created by mounds on ant communities. In this context, the following hypotheses were tested: (i) mounds with low vegetation cover have more compacted and leached soils than the surrounding lowlands; (ii) this negatively affects the distribution and diversity of ant species due to the shortage of resources for foraging or nesting, as compared to the surrounding matrix.

It provides at least two major for questions biodiversity conservation in dry ecosystems such as the Caatinga: 1) How far do the negative effects of mounds in the distribution and diversity of the ants (and other arthropods) reach? Are these negative effects limited only to mound structure or mound formation as well? In this sense, 2) what would be the best scale to study the effects of heterogeneity of the mound fields on ant communities? A larger scale study including mounds with a chronosequence of human disturbance can investigate whether the hardened soils, low vegetation cover and low ant diversity on mounds are natural features or are happening as a consequence of human activities. Such a determination would

then enable mounds to be seen as sentinels or indicators of ongoing environmental change in the Caatinga, and thereby be useful for assessing ecological conditions in conservation and restoration strategies.

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