Temperature Influence on Species Co-Occurrence Patterns in Treefall Gap and Dense Forest Ant Communities in a Terra-Firme Forest of Central Amazon, Brazil

by

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ABSTRACT

In this study we evaluated the influence of temperature and species co-occurrence on the structure of an ant community of treefall gaps and surrounding dense forests in a terra-firme forest of Central Amazon, Brazil. For this, we collected ants at different hours, and at the time of each collection we measured the temperature of the environment. Even with the difference in the temperature variation and variation throughout the day, there was no difference in the richness and abundance of ants among the environments. Also, the ant species are distributed randomly and independently of one another in both studied environments in accordance with a null model (C-score). However, although not influenced by temperature, the ant composition of treefall gaps was different from the ant community of the surrounding dense forest. Possibly the composition and ant foraging in environments of treefall gaps and surrounding dense forests are not only influenced by temperature, but also by the interaction of this factor with the structural complexity of vegetation in terms of sites available for nesting and feeding, and other microclimatic factors. This generates a difference in ant composition of both environments. In addition, the structuring of ant community in tropical rain forests may actually be stochastic or neutral within each environment.

Key Words: Tropical Rain Forest; Formicidae; Microclimatic factors; Competition; Diversity.

INTRODUCTION

In the tropics, most small natural forest disturbances are caused by falling trees, forming natural treefall gaps (Uhl *et al.* 1978, Brokaw 1985, Almeida

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1989). This stochastic event is part of the natural forest dynamic and acts as an additional factor in forest structure, changing the light intensity, temperature and humidity in these sites (Whitmore 1978, Brown 1993, Allen & Meyer 1998). When this new habitat is formed, several adapted organisms can colonize these sites, replacing one another in succession (Probert 1993, Ekstam & Forseby 1999, Andrade 2000). Among these organisms, ants emerge as one of the most prominent groups (Ward 2006). Because of their extreme abundance and diversity, ants act in the process of nutrient cycling, seed dispersal and aeration in the soil surface, and interact in various ways with other parts of the ecosystem, influencing the pattern of distribution and abundance of other taxa along succession (Hölldobler & Wilson 1990, Majer & Camer-Pescl 1991, Dáttilo *et al.* 2009).

In tropical rain forests, the ant diversity is extremely high, reaching approximately 500 species in only one collection site (Wilson 1959, Fisher 1999, Vasconcelos & Delabie 2000, Longino *et al.* 2002). The success of these organisms is mainly due to several ecological and social adaptations, including generalized feeding and nesting habits (Benson & Harada 1988, Hölldobler & Wilson 1990, Fowler *et al.* 1991). The high abundance and diversity of ants in tropical rain forests is also due to the high habitat complexity (abundance of places to nesting) and the climate stability in tropical regions over space and time, creating an ideal environment where several species specialists can establish (Benson & Harada 1988, Hölldobler & Wilson 1990, Reyes-Lopes *et al.* 2003). However, little is known about the relationship between the natural dynamics of tropical rainforests and the ant communities inside forests.

In many cases ant colonies are considered modular organisms and, in analogy, comparable to plants. This comparison is made because most ant species do not present migration behavior of the colony and their foraging is centered at a point (Andersen 1991, López 1994, Santos *et al.* 2006). Thus, competition has been identified as an important factor in the structure of ant communities (Andersen 1992, Adams 1994, Acosta *et al.* 1995, Punttila *et al.* 1996). The distribution of ant mosaics proposed by Room (1971) is defined as the distribution in patches of dominant ant species with similar ecological requirements, and therefore there is no overlap of their territories (Gause 1934, MacArthur & Levins 1964, Chesson 2000). Thus, in small spatial scales is possible that competitive exclusion occurs with some ant species

(Andersen 1995, Parr *et al.* 2000). However, beyond the competition, one of the factors that regulates the ant diversity and their foraging is the species' preference for different abiotic conditions, and several studies indicate that soil temperature is directly related to the foraging of these organisms on the soil surface (Porter & Tschinkel 1987, Marsh 1988, Andersen 1992, Wehner *et al.* 1992, Cerdá *et al.* 1998).

Due to the fact that after the opening of a clearing there is an increase in daily temperature fluctuations on the soil surface (Vázquez-Yanes & Orozco-Segovia 1982), and that the ants are sensitive to small microclimatic changes in the environment which they live (Brown 1997, Cerdá *et al.* 1997, 1998, Bestelmeye 2000), different adaptive strategies of ants that live in these two environments are expected (Aguiar & Monteza 1996). Thus, in this study, we evaluated the influence of temperature and co-occurrence structuring the ant community of treefall gaps and surrounding dense forests in a terra-firme forest of Central Amazon, Brazil.

MATERIAL AND METHODS

Study area

This study was conducted during June and July 2007 in the forest reserve #1501# (54°50'W and 02°25'S), located approximately 80 km north of Manaus city, Amazonas State, Brazil. The reserve area covers 10,000 ha of continuous forest, surrounded by a much larger area of undisturbed forest, and is part of the Biological Dynamics of Forest Fragments Project, BDFFP (INPA/Smithsonian Institution). Characterized as a primary tropical rainforest and terra-firme, it has canopy trees ranging from 30-40m in height and some emergent trees which reach 50m in height. The understory is relatively open and contains several species of palm trees (Lovejoy & Bierregaard 1990). According to the Köppen classification, the climate is tropical humid (Afi) with average annual temperature of 26.7 °C, 85% humidity and 2.200 mm of precipitation, with periods of rain between November and May and a dry season between June and October (Ribeiro 1976, Lovejoy & Bierregaard 1990, Laurance 2001).

Data collection

Five treefall gaps and five surrounding dense forests were randomly selected approximately 300-800m away from each other. All treefall gaps had an area exceeding 400 m^2 and were opened between 5 and 10 years before the present study (T.J. Izzo, pers. obs.). In each site three baits were distributed with 5g of sardines and guava in a plastic card 10 m apart from each other, forming a triangle. After an hour, all the ants present in the baits were collected. The collections were made at five different hours (7h, 10h, 14h 18h, 22h), and at the time of each sample we measured the temperature, always at a height of 5 cm above the ground. The ants collected were stored in 70% alcohol for further identification. All individuals collected were deposited in the Entomological Collection of Instituto Nacional de Pesquisas da Amazônia (CE-INPA).

Data analysis

In order to not overestimate the ant species with more efficient systems for recruiting and / or those whose colonies are closer to the bait (Romero & Jaffé 1989, Leal & Lopes 1992, Tavares *et al.* 2001, Gotelli *et al.* 2011), all quantitative matrices used in this study were calculated based on the frequency of species occurrence in the bait and not based on the number of workers.

Initially, we tested the temperature variation among the times of the two environments using an Analysis of Variance with repeated measurements (ANOVA Repeated). Subsequently, we used General Linear Models (GLM) to assess the influence of temperature, the type of environment, and the interaction of both factors on the richness and abundance of ants, through the software SYSTAT 10.0.0 (Wilkinson 1998). To summarize the composition of the ant community foraging in environments of treefall gaps and surrounding dense forests, we ordered the similarity between points using Non-Metric Multidimensional Scaling (NMDS). This type of ordination analysis is one of the most robust and often summarizes more information in less axes than other techniques for direct ordering (Legendre & Legendre 1998). The ordinations analyses were performed from a distance matrix calculated from the Sorensen's dissimilarity index (qualitative data) and Bray-Curtis's dissimilarity index (quantitative data). Additionally, we tested the difference in the ant species composition of treefall gaps and surrounding dense forests through a permutation test (10.000 permutations) based on analysis of similarities (ANOSIM) (Clarke 1993). Both the ordination and analysis of similarities were made through the software R Development Core

Team (version 2.13.1). Finally, we use the first two axes of each ordination in a Multivariate Analysis of Covariance (MANCOVA) (MANCOVA), in order to evaluate the influence of temperature and interaction between the environment and the temperature in the ants composition through the software SYSTAT 10.0.0 (Wilkinson 1998).

To test the hypothesis that the coexistence of ant species in treefall gaps and surrounding dense forests is determined by competition, we used the co-occurrence index (C-Score) through the software EcoSim 7.72 (Gotelli & Entsminger 2009). In a competitively structured community, the observed C-score index should be significantly higher than expected. When this index is less than expected competitive exclusion does not occur between the ant species (Gotelli 2000, Gotelli & Entsminger 2009). We compared the observed C-score index with 5000 replicates generated by the null model where the species occurrences and sites are fixed. This null model assumes that the presence of a given ant species does not influence the occurrence of other species, i.e. there is no evidence for deterministic process influencing species distribution (Ribas & Schoereder 2002, Gotelli & Entsminger 2009).

RESULTS

In this study we collected 37 ant species representing eight genera and 4 subfamilies. The subfamily Myrmicinae had the greatest number of taxa (81.1%), followed by Formicinae (8.1%), Ectatomminae (5.4%) and Ponerinae (5.4%). We collected 14 ant species in treefall gaps and 21 ant species in surrounding dense forests, and only six species occurred in both environments. Eight species were exclusive to treefall gaps and 17 species were exclusive to surrounding dense forests (Table 1). However, there was no difference in the richness and abundance of ants by area between the environments (ANOVA, $P > 0.05$), and both factors also did not vary with temperature and are not different between the environments (ANOVA, $P > 0.05$) (Table 2).

The temperature range in dense forest (Mean 26,1°C – Min 24,0°C, Max 28. 3°C) was lower than in the treefall gaps (Mean 27,5°C – Min 23,7°C, Max 32.3°C), and there was a difference in temperature variation per hour between the two environments ($F_{(1.137)} = 33.126$; $P < 0.001$).

Despite the overlap in some points showed by the ordination analysis, the ant community of dense forest differs from the treefall gaps both qualitatively

Table 1. Number of occurrences of ants collected in treefall gaps and surrounding dense forests environments in the months of June and July 2007 in a terra-firme forest in Central Amazon, Manaus city, Amazonas State, Brazil.

	Number of occurrences	
Ant species	Treefall gaps	Surrounding dense forests
Camponotus femoratus (Fabricius 1804)	-	19
Crematogaster sp1	25	10
Crematogaster sp2	2	4
Crematogaster sp3	-	4
Crematogaster sp4	13	-
Ectatomma quadridens (Fabricius 1793)	-	1
Ectatomma tuberculatum (Olivier 1792)	1	-
Odontomachus haematodus (Linnaeus 1758)	-	1
Odontomachus scalptus Brown 1978	1	-
Paratrechina sp1	3	2
Paratrechina sp2	1	-
Pheidole sp1	-	3
Pheidole sp2	-	3
Pheidole sp3	-	7
Pheidole sp4	-	2
Pheidole sp5	1	2
Pheidole sp6	-	3
Pheidole sp7	-	5
Pheidole sp8	-	2
Pheidole sp9	-	1
Pheidole sp10	-	2
Pheidole sp11	-	1
Pheidole sp12	15	3
Pheidole sp 13	-	1
Pheidole sp 14	3	-
Pheidole sp 15	1	-
Pheidole sp16	6	1
Pheidole sp17	1	-
Pheidole sp18	1	-
Pheidole sp19	1	-
Pheidole sp20	1	-
Solenopsis geminata (Forel 1893)	1	-
Solenopsis sp1	1	4
Solenopsis sp2	-	3
Trachymyrmex cornetzi (Forel 1912)	-	2
Trachymyrmex sp1	-	1
Trachymyrmex sp2	1	1

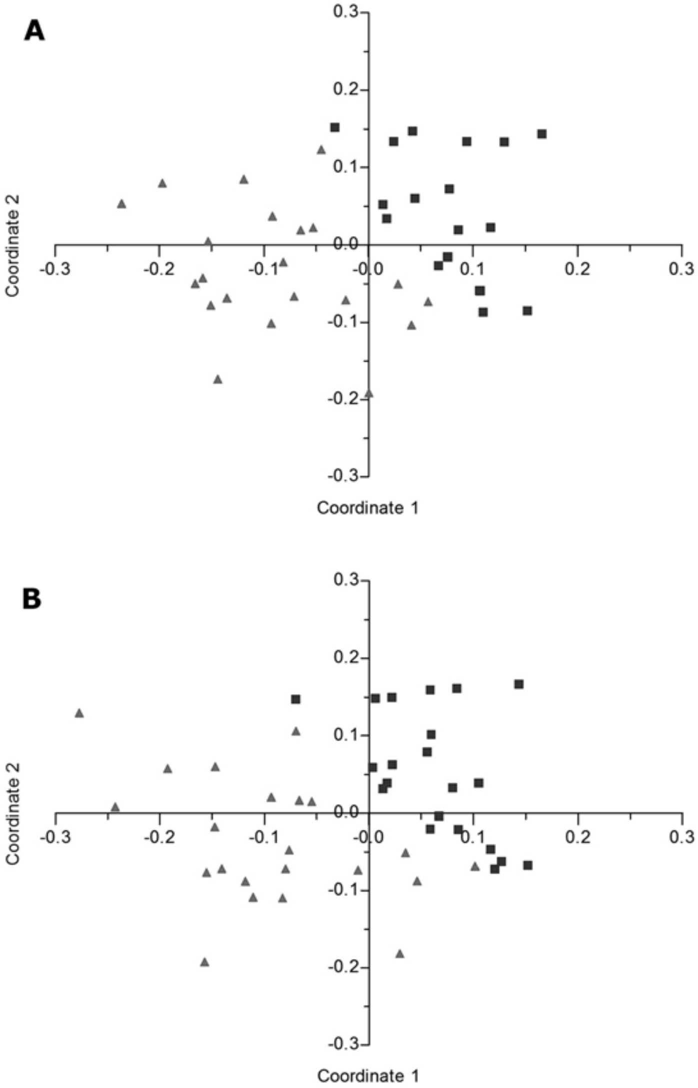

Fig. 1. Non-metric multidimensional scaling (NMDS) of ants collected in treefall gaps (triangles) and surrounding dense forests (squares) in June and July 2007 in a terra-firme forest in Central Amazon, Manaus city, Amazonas State, Brazil. This ordination analysis was calculated from the (A) Sorensen's dissimilarity index (Stress= 0.2631 ; Axis 1 + Axis 2= 49.5% of explanation) and (B) Bray-Curtis's dissimilarity index (Stress= 0.2635 ; Axis 1 + Axis 2= 49.3% of explanation).

Table 2. General Linear Models (GLM) to assess the influence of temperature, the type of environment (treefall gaps and surrounding dense forests), and the interaction of both factors on the richness and abundance of ants.

Response	Effect	DF	Mean Squares	F-ratio	P-value
Richness	Environment	1	2.043	1.250	0.269
	Temperature	1	0.242	0.148	0.702
	Environment*Temperature	1	2.452	1.500	0.227
	Error	46	1.634		
Abundance	Environment	1	2.492	1.885	0.176
	Temperature	1	1.269	0.960	0.332
	Environment*Temperature	1	2.771	2.096	0.154
	Error	46	1.322		

(NMDS, followed by ANOSIM; $P < 0.001$) and quantitatively (NMDS, followed by ANOSIM; $P < 0.001$) (Fig. 1). In qualitative data, the temperature did not influence the species composition of ants (MANCOVA, Pillai-Trace: $F_{(0.007)} = 1.037$; $P = 0.363$), and the composition did not change with temperature differences between the environments (MANCOVA, Pillai-Trace : $F_{(0.007)} = 0.279$; $P = 0.345$). For the quantitative matrix, there was no influence of temperature on the species composition of ants (MANCOVA, Pillai-Trace: $F_{(0.034)} = 0.793$; $P = 0.459$) and the composition did not change with temperature differences between the environments (MANCOVA, Pillai-Trace : $F_{(0.051)} = 1.197$; $P = 0.312$).

Our data indicate that competition does not seem to be the principal factor in structuring of ant communities in treefall gaps and surrounding dense forests. The simulations performed for the ant community associated with the treefall gaps showed that the observed C-score index is lower than expected ($P = 0.001$) if the competition was a factor structuring the ant community (Fig. 2A). In ant community associated with dense forests, the simulations realized showed that the observed C-score index lay within the 95% limits of random frequency obtained from the null model ($P = 0.75$) (Fig. 2B).

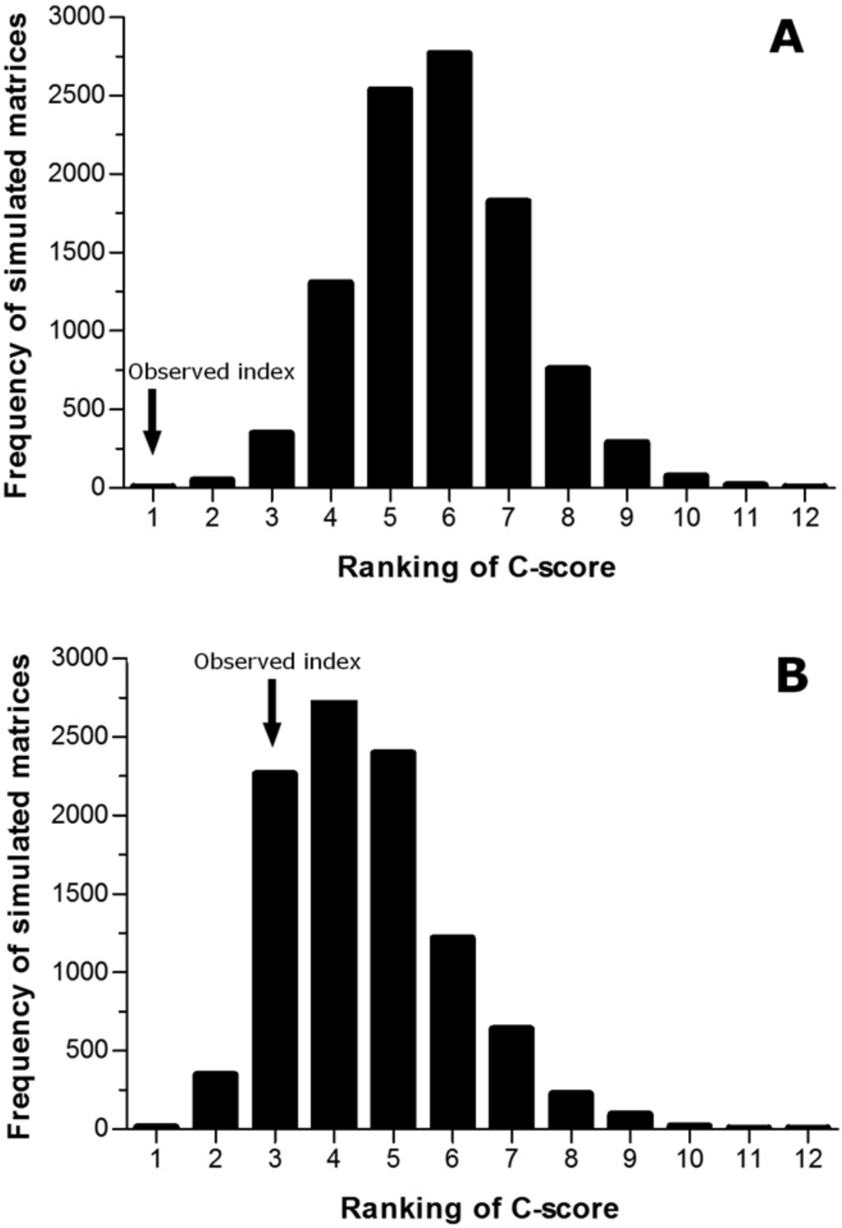

Fig.2. Frequency distribution of the co-occurrence C-score index obtained from 5000 replicates generated by the null model in the ant community associated with A) treefall gaps and B) surrounding dense forests in June and July 2007 in a terra-firme forest in Central Amazon, Manaus city, Amazonas State, Brazil. Arrows represent the observed C-score index.

DISCUSSION

Many studies have shown the factors that determine the ant diversity in different spatial scales (Hölldobler & Wilson 1990, Andersen 1997, Cerdá 1997, Gibb & Hochuli 2002, Ribas *et al.* 2003, Floren & Linsenmair 2005, Kaspari 2005). These factors act differently in different spatial scales and vegetation types (Santos *et al.* 2006). In this study, in a small spatial scale, even with the difference in the amplitude and the thermic variation between the treefall gaps and surrounding dense forests environments, we did not observe a modification of the ant community as a function of temperature, but just due to strong differences on habitat structure. Some studies have shown that the composition and foraging ants in treefall gaps environments are not only influenced by microclimatic factors, but also by the interaction of these factors with the structural complexity of vegetation in terms of availability of food and nesting sites (Greenslade & Halliday 1983, Andersen 1986, Aguiar & Monteza 1996, Basu 1997). Thus, many factors act together so that the composition of ant species differs between forest clearings and around tropical forests (Aguiar &Montez 1996), as observed in our results. In regions with large climatic variations throughout the day and year, the temperature can directly influence the foraging strategy of ants, and change the hierarchical level between the dominant ant species (Herbers 1989, Hölldobler & Wilson1990, Cerdá *et al.* 1997, 1998).

On a broader level, some studies have shown that competition is the only or most important factor regulating the ant diversity (Room 1971, Andersen 1992, Majer *et al.* 1994, Acosta *et al,* 1995, Djieto-Lordon & Dejean 1999, Delabie *et al.* 2000; Albrecht & Gotelli 2001). However, variations in environmental conditions, ecological, spatial, beyond random events can modulate the importance of competition and the ant community structure in one site (Hölldobler & Wilson 1990, Morrison 1996, Basu 1997). Our work corroborates with other work available in the literature that there is not substantial evidence that competition influences ant community structure at different spatial scales (Levings & Traniello 1981, Fellers 1987, Ryti & Case 1992, Punttila *et al.* 1996; Ribas & Schoereder 2002). In treefall gap environments, there was a great co-occurrence of ant species, possibly due to the fact that most species in disturbed environments are resource and habitat generalists (Fowler 1990, Andersen 1995, King *et al.* 1998, Vasconcelos 1999, Silvestre *et al.* 2003, Dáttilo *et al.* 2011). That means limitation of a particular resource that can be dominated by some ant species does not necessarily cause the elimination of other species. So, the ants associated with these environments may use different food resources and change, even temporarily, their diets, avoiding competition and facilitating the co-occurrence (Herbers 1989, Yanoviak & Kaspari 2000, Albrecht & Gotelli 2001, Santos *et al.* 2006). On the other hand, in surrounding dense forests, the results showed that the co-occurrence observed lay within the 95% limits of random frequency and suggest that it is not always the biological processes which determines the spatial distribution of ants. Ribas & Schoereder (2002) tested the hypothesis of competition structuring the ant community in 14 different tropical rain forests and also obtained through simulations by null models, and the results indicate that the ant mosaic theory of structuring the ant community does not apply to these regions. Given the high availability and spatial distribution of food resources, beyond the climatic conditions equilibrium, our study suggests that the structure of ant communities in tropical rainforests may really be stochastic or neutral within each environment (Floren & Linsenmair 2000, Floren *et al.* 2001, Hubble 2001).

Finally, as individuals differ in the probability of colonizing a type of environment due to dispersal ability and the effects of variation between environments, we expect that the ant composition is different in treefall gaps and surrounding dense forest environments (Olden *et al.* 2001, Bruna *et al.* 2011). The foraging and colonization of the environment immediately after the opening of the one treefall gap can be determining factors in the establishment of the colony as we observed, once ant species that occur in treefall gaps are different from the surrounding dense forests (Aguiar & Monteza 1996). So, some generalist species colonize treefall gaps environments, while habitat specialists probably can not survive and/or establish nests. Additionally, the natural regeneration that occurs within the treefall gaps influencing important parameters of composition and distribution of the ant species that live there (Pearson *et al.* 2003). We suggest for future studies, assessment of how the regeneration of treefall gaps influence the processes of substitution and competition of ants inside the tropical rainforests, since such events are part of the natural dynamics of these forests.

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