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Composition and Richness of Arboreal Ants in Fragments of Brazilian Caatinga: Effects of Secondary Succession

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Abstract

Ecological succession is a complex process involving mainly some changes in the structure of plant community, with subsequent changes in resource availability as well as in the interactions among organisms which are also important factors determining the structure of arboreal ant assemblages, but little is known about the consequences of secondary succession on ant assemblages in Tropical Dry Forests (TDFs), such as the Brazilian Caatinga. Here we investigate the effects of ecological succession on the richness and species composition of arboreal ants in fragments of Caatinga, testing the following hypothesis: i) the species richness of arboreal ants increases along a gradient of secondary succession, in response to habitat complexity and season; ii) species composition of arboreal ants differs among stages of secondary succession due to differences in vegetation structure in theses stages and seasonality. This study was conducted in 15 plots distributed in three areas with different stages of secondary succession (early, intermediate and late). Tree species richness and density were used as surrogates of habitat complexity. Ants were sampled using the technique of beating the foliage and baited pitfall traps, where five trees were sampled per plot, totaling 75 individual trees sampled. We sampled 37 species of ants, distributed in 16 genera and five subfamilies. Ant species richness differed among stages of succession and seasons, with higher number of species in the late succession and rainy period, also increasing with habitat complexity. We conclude that the structure of arboreal ants assemblage was related to ecological succession of vegetation, mainly in the rainy season. Fifteen years of secondary regeneration are enough to increase species richness and maybe to restore species composition of arboreal ants but secondary habitats are also important to biodiversity maintenance of this group in Caatinga.

Introduction

There is a consensus that along a gradient of secondary succession, environments in late stages of regeneration tend to have greater species richness of arthropods than more disturbed habitats (in early stages of succession). Late succession environments generally leads to a greater richness and density of plant species, increasing availability of food resources and nesting sites (Bazzaz, 1975; Vasconcelos, 1999; Klimes et al., 2012). The idea that more arthropods species can be find in environments with high complexity (i.e. high species richness and/or abundance of trees) along a successional gradient has been demonstrated in studies using different groups of insects such as beetles, termites, butterflies (Romero-Alcaraz & Avila, 2000; Tewset al., 2004; Quesada et al., 2009; Neves et al., 2010a; Vasconcellos et al., 2010; Neves et al., 2014). Among these groups, ants have been the subject of several studies that seek to understand how species richness and composition has been influenced by vegetation structure (Leal, 2003; Ribas et al., 2003; Corrêa, 2006; Ribas & Schoereder, 2007; Vargas et al., 2007; Neves et al., 2010b; Gomes et al., 2014; Klimes et al., 2012).

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Ants represent an important group of terrestrial organisms due to several factors, such as their high taxonomic diversity (Erwin, 1989), their contributions to ecological processes (Hölldobler & Wilson, 1990) and their sensitiveness to variations of landscape structure (Lindsey & Skinner, 2001; Ribas et al. 2003). Ant species richness has usually been positively associated with habitat structure and its association is more pronounced at local scale, mainly at sites with higher resource availability, diversity of microhabitats and a greater number of nesting sites (Ribas et al., 2003; Marques & Del-Claro, 2006; Ribas & Schoereder, 2007; Pacheco & Vasconcelos, 2012; Fagundes et al., 2015). Arboreal ants, however, commonly show a strong territorial behavior (Schoener, 1970; Bernstein, 1975; Espírito-Santo et al., 2009; Ribeiro et al., 2013a; Dáttilo et al., 2015), and changes in vegetation structure due to ecological succession may result in an increase of aggression and monopolization of space, leading a shift in the species composition.

Tropical dry forests (TDFs) cover significant land areas in Brazil and provide a habitat for a diverse number of species. The Brazilian Caatinga is a mosaic of scrub vegetation and patches of dry forest and covers over 800,000 km^2, of the Brazilian territory (Sampaio, 1995). This biome undergo 7-11 months of dry season (Prado et al., 2003), and such seasonal variation has a negative impact in the production and maintenance of the leaves, with most tree species losing their leaves during the dry months, diminishing connectivity between tree canopies. In these periods, when the resources are scarce and the abiotic conditions are stressful, arboreal ants could have different survival strategies, such as changing daily activity (e.g. diurnal to nocturnal pattern) (Dáttilo et al., 2015), expand the foraging area to alternative strata (e.g. vertical stratification) (Dejean et al., 2003; Campos et al., 2008; Silva et al., 2014), or move to more favorable adjacent habitats to search for resources (Neves et al., 2010b). For example, trees in early successional stages would be occupied by both ground-dwelling and arboreal ants, whereas exclusive arboreal ants predominate in late-stage trees (Dejean et al., 2003). However, effects of seasonality and environmental changes in areas of TDFs, along a successional gradient on the structure of ant assemblages have been poorly documented (Lewinsohn et al., 2005; Neves et al., 2010b).

Thus, the aim of this study was to investigate the effects of ecological succession on the structure of arboreal ant assemblages in areas of Caatinga, testing the following hypotheses: i) the species richness of arboreal ants increases along a gradient of secondary succession, in response to season (dry and rainy), tree species richness and/or density; ii) species composition of arboreal ants differs among seasons and stages of secondary succession.

Material and Methods

Study area

The study was conducted in the state of Sergipe, northeastern Brazil encompassing three fragments of Caatinga with different stages of plant regeneration surrounded by a matrix of active or abandoned pastures (Ribeiro et al., 2013b). Caatinga is a Tropical Dry Forest that covers approximately 9% of the Brazilian territory, characterized by a Tropical Semiarid climate (Bshi), annual rainfall ranging from 250 to 900 mm and mean temperature of 24°C and 26°C (Andrade-Lima, 1981; Sampaio, 1995; Pennington et al., 2000). According to Oliveira et al. (2013) the soil type is classified as Eutrophic Litholic Neosol.

The stages of succession were divided in Early, intermediate and late. The early stage (20 ha) is characterized by a abandoned pasture with three years of plant recovery, composed of sparse patches of trees with open canopy and 2 meters of high. Intermediary area is located 2.5 km apart from the early stage within a Conservation Unit (Monumento Natural Grota do Angico), in the municipality of Poço Redondo (9º 41'S and 38º 31'W) covering 2,183 ha. This area is composed of deciduous trees 2-4 m in height and with approximately 12-15 years of regeneration. The late successional area is a forest fragment (115 ha) with more than 40 years of forest regeneration, located 30 km far away from the other two areas (10° 02'S 37° 24'W). The fragment is characterized by taller deciduous trees which form a canopy 4-15 m high, on a private farm.

Sampling design

Sampling areas consisted of 15 plots with 50 m x 20 m (0.1 ha each), being five plots per stage of succession, with a minimum distance of 200 m between each plot. Tree species richness and abundance (circumference at breast height - CBH > 6 cm) were used as surrogate of vegetation structure. In each plot, we arbitrarily chose five trees (CBH > 6 cm, regardless of the species), at least 10 m apart from each other as sampling points. Sampling of ants was conducted in six sample periods: February/2011, March/2012 and November/2013 (dry season), May/2011, July/2012 and June/2013 (rainy season).

Ant sampling was made using a entomological umbrella and pitfall traps. The chosen trees were beaten over the umbrella with a stick. We standardized the sampling effort according to the number of secondary branches per tree, being 30 beats for trees with 1–5 branches (n = 60), including all branches. For the other trees with 6–10 branches (n = 15), we selected three sections of the tree canopy and performed 10 beatings in each section, totaling 30 beatings per tree. Thus, each tree was beaten 30 times, regardless of its size (Sousa-Souto et al., 2014). In addition, we used pitfall traps on the same five trees. These traps consisted of plastic cups (350 ml) with water and detergent (2%) baited with sardine and honey (see Ribas et al., 2003). These traps were left in the field for a period of 48 hours. Traps were set with a nylon thread on tree trunks at breast height. Ants were identified with taxonomic keys (Bolton, 1994; Fernández, 2003) and by comparison with specimens from the collection of the Laboratório de Mirmecologia of the CEPEC/ CEPLAC, Ilhéus, Bahia, Brazil. Voucher specimens of all species are deposited in Laboratório de Entomologia of the Federal University of Sergipe.

Data analysis

To compare the species richness of ants among the three successional stages (early, intermediate and late) and between seasons, we used liner mixed effects (LME) due to the pseudoreplication of plots in different seasons (dry and wet). Thus, ant species richness was treated as fixed effects, while plots and seasons were the random effects. In addition, we tested the response of ant species richness to richness and abundance of trees using generalized linear models (GLM's). In these models, ant species richness was used as the response variable and the species richness and abundance of trees were treated as explanatory variables. The minimum adequate models (MAM) were obtained by extracting non-significant terms ($p > 0.05$) from the full model (Crawley, 2013).

We tested if accumulated species composition of arboreal ants was affected by secondary succession, season, tree species richness and density using a PERMANOVA — permutational multivariate analysis of variance (Anderson, 2001). A non-metric multidimensional scaling (NMDS) was used to represent the results of the PERMANOVA (K = 2). In these analyses, the ordination of species composition was undertaken using the Jaccard index. All statistical analyses were conducted with the R software (R Development Core Team, 2015).

Results

A total of 37 species of ants were sampled, belonging to 16 genera and five subfamilies (Table 1). Myrmicinae was the subfamily with the largest number of species, representing approximately 55% of all species collected. *Pheidole* and *Camponotus* were the richest genera, with seven and six species, respectively. Only 12 species were common to all successional stages: *Camponotus arboreus, C. atriceps, C. cingulatus, C. melanoticus, C. senex, C. vittatus, Crematogaster stolli, C. victima, Pheidole radoszkowskii, Solenopsis tridens*, *Pseudomyrmex gracilis*, and *Pseudomyrmex rochai*.

In the initial stage area16 species were sampled, where three were exclusively sampled in this stage of succession. In the same way, intermediate stage had 16 species sampled being just one exclusively found in that habitat. In the late stage of succession, 33 species were collected, with 17 species sampled exclusively in that environment (Table 1).

The species richness of arboreal ants differed among stages of succession ($F = 8.3$; $p < 0.01$) as well as between seasons ($F = 72.1$; $p < 0.001$). In the LME model, interaction between secondary succession and season was also significant ($F = 22.4$; $p < 0.001$), indicating that the response of ant species richness was different depending of the stage of succession and season. Ant species richness was higher in wet than dry season in intermediary and late forests fragments, while species richness did not differ among stages in the dry season (Fig 1).

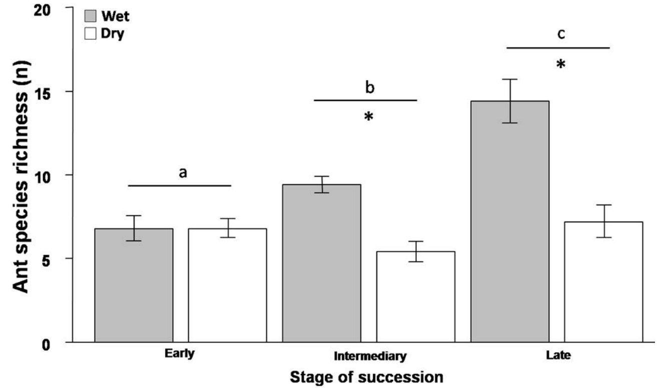

Fig 1. Species richness of arboreal ants in response to season (dry and wet) and among three forest fragments of Caatinga, with different stages of succession. Different letters above bars indicate significant differences amongst successional stages, while asterisks indicate differences between seasons within a same stage.

Besides, differences in habitat structure (tree species richness and density) had affected positively the species richness of arboreal ants ($F = 5.8$; $p = 0.03$ and $F = 17.1$; $p = 0.02$, respectively) (Fig2).

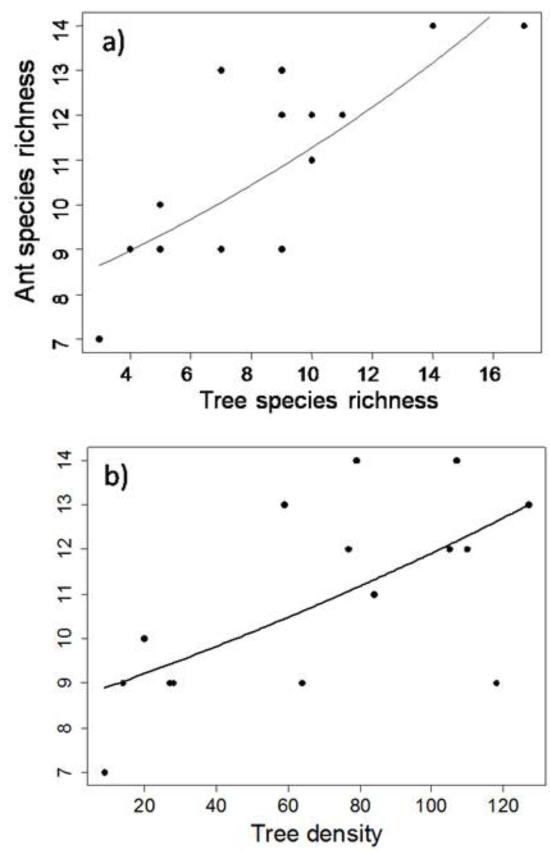

Fig 2. Species richness of arboreal ants in response to (a) tree species richness and (b) tree density among 15 plots in fragments of Caatinga.

Regarding species composition, arboreal ants presented differences among successional stages and these differences were in response to changes of tree density, tree species richness and season (PERMANOVA; Table 2; Figure 3).

Table 1 - Relative frequency of arboreal ants collected in three areas with different stages of secondary succession (Early, Intermediary and Late succession) in areas of Caatinga of Sergipe.

Subfamily	Species	Treatment			
		Code	Early	Intermediary	Late
Formicinae	*Brachymyrmex*sp.1	sp1	0.1	-	-
	Camponotus arboreus	sp2	0.1	0.5	0.1
	Camponotus atriceps	sp3	0.5	0.1	0.5
	Camponotus cingulatus	sp4	0.8	0.1	0.3
	Camponotus melanoticus	sp5	0.2	1.0	0.3
	Camponotus senex	sp6	1.0	1.0	0.6
	Camponotus vittatus	sp7	0.9	0.9	0.7
Ectatomminae	*Ectatomma suzanae*	sp8	-	0.1	0.6
	Gnamptogenys sulcata	sp9	0.3	-	-
	Gnamptogenys moelleri	sp10	-	-	0.6
Myrmicinae	*Cephalotes minutus*	sp11	-	0.4	0.9
	Cephalotes persimilis	Sp12	-	0.1	-
	Cyphomyrmex transversus	sp13	-	-	0.2
	Crematogaster chodati	sp14	-	-	0.3
	Crematogaster distans	sp15	-	-	0.6
	Crematogaster sp.1	Sp16	-	-	0.1
	Crematogaster stolli	sp17	0.4	0.5	0.1
	Crematogaster victima	sp18	0.3	0.7	0.6
	Nesomyrmex spininodis	sp19	-	-	0.1
	*Pheidole (*gr. Diligens*)* sp.1	sp20	0.1	0.2	-
	Pheidole (gr. Fallax) sp.2	sp21	-	-	0.5
	Pheidole (gr. Fallax) sp.3	sp22	-	-	0.4
	Pheidole (gr. Fallax) sp.4	sp23	-	-	0.1
	Pheidole sp.1	sp24	-	-	0.1
	Pheidole sp.2	sp25	-	-	0.3
	Pheidole radoszkowskii	sp26	0.8	0.5	0.8
	Solenopsis tridens	sp27	0.1	0.3	0.2
	Solenopsis globularia	sp28	-	-	0.4
	Strumigenys sp.1	sp29	-	-	0.2
	Wasmannia auropunctata	sp30	-	-	0.3
Pseudomyrmecinae	*Pseudomyrmex gracilis*	sp31	0.7	0.4	0.3
	Pseudomyrmex rochai	sp32	0.4	0.4	0.1
	Pseudomyrmex symplex	sp33	-	-	0.1
	Pseudomyrmex termitarius	sp34	0.1	-	0.1
Dolichoderinae	*Dorymiyrmex thoracicus*	sp35	-	-	0.1
	Dolichoderus voraginosus	sp36	-	0.1	0.1
	Tapinoma melanocephalum	sp37	-	-	0.1

Table 2 - PERMANOVA main tests for differences in assemblage composition of arboreal ants among successional stages, season and habitat structure (plant species richness and density), in a semiarid Caatinga, state of Sergipe, Brazil.

Response variable	Terms of the model	df	F-model	R^2	*P*
Ant composition	Stage of succession	2	3.52	0.17	0.001
	Plant species richness	1	1.83	0.05	0.04
	Plant abundance	1	5.10	0.12	0.001
	Season	1	3.54	0.08	0.001

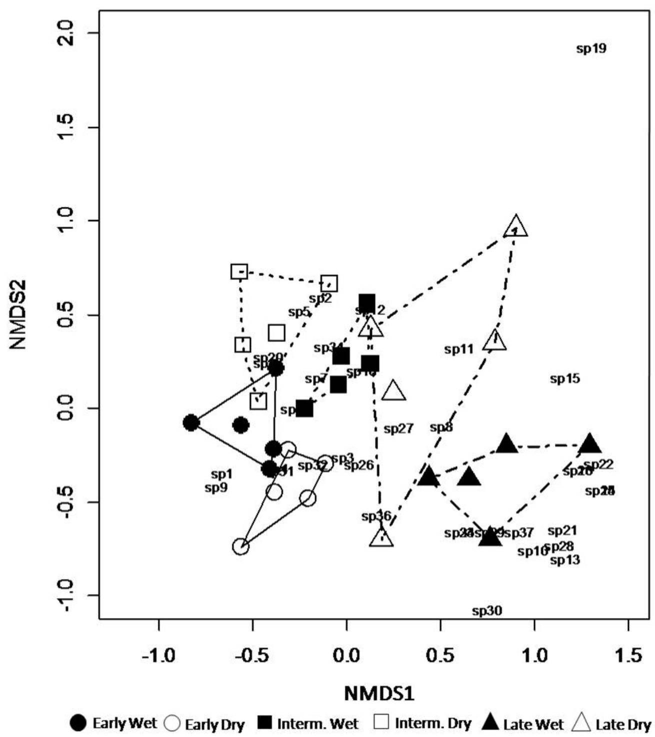

Fig 3. NMDS ordination of the 37 ant species along three successional gradients (Early, Intermediate and Late) in a Caatinga environment, between dry and wet season.

Discussion

Considering that secondary succession is a process, several factors that arise as a consequence of this ecological process may act individually or together modifying the structure of ant assemblages along the successional stages. In the present study we tested the influence of two of these factors: habitat complexity (herein referred to as species richness and density of trees) and seasonality as drivers of change in the diversity of ants in areas of Caatinga and we found that the factors above contribute to the increase in species richness of ants as well as for modification of its composition along the successional gradient, with strong influence of the rainy season. Thus, for arboreal ants, the ecological succession in areas of Caatinga has the same patterns already known for other Brazilian biomes that are the increase of species richness and changes in species composition along the gradient of forest regeneration. The species richness of arboreal ants sampled in this study (n = 37) can be considered low compared to other studies done in Cerrado or Atlantic Forest, using a similar sampling method. In fragments of Atlantic Forest, for example, species richness may vary from 69 to 153 (Resende et al., 2013; Vasconcelos et al., 2014), whereas in areas of Brazilian savanna (Cerrado) species richness of arboreal ants ranges from 37 to 95 (Ribas et al., 2003; Frizzo et al., 2012). However, for Tropical Dry Forests areas, such as Caatinga, the number of arboreal ants sampled is generally low, ranging from 24 to a maximum of 43 species (Neves et al., 2010c; Neves et al., 2013; Silva et al., 2014), indicating that Caatinga environments, may naturally harbor a smaller ant richness when compared to other environments, probably due to habitat limitations such as drastic variation in resources and conditions during the season and between years (Quesada et al., 2009). Of all ant species sampled, seventeen were unique of the area of late succession, indicating that these species could be bioindicators of advanced stages of forest regeneration in Caatinga. However, *W. auropunctata* was also found in areas of early forest regeneration in Caatinga (Neves et al., 2010b) as well as two species (*C. distans* and *C. transversus*) were also found in fragments with early forest regeneration in Atlantic Forest fragments in Sergipe (Gomes et al., 2014), suggesting that the occurrence and dispersion of some potential species used as bioindicators may vary depending on the scale and environment.

The results presented in figures 1 and 2 confirm some studies showing a general pattern that areas of advanced stages of forest regeneration tend to harbor greater species richness when compared to simpler environments (Bazzaz, 1975; Vasconcelos, 1999; Klimes et al., 2012; Gomes et al., 2014), due to environmental factors such as high habitat complexity and high resource availability (Kalacska et al., 2004; Quesada et al., 2009). In the present study, we found that areas considered at late stages of succession have greater species richness of arboreal ants compared with environments in recent forest regeneration. This result indicates that changes in habitat structure, promoted by the increment of variables such as richness and abundance of trees, along a gradient of secondary succession favor directly and indirectly the increase of species richness of ants, corroborating other studies (Lassau & Hochuli, 2005; Ribas et al., 2003; Vargas et al., 2007; Klimes et al., 2012).

Seasonality in our study area was also an important driver of the biodiversity of arboreal ants, accounting for a decrease of 40 to 50% in species richness of ants in the dry season in the intermediate and late successional stages, respectively. This reduction in species richness was due to the drastic loss of leaves in most tree species during the dry season, diminishing connectivity between tree canopies with a consequent reduction of resource availability in these areas. Those differences can be a result of variations in the exploitation of resources between seasons and due to vertical migration of some ant species from soil and shrub layer to canopy. Further studies, however, are necessary to test how of these factors (variation in the use of resources or vertical migration) are determinant in Caatinga, since there are few information about the effects of seasonality on the ant activity and structure of communities in tropical dry forests (Neves et al., 2010b).

Differences in species richness of ants between dry and rainy seasons, however, did not occur in the initial succession area. This may reflect a higher occurrence of non-specialist ants in the arboreal stratum, with predominance of species adapted to search for food in the ground or shrub vegetation. Thus, in a scenario of high unpredictability of resource supply, is common that generalist ground-nesting ants start to climb the trees more often, and start to monopolize resources (trees) (Martinez, 2015). This behavior was previously reported by Martinez (2015) and may explain the low diversity of ants in Caatinga, considering that in our study area some predominantly ground-nesting ants were sampled in the trees, such as *Cyphomyrmex transversus*, *Strumigenys* sp.1, *Gnamptogenys sulcata* and *G. moelleri*.

As the forest regeneration occurs, gradual changes take place in the composition, abundance and richness of vegetation, thus driving changes in species composition in the assemblages of organisms associated (Bazzaz, 1975; Neves et al., 2014; Sousa-Souto et al., 2014). These changes become clear since we observe the differences in species composition of arboreal ants between different successional stages. Similar results were observed in previous studies (Arnan et al., 2011; Neves et al., 2013; Sousa-Souto et al., 2014), indicating that changes in habitat structure tends to affect the species composition of ants. This turnover of ant species can be determined by factors specific to each successional stage (e.g. microclimatic gradients, especially moisture and temperature) or each individual tree species (i.e. architectural tree characteristics), since resource specialization performed by some ant species can influence the distribution of less competitive species in the canopies (Ribas & Schoereder, 2002; Campos et al., 2006; Neves et al., 2010b).

This study strengthens the evidence for a regional ecological pattern, in which changes of the vegetation along the ecological succession have direct and indirect consequences for changes in the fauna of arboreal ants with regards of differences in species richness and composition of ant assemblages in dry forests, with pronounced effects in the rainy season. Besides, this study was the first to assess the effects of ecological succession on the assemblage of arboreal ants in area of Caatinga in Sergipe.

In conclusion, habitat complexity and heterogeneity resulting of ecological succession can be considered an important factor in determining patterns of richness and species composition of arboreal ants in Caatinga, where each area tends to have specific characteristics. Based on these results it can be stated that the conservation of areas with different stages of forest regeneration (with a progressive focus on late successional areas) is crucial, since such areas would preserve most ant species associated with vegetation.

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