



RESEARCH ARTICLE - ANTS

Does ant community richness and composition respond to phytophysiological complexity and seasonality in xeric environments?

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Article History

Edited by

Kleber Del-Claro, UFU, Brazil

Received 16 May 2014

Initial acceptance 07 June 2014

Final acceptance 18 June 2014

Keywords

Environmental Heterogeneity, Species Composition, Formicidae, Seasonality

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Abstract

This study aimed to analyze how the vegetation structure (physiognomy) and seasonal changes between seasons (wet and dry) influence richness, diversity and composition of ant species of arboreal and shrubby savannah (Caatinga) environments. The vegetation structure was significantly different among the three strata for all parameters (mean diameter of vegetation, level of herbaceous cover, degree of coverage and depth of litter and percentage of canopy cover). We collected 127 ant species. The mean number of species was approximately two times higher in the rainy season than in the dry season. There was no difference in species richness between the arboreal and shrubby Caatinga physiognomies nor interaction between season and physiognomy. Despite the similarity in richness, species composition differed between physiognomies, however we found no difference in composition between seasons. The seasonal differentiation may be mainly related to the variation in the overall numbers of individuals circulating in the environment, since the enhancement of resource availability during rainy season allows the colony to grow or expand foraging activities, which increases local diversity. Water restriction explains the limited diversity in both environments, while the occurrence of species with greater resource specificity may determine differences in ant composition. Differences in composition of each of Caatinga's physiognomy enhance beta diversity, therefore, raising the overall diversity in the Caatinga Domain.

Introduction

It is common that communities suffer changes in species composition and richness in seasonal environments, such as tropical dry forests (Murphy & Lugo, 1986). A remarkable feature of these vegetation types is the loss of leaves by trees during the dry season (Veloso et al., 1991), which interspersed with wetter periods and higher productivity, determine changes in the amount and quality of resources and, consequently, the structure of local communities (Sánchez-Azofeifa et al., 2005). This explains why certain species may specialize in the use of resources under more severe conditions, resulting in a temporal partition of the same, reflecting a temporal variation of community composition (Pianka, 1980). Apart from climate change, another factor that can influence the animal community is the structural complexity of vegetation. The ecological prediction states that the occurrence of more spe-

cies in a community is seen as a response to the greater complexity of vegetation structure (Pacheco et al., 2009; Corrêa et al., 2006), which provides a greater amount of realizable niches by species of animals and therefore a greater number of species in a given community (Tews et al., 2004). To test this hypothesis, several studies involving the comparison of areas with distinct physiognomies have been done throughout the world, using ant communities, such as Armbrrecht and Ulloa-Chacón (1999) in Colombia; Fisher and Robertson (2002) in Madagascar; Wilkie et al. (2009) in peruvian Amazonic Forest; Lindsey and Shinner (2001) in South Africa. In Brazil we highlight the studies of Fowler et al. (2000) comparing forests from Bahia and Pará States; Corrêa et al. (2006) in forest patches from Mato Grosso do Sul and Delabie et al. (2007) comparing shaded cocoa agroecosystem developed under Atlantic Forest vegetation or other native vegetation in Bahia State.

The Caatinga, a native dryland registered in the North-



eastern Brazil, shows a marked variation in its vegetation structure (Andrade-Lima, 1981), particularly with regard to the density and size of the plants. These differences can be perceived at the local level, where even within a few dozen meters we recognize differences, usually related to a clearly identifiable environmental change as rock extrusions ('lajedos' formations), that determine shallow soils and lower water availability (Amorim et al., 2005). However, studies with animal communities are still incipient, particularly in relation to communities of ants (Neves et al., 2006; Leal, 2003).

In this context, the present study attempted to answer the following question: Does the type of vegetation (physiognomy) that makes up the Caatinga and seasonal variations between the dry and rainy seasons in this environment, influence the richness, diversity and species composition of ants? To answer this question, the following hypotheses were formulated: The richness, diversity and composition of ant species respond positively to the increased structural complexity of the environment and negatively to conditions of the dry season due to the scarcity of food and nesting resources.

Material and Methods

Study Area

In this study, we compared two physiognomies of Caatinga, an arboreal and a shrubby Caatinga, both located in the city of Milagres, Bahia, Brazil (12°52'36S 39°51'22W). The Arboreal Caatinga is characterized by having tall trees reaching up to 20 meters, straight stems and understory consisting of smaller trees and ephemeral subshrubs (Ferreira, 1997). The shrubby Caatinga, in turn, is marked by more sparse trees and greater representation of Cactaceae and Euphorbiaceae with a formation that resembles the vegetation of fields (Ross, 2001).

The region has a semi-arid tropical climate with an average temperature of 24.3°C and average rainfall of 551 mm/year, although large variations between years may occur (142 to 1206 mm/year). The rainy season generally extends from December to February, although there are annual variations, with at least five dry months during the year (Bahia, 1994).

In order to characterize each vegetation type in each sampled area we evaluated vegetation variables which were compared using two-sample independent tests (t test or Mann-Whitney): CBH (Circumference at Breast Height), herbaceous cover, litter cover, litter depth and percent cover of vegetation canopy, measured at each sample point of fauna. CBH of trees was measured at 1.30m above ground, within a 5m radius circular plot (78,5m²) marked from the sampling points; in plants smaller than 1.50m in height, CBH was replaced by the circumference of the trunk below the first branch (Soares, 1999). The herbaceous cover is given by counting the herbaceous plants in a radius of 1.50m from the sample point. Coverage of litter was measured accord-

ing to the scale of Fornier (1974): 1 (0-25%=small); 2 (26-50%=medium 1); 3 (51-75%=medium 2); 4 (76-100%=large). The depth of the litter was classified according to Pacheco et al. (2009) comprising four classes of arbitrary amplitude: very shallow (0-2cm), shallow (2-4cm), deep (4-6cm) and very deep (>6cm). The percentage cover of the vegetation canopy was evaluated through a modification of the methodology for indirect estimation of canopy proposed by Monte et al (2007). We used a Sony Cybershot camera (7.2 MP) to capture the canopy image, and through the Photoshop 7.0 software we created a binary image (black-white) in order to quantify the amount of black pixels, estimating canopy coverage.

Ant sampling

Between May 2009 and January 2010 we carried out four field incursions, two during the dry season and two during the rainy season. In each incursion we sampled the ant fauna associated with three areas of arboreal Caatinga and three areas of shrubby Caatinga.

Samples were taken on a transect of 350 meters in each area, each transect containing 15 pitfall traps 25m distant from one another. The traps were kept active for 48 hours in the field. Additionally, we installed 15 traps with attractive bait sardines in vegetable oil (1cm³), at each transect, exposed for a period of 30min. To avoid interference, the baits were installed only after the removal of the pitfalls. This collection protocol had three replicates at each physiognomy and repeated in all four incursions in the field totaling 12 transects in arboreal Caatinga and 12 transects in the shrubby Caatinga.

Collected ants were identified following the classification proposed by Bolton et al. (2006) and witness individuals were deposited in the Prof. Johann Becker Entomological Collection from Zoology Museum of the Universidade Estadual de Feira de Santana (MZFS) and in the entomological collection from the Myrmecology Laboratory from the Comissão Executiva de Pesquisa da Lavoura Cacaueira (CEPEC/CEPLAC), in Itabuna, Bahia.

Data Analysis

We tested our hypothesis with analyzes based on the components of community structure. The first analysis was based on species richness and used the sample points as local units. For this, we used a generalized linear mixed model with Poisson distribution and log link function to assess the influence of vegetation type and season (explanatory variables) on species richness (response variable). Furthermore, we use the sampling points, and collection areas incursions as random factors to control the temporal pseudoreplication. We conducted this analysis in R software (R Development Core Team, 2013) using the lme4 package (Bates et al., 2013).

The second analysis was based on species composition and areas used as sampling points. For this purpose, we build a similarity matrix using the Jaccard index and from this we performed a non-metric multidimensional scaling (NMDS). This technique is an ordering method more robust to non-linear situations and often summarizes more information in fewer axes than other indirect ordination techniques (Legendre & Legendre, 1998). We tested changes in species composition between seasons (dry and wet) and between vegetation types (arboreal and shrubby Caatinga) using a two level similarity analysis (Two-way ANOSIM). We conducted this analysis using Primer® 6.0 software (Clarke & Gorley, 2006).

Results

Vegetation structure

The vegetation structure of arboreal and shrubby Caatinga were different in all traits, with the arboreal physiognomy presenting a CBH 1.4 times greater than in shrubby Caatinga (arboreal = 30.0 ± 21.4 mm; shrubby = 42.2 ± 22.03 mm; $t = 2.652$; $n = 45$; $P \leq 0.001$), herbaceous cover twice as large (arboreal = 1.9 ± 0.9 , shrubby = 0.7 ± 0.4 ; $t = 7.0$; $n = 45$; $P < 0.001$), larger leaf litter coverage ($U = 122.5$; $n = 90$; $P < 0.001$), larger leaf litter depth ($U = 701$; $n = 90$; $P < 0.001$), and canopy coverage was two times larger (arboreal = $70.9 \pm 9.2\%$, shrubby = $33.6 \pm 22.2\%$, $t = 14.74$; $d.f. = 118.57$; $P < 0.001$).

Mirmecofauna

We collected 127 ant species (Appendix 1), with the most frequent species being *Dinoponera quadriceps* (68%), *Camponotus* sp6 (56%) and *Ectatomma muticum* (41%). A total of 32 ant species was recorded exclusively on arboreal Caatinga and 29 species exclusively in the area of shrubby Caatinga. Between stations, 18 species of ants were collected only in the dry season and 20 species of ants were collected exclusively in the wet season.

The mean number of species by point sampled was approximately two times higher in the wet season than in the dry season ($\chi^2 = 5.45$; $d.f. = 1$; $P < 0.05$). Moreover, there was no difference in species richness among the Caatinga physiognomies ($\chi^2 = 0.4796$; $d.f. = 1$; $P = 0.49$) nor interaction between physiognomy and season ($\chi^2 = 6.95$; $d.f. = 3$; $P = 0.07$) (Fig. 1).

Despite the similarity in richness, composition of ant species differed between the physiognomies ($R = 0.849$; $P < 0.01$), however we found no difference in species composition of ants between the dry and wet seasons ($R = 0.118$; $P = 0.10$) (Fig. 2).

Discussion

The fact that there were differences in species composition between the physiognomies, despite the similarity of species richness, indicates that there are two distinct communities in the Caatinga - a specialist in arboreal Caatinga

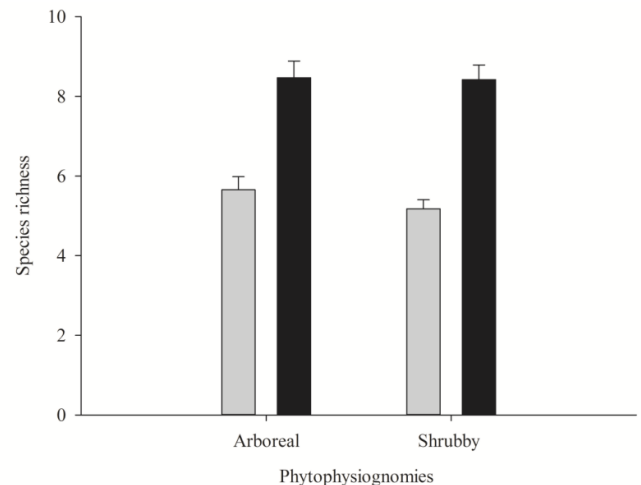


Figure 1. Mean of ant species richness for point sampled in two Caatinga phytophysiognomies (arboreal and shrubby) ($\chi^2 = 0.4796$; $d.f. = 1$; $P = 0.49$) in dry (gray columns) and rainy (black columns) seasons. The mean number of species for point sampled was approximately two times higher in the wet season than in the dry season ($\chi^2 = 5.45$; $d.f. = 1$; $P < 0.05$). Bars represent standard errors.

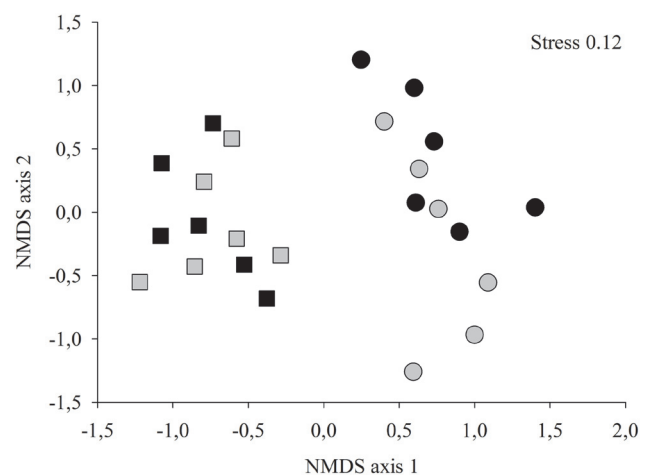


Fig 2. Non-metric dimensional scaling (NMDS) based on Jaccard Similarity Index, comparing ant species composition in Milagres, Bahia, Brazil. Circles represent arboreal Caatinga and squares represent shrubby Caatinga. Dry season in gray and rainy season in black.

and another in shrubby Caatinga. Increasing environmental complexity can change the types of resources and their availability. Once the resources are different, the environment may become less advantageous to the dominant species and completely change the structure and composition of the community (Perfecto & Vandermeer, 1996). An example of how the heterogeneity of vegetation may determine the occurrence of specialist species is the presence of *Gnamptogenys concinna* in the area of arboreal Caatinga. It was believed that this ant species was restricted to wet forest environments, and recently recorded for the state of Bahia in cacao shaded

by large trees (Delabie et al., 2010). *G. concinna* is the only one belonging to the arboreal specialist genus (Lattke, 1990; Longino, 1998), with strong links with canopies with high numbers of epiphytes of the families Bromeliaceae and Orchidaceae (Delabie et al., 2010). A link to these epiphytes may explain its occurrence in the area of arboreal Caatinga, considering that the area where it was found has a canopy with lots of large epiphytic Bromeliaceae.

Studies focusing on the influence of grazing on the ant community in semi-arid regions also found effects restricted to species composition (Bestelmeyer & Wiens, 2001). However, in the present study species richness was similar because once the two areas are subject to stress caused by lack of rain, the food resources must be scarce in both environments.

We found no effect of the interaction between environmental complexity and seasonality on the ant diversity, but we found a difference in the richness of ant species between seasons, but without a difference in species composition. Due to the unpredictability in the acquisition of resources caused by the shortage of rainfall, most species in Caatinga should be able to pull through in xeric conditions (like ants in american desertlands e.g: Whitford et al., 1999), and the species should only reduce the number of active individuals in the colony during the dry season and invest in foraging activities when the environment has more resources (Bernstein, 1979). If there are less active individuals, the probability of finding more species will be smaller. It is worthwhile to point out that, although fluctuations in abundance may occur between seasons, we work only with occurrences, missing evidence to support this hypothesis. A study addressing ants that use floral resources in a tropical dry forest demonstrated that dietary overlap is higher in the dry season (Brito et al., 2012) indicating a decrease in food resources.

Since there are large differences in species composition in the two physiognomies, this leads to an increase in beta diversity of Caatinga on a regional scale, similar to what happened with other groups such as bees (Martins, 2002). Given that there is more than one type of physiognomy in the Caatinga, the importance of environmental heterogeneity for increasing beta diversity in the region shown in the present study may be underestimated.

Two factors influence the effect of the plant structure on ants and are characteristics that distinguish arboreal and shrubby Caatinga. The first is the increase in shading in the environment caused by the presence of trees (Reyes-López et al., 2003). The second is the deposition of litter which is a factor that positively influence the activity of ant species (Perfecto & Vandermeer, 1996). Similar to that reported in this study, other studies have also found no influence of environmental complexity in species richness of ants (Corrêa et al., 2006; Neves & Braga, 2010). However, the use of only one feature as a surrogate of environmental complexity may fail to find an effect even if it exists (see discussion on the review by Tews et al., 2004), so an indirect analysis can more

easily detect the environmental heterogeneity even without setting a key structure, provided focusing on the species composition.

Our study shows the following pattern: while the variation in rainfall is responsible for the increase in the number of species that may be present in the environment on a local scale, the difference of environmental complexity on both physiognomies is detectable in species composition and is responsible for increasing the beta diversity through differences in species composition.

Acknowledgments

Many colleagues contributed to this study in different ways, especially J.J. Resende who helped during sampling. We thank two anonymous reviewers for valuable comments. The Brazilian National Council for Scientific and Technological Development (CNPq) supported this study. G.M.M. Santos received productivity fellowship from CNPq.

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Appendix 1. List of ant species collected in areas of Arboreal Caatinga and Shrubby Caatinga, during dry and rainy seasons in Milagres, Bahia, Brazil.

Species	Phytophysiognomy			
	Arboreal Caatinga		Shrubby Caatinga	
	Dry Season	Rainy Season	Dry Season	Rainy Season
<i>Acanthoponera</i> sp01	X			X
<i>Acanthostichus</i> sp01	X			
<i>Acromyrmex</i> sp01			X	X
<i>Anochetus</i> sp02	X			
<i>Apterostigma</i> sp01	X			
<i>Atta sexdens rubropilosa</i>	X	X	X	X
<i>Azteca</i> sp01		X		
<i>Azteca</i> sp02		X		
<i>Azteca</i> sp03		X		
<i>Brachymyrmex</i> sp01	X	X		
<i>Brachymyrmex</i> sp02		X		
<i>Brachymyrmex</i> sp03			X	X
<i>Brachymyrmex</i> sp04			X	X
<i>Camponotus</i> sp01	X	X	X	X
<i>Camponotus</i> sp02	X	X	X	X
<i>Camponotus</i> sp03	X	X	X	X
<i>Camponotus</i> sp04	X	X	X	X
<i>Camponotus</i> sp05	X	X	X	
<i>Camponotus</i> sp06	X	X	X	X
<i>Camponotus</i> sp07	X		X	X
<i>Camponotus</i> sp08	X	X	X	X
<i>Cephalotes</i> prox. <i>goeldi</i>	X	X		
<i>Cephalotes atratus</i>	X	X		
<i>Cephalotes clypeatus</i>		X	X	X
<i>Cephalotes depressus</i>	X	X		X
<i>Cephalotes grandinosus</i>		X		X
<i>Cephalotes minutus</i>	X	X	X	X
<i>Cephalotes pussilus</i>	X	X	X	X
<i>Cephalotes</i> sp01	X			
<i>Cephalotes ustus</i>		X		
<i>Crematogaster</i> sp01	X		X	X
<i>Crematogaster</i> sp02		X	X	X
<i>Crematogaster</i> sp03			X	X
<i>Crematogaster</i> sp04				X
<i>Crematogaster</i> sp05			X	X
<i>Crematogaster</i> sp06	X	X	X	X
<i>Crematogaster</i> sp07	X	X		X
<i>Cyphomyrmex</i> sp01			X	X
<i>Cyphomyrmex</i> sp02			X	X
<i>Dinoponera quadriceps</i>	X	X	X	X
<i>Dorymyrmex</i> sp01			X	X
<i>Dorymyrmex thoracicus</i>			X	X

<i>Ectatomma edentatum</i>	X	X	X	X
<i>Ectatomma muticum</i>	X	X	X	X
<i>Ectatomma</i> sp01			X	X
<i>Ectatomma</i> sp02			X	X
<i>Ectatomma suzanae</i>	X	X	X	X
<i>Forelius brasiliensis</i>			X	X
<i>Gnamptogenys concinna</i>	X			
<i>Gnamptogenys</i> sp01			X	X
<i>Gnamptogenys</i> sp02			X	
<i>Hylomyrma balzani</i>	X	X		X
<i>Hylomyrma</i> sp01	X			
<i>Labidus coecus</i>	X	X		
<i>Labidus mars</i>	X			
<i>Labidus praedator</i>	X	X		
<i>Linepithema humile</i>		X		
<i>Linepithema</i> sp01		X	X	X
<i>Linepithema</i> sp02		X	X	X
<i>Linepithema</i> sp03				X
<i>Linepithema</i> sp04			X	
<i>Mycetophylax</i> sp01				X
<i>Neivamyrmex</i> sp01	X		X	
<i>Nylanderia</i> sp01	X	X		
<i>Ochetomyrmex</i> sp01		X		
<i>Octostruma</i> sp03		X		
<i>Odontomachus chelifer</i>	X	X		
<i>Odontomachus haematodus</i>	X	X	X	X
<i>Oxyepoecus</i> sp02				X
<i>Pachycondyla bucki</i>	X	X		
<i>Pachycondyla</i> prox. <i>magnifica</i>	X			
<i>Pachycondyla</i> prox. <i>venusta</i>		X	X	X
<i>Pachycondyla striata</i>		X		
<i>Pheidole</i> sp01	X	X	X	X
<i>Pheidole</i> sp02	X	X	X	X
<i>Pheidole</i> sp03	X	X	X	X
<i>Pheidole</i> sp04	X	X		X
<i>Pheidole</i> sp05	X	X	X	
<i>Pheidole</i> sp06				X
<i>Pheidole</i> sp07	X	X	X	X
<i>Pheidole</i> sp08	X	X		X
<i>Pheidole</i> sp09	X	X		X
<i>Pheidole</i> sp10	X	X	X	X
<i>Pheidole</i> sp11			X	X
<i>Pheidole</i> sp12	X	X	X	X
<i>Pheidole</i> sp13	X	X	X	X
<i>Pheidole</i> sp14	X	X	X	X
<i>Pheidole</i> sp15	X	X	X	
<i>Pheidole</i> sp16	X		X	X

<i>Pheidole</i> sp17	X	X		
<i>Pheidole</i> sp18			X	
<i>Pheidole</i> sp19	X	X	X	X
<i>Pheidole</i> sp20	X			X
<i>Pheidole</i> sp21	X	X	X	X
<i>Pheidole</i> sp22	X	X	X	X
<i>Pheidole</i> sp23	X	X	X	X
<i>Pheidole</i> sp24	X	X	X	X
<i>Pheidole</i> sp25	X		X	
<i>Pogonomyrmex (E.) naogeli</i>	X		X	X
<i>Procryptocerus</i> sp01	X			
<i>Pseudomyrmex elongatus</i>		X		X
<i>Pseudomyrmex gracilis</i>				X
<i>Pseudomyrmex</i> sp01	X	X	X	X
<i>Pseudomyrmex</i> sp02			X	X
<i>Pseudomyrmex</i> sp03	X			
<i>Pseudomyrmex</i> sp04		X		X
<i>Pseudomyrmex</i> sp05	X			
<i>Pseudomyrmex tenuis</i>	X	X		X
<i>Pseudomyrmex termitarius</i>			X	X
<i>Rogeria</i> sp01	X			
<i>Solenopsis</i> sp02	X	X	X	X
<i>Solenopsis</i> sp03	X	X	X	X
<i>Solenopsis</i> sp04	X	X	X	X
<i>Solenopsis</i> sp05		X	X	X
<i>Solenopsis</i> sp06	X		X	X
<i>Solenopsis</i> sp07	X	X	X	X
<i>Solenopsis</i> sp08				X
<i>Solenopsis</i> sp09		X	X	
<i>Strumigenys</i> sp02				X
<i>Tapinoma</i> sp01				X
<i>Tapinoma</i> sp02	X			X
<i>Tapinoma</i> sp03			X	X
<i>Trachymyrmex</i> sp01	X	X	X	X
<i>Trachymyrmex</i> sp02	X		X	
<i>Wasmannia</i> sp01		X	X	X
<i>Wasmannia</i> sp02		X	X	X
<i>Wasmannia</i> sp03		X	X	