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Applicability of the Ant Mosaic theory on floor litter in a forest of Central Amazon, Brazil.

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Abstract

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The spatial distribution pattern of ants is apparently very influenced by competition in habitats with few species, and on the crowns of tropical trees. However, we tested if the mosaic theory applies also to tropical species which forage and nest on the litter accumulated on the base of palms and the litter distributed on the forest floor. A total of 160 samples were collected in a primary upland forest from Amazonas state, Brazil. The analysis of interspecific association is according to Majer et al. (1994). Weak interaction traces among species pairs were found. The only significant association after correction for multiple tests was a positive correlation on the abundance of *Camponotus femoratus* and *Crematogaster carinata*. With this results, we concluded that the mosaic of ant species does not apparently exist on the forest floor.

Additional key words: *Attalea attaleoides*, competition, Formicidae, palm base, upland forest.

Resumo

Franken EP, Gasnier TRJ. 2010. Aplicabilidade da teoria do mosaico de formigas em serapilheira de chão em uma floresta da Amazônia Central, Brasil. Entomotropica 25(1): 37-42.

O padrão de distribuição espacial das formigas parece ser fortemente influenciado pela competição em habitats com poucas espécies e nas copas das árvores tropicais. Entretanto, nós testamos se a teoria do mosaico também pode ser aplicada às espécies tropicais que forrageiam e nidificam na serapilheira acumulada na base de palmeiras e na serapilheira distribuída no chão da floresta. Um total de 160 amostras foram coletadas em floresta primária de terra firme no estado do Amazonas, Brasil. A análise de associação interespecífica está de acordo com Majer et al. (1994). Foram encontrados fracos indícios de interação entre os pares de espécies. A única associação significante após a correção para testes múltiplos foi a correlação positiva na abundância de *Camponotus femoratus* e *Crematogaster carinata*. A partir destes resultados, concluímos que o mosaico de espécies de formigas aparentemente não existe no chão da floresta.

Palavras-chave adicionais: *Attalea attaleoides*, competição, Formicidae, base de palmeira, floresta de terra firme.

Introduction

It is believed that the spatial distribution of ant species in an environment is determined by patterns of competitive dominance (Savolainen and Vepsäläinen 1998). Dominant species can

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exclude subordinate species from their territory or reduce their foraging success (Sanders and Gordon 2000). This hierarchy results in different assemblages of ants regulated by different dominant species. This process generates an ant mosaic which consists of mutually exclusive territories by dominant ant species. These dominants are associated with a set of characteristic subdominant species (Room 1971, Leston 1973, Majer 1976, Majer and Camer-Pesci 1991).

The ant mosaic theory is based on the premise that the subdominant and non-dominant species must be associated to a particular dominant species which minimizes the interspecific competition, comprising a limited number of dominant species (Room 1971, Majer 1976, Leston 1978, Majer and Camer-Pesci 1991, Majer et al. 1994). So, the mosaic is inter and intraspecific, where most of the subdominant and non-dominant species are specialized in exploring a niche different from the one used by the sympatric dominant species. These subdominant and non-dominant species are specialized in exploiting a different part of the environment, in relation to that used by the sympatric dominant ant, and the superimposition on the use of resources doesn't occur (Majer 1976). The usual hostility which was observed between dominants was not exhibited. When workers of the two species met while foraging, they performed antennal inspection and then continued foraging (Room 1971). The association among species also has an effect on their spatial distribution, resulting in an irregular distribution of the colonies, particularly on the crown of the trees, and to some extension on the floor level (Delabie et al. 2000). The hierarchies, and consequently the mosaics, are not rigid patterns, and can vary locally and regionally according to the type of habitat and the combination of species-specific factors (Floren and Linsenmair 2000, Sanders and Gordon 2000).

The forest floor is not a much uniform habitat, showing a large spatial heterogeneity in the amount of soil surface litter that is observed in Central Amazonian rainforests (Höfer et al. 1996). Among the great variety of microhabitats formed by the irregular distribution of litter of the forest floor litter, the accumulations on the base of acaulescent palms can show a differentiated organization due to this being a restricted environment, and consequently easier to defend. In the acaulescent palms the stem is reduced to a short subterranean axis, but the leaves are large and are disposed in such a way that gives to palm the appearance of a funnel (Figure 1). These palms act as efficient litter traps, funneling leaves and small branches falling from the overstory directly to the palm root zone, which is different from the one typically found on the floor (Vasconcelos 1990). For the sampling of this work, we selected specimens of the acaulescent palm *Attalea attaleoides* (Barb. Rodr.) Wess. Boer, since it is one of the dominant species of the understorey (Kahn and Castro 1985).

The spatial distribution pattern of ants is apparently very influenced by competition in habitats with few species and on the crowns of tropical trees. However, there are few studies to verify if the mosaic theory applies also to tropical species which forage and nest on the floor. In this work we examine if the ant mosaic theory can be applied to two floor litter microhabitats in a upland forest in Central Amazon: the litter accumulated on the base of palms and the litter distributed in the forest floor.

Materials and Methods

Sampling was carried out from June 22 to December 3, 2004 in the Experimental Farm of the Federal University of Amazonas, located on km 38 of the BR-174 federal highway. Vegetation at the site is primary upland forest. We made a transect and the first 80 *Attalea attaleoides* palms where marked. Palm

Table 1. Correlation between most representative ant species (10 or more occurences). Type of association (TA): N – negative, P – positive; Microhabitat (MH): LN – 1 m^2 of litter next to *Attalea attaleoides*, LB – litter accumulated on the base of *Attalea attaleoides*; χ^2 – chi-square values; P – significance values (only P < 0,05); Significance recalculated for 144 tests (Sign.): - absent, + present.

Pairs of species	TA	MH	χ^2	P	Sign.
Pheidole sp.12 – *Pyramica denticulata*	P	LN	4,698	0,030	-
Pheidole sp.12 – *Crematogaster nigropilosa*	P	LN	5,169	0,023	-
Pyramica denticulata – *Crematogaster minutissima*	P	LN	7,408	0,006	-
Paratrechina sp.3 – *Solenopsis (Dipl.)* sp.9	P	LB	4,693	0,030	-
Paratrechina sp.5 – *Crematogaster minutissima*	P	LB	6,299	0,012	-
Camponotus femoratus – *Crematogaster carinata*	P	LB	18,085	<0,001	+
Crematogaster brasiliensis – *Crematogaster carinata*	N	LB	8,932	0,003	-

sampling sequence was radom. In each palm it was extracted a sample comprising the total volume of the litter accumulated in its base and a second sample taken 1 m away from the palm base (1 m^2 of soil litter), totalizing 160 samples. The ants were removed by hand picking. The analysis of interspecific association is according to Majer et al. (1994), where only the species data which occurred in ten or more samples for each microhabitat were used. The values for positive or negative association among species were obtained using the χ^2 analysis with Yates' correction applied. This index shows that the dominant species are going to exhibit negative associations with other dominating and/or subordinate species. The sequential Bonferroni correction was used in order to adjust the significance value (P) in multiple tests and to reduce the probability of spurious results generated purely by chance (Rice 1989).

Results and Discussion

Weak interaction traces among species pairs on the two analyzed microhabitat categories were found (Table 1). Multiple tests must be interpreted with caution, e.g. Ribas and Schoereder (2002) describe that, in the literature tested by them, the co-occurrence of species does not differ from those expected randomly. Among the analyzed correlations, no associations occurred above the values previewed at random for P<0.05. So, we can interpret that the interactions among most of the species pairs must be considered weak or insignificant. According to Moran (2003), the "significant" associations found must be interpreted with this in mind, being important, however, to present them because they can reveal tendencies to be considered in future studies.

In the adjacent litter, 66 tests, including 12 ant species, were carried out (Table 1). In this portion occurred three positive associations, being two of them between *Pheidole* sp. 12 co-occurring with *Pyramica denticulata* (Mayr, 1887) and *Crematogaster nigropilosa* Mayr, 1870 and another one with *P. denticulata* and *Crematogaster minutissima* Mayr, 1870. In the litter accumulated on the base of the palm 78 tests including 13 ant species were carried out (Table 1). In this portion, three positive and one negative association occurred, being *Paratrechina* sp. 3 co-occurring with *Solenopsis* (*Diplorhoptrum*) sp. 9, *Paratrechina* sp. 5, co-occurring with *C. minutissima*, *Camponotus femoratus* (Fabricius, 1804) co-occurring with *Crematogaster carinata* Mayr, 1862 and *Crematogaster brasiliensis* Mayr, 1878 avoiding *C. carinata*, indicating that these association events can be rare on the forest floor.

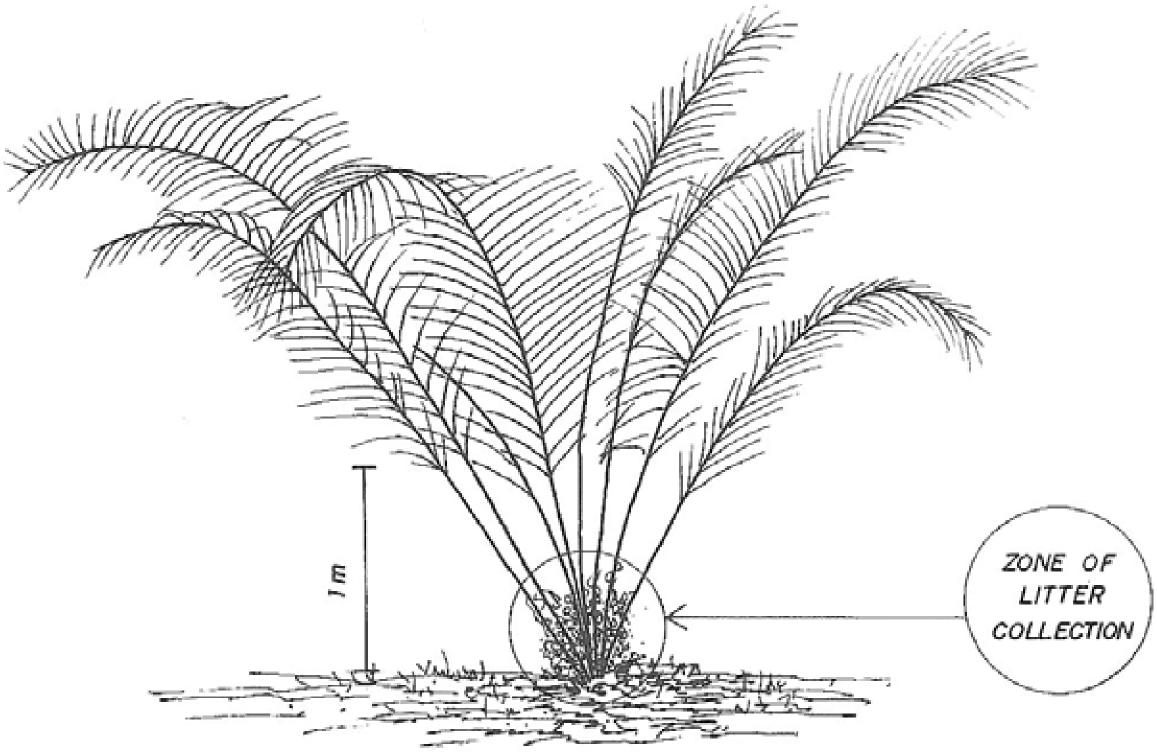

Figure 1. General aspect of a acaulescent palm (from Vasconcelos 1990).

In Table 1 it can be seen that *Crematogaster* predominated among the "significant" associations. About 70% of the significant species pairs for α=0.05 were related to some species of this genus. This can indicate that these ants have a greater ability to interact with other species of different genus. It must be considered, however, that these were the most abundant and common species in the samples, being 4 species (*C. brasiliensis*, *C. carinata*, *C. minutissima* and *C. nigropilosa*) analyzed from the adjacent and accumulated litter.

The only significant association after correction for multiple tests was a positive correlation on the abundance of *C. femoratus* and *C. carinata* (Table 1). This strong association can be explained based on behavioral data obtained by other authors. Majer et al. (1994), for example, observed that among the six ant species considered as dominants in terms of biomass, three species belonged to the genus *Crematogaster*. In this same study, three species of the genus *Camponotus* were considered as sub-dominants. In these circumstances, we can suppose that this coexistence is possible due to *C. femoratus* show a submissive behavior, and *C. carinata* show an encounter behavior. According to Fellers (1987), submissive ants possess abilities to find out and quickly use food resources. This same article describes that some encounter species are the last to reach the baits, but, when it happens, they invariably control the resources due to their numerical dominance.

The mosaic of ant species which is evident in some tropical species (Leston 1978; Majer 1976; Majer and Camer-Pesci 1991; Majer et al. 1994) does not apparently exist on the forest floor (Jackson 1984). Our results corroborate this, as we have only found one significant evidence of association between species. This might have occurred due to a litter colony probably finding a broad and unpredictable variety of species during its (Levings 1983). According to Jackson (1984), negative associations occur on a lesser scale on the floor, differing from the monopoly of large areas on the crowns of the trees by arboricolous species, which can be the result of processes, other than competition. So, the complex forest dynamics must lead to various possible stable communities, each one with an unpredictable species composition (Floren and Linsenmair 2000). The species which nest and forage on the forest floor, although some may be relatively aggressive, are not truly territorial (Levings 1983; Jackson 1984), showing less agressivity when compared to arboricolous ants, defending only the nest and the food resources, unevenly distributed, from the approaching intruders (Hölldobler and Lumsden 1980; Yanoviak and Kaspari 2000). The defense of territories on the floor (bidimensional) probably is impracticable due to the need of a greater density of workers in obtaining the same reward as the territories on the trees (tridimensional), once that the tree branches architecture facilitates the defense, being necessary that the ants only remain still on strategic spots to intercept the intruders (Jackson 1984).

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