RENATA BERNARDES FARIA CAMPOS

FATORES DETERMINANTES DA RIQUEZA E COMPOSIÇÃO LOCAL DA COMUNIDADE DE FORMIGAS DE SERAPILHEIRA

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de Magister Scientiae.

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Prof. Carlos F. Sperber (Conselheiro)	Prof. Og F. F. Souza (Conselheiro)
Prof. Julio N. C. Louzada	Prof. Angelo Pallini Filho

Prof. José H. Schoereder
(Orientador)

Dedico este trabalho aos que me fizeram
descobrir o verdadeiro sentido da palavra
amizade: Carla, Zhé e Tathi
Amo vocês...

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RESUMO

CAMPOS, Renata Bernardes Faria, M.S., Universidade Federal de Viçosa, fevereiro de 2002. **Fatores determinantes da riqueza e composição local da comunidade de formigas de serapilheira.** Orientador: José Henrique Schoereder. Conselheiros: Carlos Frankl Sperber e Og Francisco Fonseca de Souza.

Esta tese teve por objetivo testar a importância de fatores locais para a riqueza e estrutura da comunidade de formigas em ambiente de serapilheira. No primeiro capítulo a hipótese de que a disponibilidade e heterogeneidade local de recursos determinam a riqueza local de espécies de formigas foi testada, utilizando o peso da serapilheira como medida indireta de disponibilidade de recursos. Foi encontrada uma relação positiva estatisticamente significativa entre o peso seco da serapilheira e a riqueza local de espécies de formigas. As análises não mostraram maior importância de nenhuma das frações da serapilheira (folhas, frutos, ramos, detritos), também não foram encontrados efeitos da heterogeneidade da serapilheira sobre a riqueza local de espécies de formigas. A ausência do efeito da heterogeneidade é uma evidência de que a escala utilizada nesta tese é apropriada para o estudo de processos locais. No segundo capítulo a hipótese de que a dinâmica local de imigração e extinção determina a riqueza local de espécies de formigas em serapilheira foi testada experimentalmente. A hipótese complementar de que a disponibilidade e heterogeneidade local de recursos afetam a dinâmica local desta comunidade também foi testada. O estudo da dinâmica da comunidade não mostrou um efeito significativo das extinções locais sobre a riqueza local pelo período de dois meses. Os resultados evidenciaram que a dinâmica das espécies de serapilheira parece ser mais afetada pelos movimentos das espécies do que pela extinção local. O experimento com recolonização mostrou que há migração para áreas onde há remoção de espécies, entretanto dois meses (duração do experimento) não foi um período de tempo suficiente para recuperar a riqueza local encontrada antes do distúrbio. A recolonização foi independente da abundância, composição e heterogeneidade da serapilheira, reforçando os resultados do primeiro capítulo. A composição da comunidade após a migração também foi alterada, ou seja, as espécies que recolonizaram uma área não foram as mesmas que habitavam aquele local antes do distúrbio. Este fato mostrou que perturbações em pequena escala podem ser um fator importante para a estrutura desta comunidade. É provável que após um distúrbio a comunidade mude ao longo do tempo, desta forma é possível que a comunidade de

serapilheira seja formada por um mosaico de manchas em diferentes estágios de sucessão.

ABSTRACT

CAMPOS, Renata Bernardes Faria, M.S., Universidade Federal de Viçosa, February 2002. **Determinant factors of local richness and composition in litter ant communities.** Adviser: José Henrique Schoereder. Committee Members: Carlos Frankl Sperber e Og Francisco Fonseca de Souza.

The aim of this thesis was to test the importance of local factors to ant species richness determination in litter communities. In the first chapter the hypothesis of local availability and heterogeneity of resources to determine local species richness was tested, using litter weight as an indirect of resource availability. A significant positive relationship between litter dry weight and local species richness was found. The analyses did not evidence the effect of any of the litter fractions, nor of litter heterogeneity on local ant species richness. The absence of litter heterogeneity effect is evidence that the spatial scale used in this work is appropriate to the study of local processes. The hypothesis that local dynamics of immigration and extinction determine the local litter ant species richness was experimentally tested in the second chapter. The complementary hypothesis that local resource availability and heterogeneity affect local dynamics of this community was also tested. The study of community dynamics did not show a significant effect of extinction on local species richness in a two months period. The results evidenced that litter species dynamics seems to be more affected by species movements than by local extinction. The re-colonization experiment showed that migration occurred to areas where the ants were removed, although two months was not time enough to recover the species richness found before the disturbance. Re-colonization is independent of litter abundance, composition and heterogeneity, stressing the results from the first chapter. The community composition after migration was also altered, this means that species re-colonizing a given area are not the same than those living in the same area before disturbance. This shows that small-scale disturbances may be an important factor to community structuring. It is probable that after disturbance community changes along time. In that case litter ant communities would be formed by a mosaic of patches in different successional stages. Studies on species composition that re-colonize an area after a disturbance may show the successional pattern and give important information on the mechanisms by which dynamics of such communities determine local species richness.

INTRODUÇÃO GERAL

O estudo da biodiversidade tem sido, desde o começo do século passado, um dos pontos mais importantes no estudo de comunidades. Padrões de riqueza de espécies têm recebido a atenção de muitos pesquisadores (Cornell & Lawton 1992; Levings & Windsor 1984; Schluter & Ricklefs 1993; Srivastava 1999; Tilman & Pacala 1993), entretanto estudos sobre os mecanismos pelos quais a riqueza é gerada e mantida são fundamentais, entretanto pouco conclusivos. O estudo destes mecanismos se torna necessário, uma vez que não basta saber apenas onde há maior biodiversidade, mas que mecanismos são responsáveis pelos padrões de riqueza de espécies.

Os fatores que influenciam a estrutura, gerando e mantendo a diversidade das comunidades atuam em várias escalas espaciais. Estas escalas podem ser divididas em locais, regionais e globais. Embora esta divisão dos processos seja arbitrária, podemos dizer, de uma forma geral, que os fatores históricos e globais são aqueles que atuam em escala ampla como a evolução. Na escala regional predominam processos biogeográficos como as migrações. Os processos ecológicos, como competição, mutualismo, predação e distúrbios em pequena escala, atuam em escala local e regional(Schluter & Ricklefs 1993).

A comunidade da serapilheira tem despertado a atenção de pesquisadores por sua grande biodiversidade e importância ecológica. Na serapilheira acontecem processos importantes como a decomposição de matéria orgânica com o fornecimento de nutrientes para o solo (Copley 2000). As formigas constituem uma abundante parte dessa comunidade (York 1999), onde apresentam grande importância ecológica, já que podem ser responsáveis pela regulação da composição e abundância de comunidades de outros insetos e mesmo plantas (Levins et al. 1973; Hölldobler & Wilson 1990)

Fatores locais, como interações entre populações têm sido considerados forças muito importantes para a estrutura e manutenção local da riqueza de espécies das comunidades de formigas. Entretanto, estudos com formigas em serapilheira e solo não demonstram evidências de que interações como a competição sejam um fator estruturador destas comunidades (Yanoviak & Kaspari 2000; Soares & Schoereder 2001; Soares et al. 2001). Assim, a diversidade local dessas espécies pode ser relacionada com características do ambiente, que por sua vez podem estar afetando a comunidade direta ou indiretamente (Fig. 1).

Fatores como a quantidade, disponibilidade e heterogeneidade espacial nas taxas de recursos, assim como a condições microclimáticas podem ser importantes na determinação da riqueza local de espécies de formigas em serapilheira (Levings & Windsor 1984; Fowler & Delabie 1995; Andrew et al. 2000; Soares et al. 2001). No caso de formigas de serapilheira recursos como alimento e local para nidificação, são efêmeros, mas há uma renovação constante com possível manutenção de abundância. Sabe-se que há uma grande variação na riqueza local de espécies, e indícios de que há um maior número de ninhos em determinadas frações da serapilheira(Soares & Schoereder 2001). Entretanto, não existem estudos testando a importância da abundância, composição e/ou heterogeneidade da serapilheira na estruturação das comunidades de formigas.

A ocorrência de distúrbios nessas comunidades e a dinâmica local de extinção e imigração também podem explicar a riqueza local de espécies (Fig 2). A ocorrência de distúrbios na comunidade pode explicar a ausência de competição, uma vez que causam a redução ou o deslocamento das populações, retardando o processo de exclusão (Connell 1961). A constante queda de galhos e folhas torna a serapilheira um ambiente freqüentemente alterado. Membros da subfamília Ecitoninae, conhecidas como formigas de correição também são causadores de distúrbios (Hirosawa et al. 2000). Elas causam grande impacto uma vez que, ao passar por uma área, sua trilha remove ou reduz o tamanho de colônias situadas no chão da floresta (Sudd & Franks 1987).

Esta tese teve por objetivo testar a importância de fatores locais para a riqueza e estrutura da comunidade de formigas em ambiente de serapilheira. A tese está dividida em dois capítulos que investigam fatores e mecanismos complementares para a explicação da riqueza desta comunidade. Os capítulos foram escritos em forma de artigos científicos, cada capítulo segundo o formato de uma revista.

O primeiro capítulo tem por objetivo testar a hipótese de que a disponibilidade e heterogeneidade local de recursos determinam a riqueza local de espécies de formigas. Este capítulo está escrito seguindo o formato da revista Sociobiology, onde será submetido.

O segundo capítulo testa experimentalmente a hipótese de que a dinâmica de imigração e extinção determina a riqueza local de espécies de formigas em serapilheira. Testa também, a hipótese complementar de que a disponibilidade e heterogeneidade local de recursos afetam a dinâmica local desta comunidade. Este capítulo está no formato da revista Austral Ecology, onde será submetido.

Figura 1 - Fluxograma mostrando possíveis fatores determinantes da riqueza local de espécies testados pelo primeiro capítulo. Estes fatores estão relacionados com a estrutura física da serapilheira.

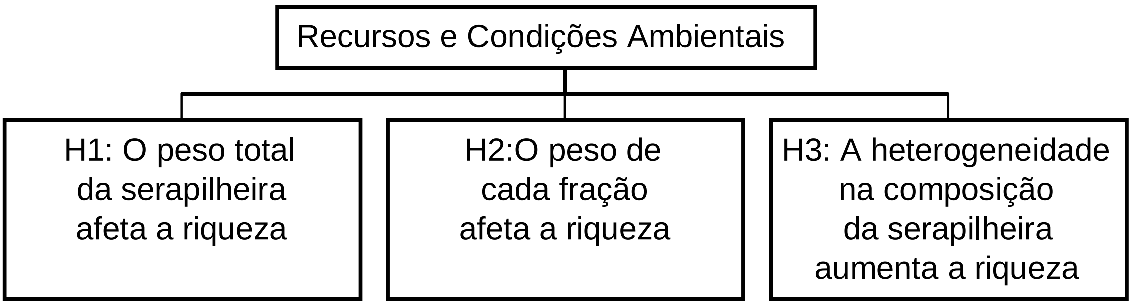
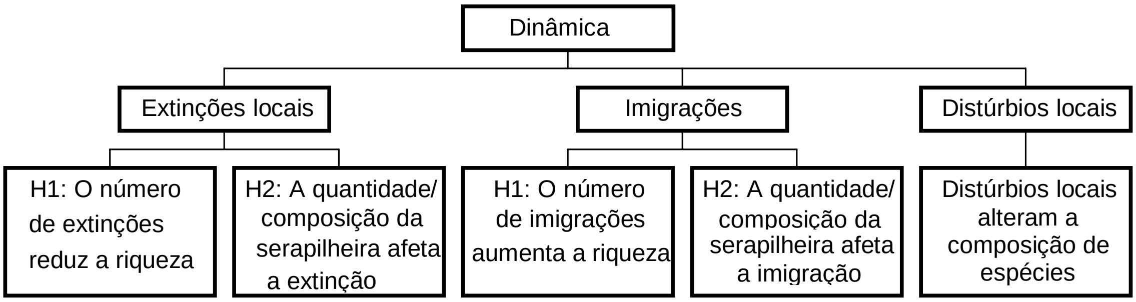


Figura 2 - Fluxograma mostrando possíveis fatores determinantes da riqueza local de espécies testados pelo segundo capítulo. Estes fatores estão relacionados com a dinâmica da comunidade de formigas.



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CAPÍTULO 1

Local determinants of species richness in litter ant communities (Hymenoptera: Formicidae)

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Abstract. In this paper we asked the question why does local biodiversity of litter ants vary. We tested the hypotheses that local resource availability and heterogeneity to species richness determination, using litter weight as a surrogate of resource availability. Litter ants were sampled in a forest remnant and extracted using Berlese funnels. Total litter weight, weight of litter fractions, and local heterogeneity of litter were used as explanatory variables in regression tests, using local ant species richness as response variable. Only total litter weight produced significant results, even though little species richness variation was explained by this variable. We discussed these results concluding that small scale disturbances may be the responsible for local ant species richness variation.

Keywords. Biodiversity determinants; Disturbance; Heterogeneity; Local processes, Resource availability.

Factors determining biodiversity may act on different spatial and temporal scales, which are usually divided in local, regional, global and historical scales (Rosenzweig 1995). Ecological processes such as species interactions and small scale disturbances are considered local processes, which interact with other processes acting in larger scales to determine how many species will be present in a given site and time (Schluter & Ricklefs 1993, Cornell & Lawton 1992).

Forest litter is presently considered a frontier in biodiversity studies, because it presents an enormous biodiversity and is believed to shelter several important processes of the forest, such as nutrient and soil dynamics (Copley 2000). An important fraction of litter macroarthropod communities is composed by ants (York 1999), considerable attention being given to ground-dwelling ant communities and to factors determining their biodiversity (Levings 1983; Carvalho & Vasconcelos 1999). Local factors such as conditions and resources are usually regarded as key factors determining ant biodiversity (Levings & Windsor 1984, Fowler & Delabie 1995; Andrew et al., 2000; Soares et al. 2001).

Conditions in litter are very dependent on its composition and abundance, and it is known that litter is responsible for the reduction of variations in soil temperature, moisture and light (Facelli & Pickett 1991). Therefore, the amount and composition of litter in a given site may affect ant colony survival due to microclimatic effects.

Resource availability may influence the occurrence of interspecific competition (Tilman & Pacala 1993), because competition only occurs with limiting resources to the involved species. Therefore, the more available the resources the less probable that competition will be an important determining factor. Litter ant communities are composed by several guilds of detritivorous, granivorous, predators, opportunists and generalists ants, and the resource for them is within litter (Delabie et al. 2000). Litter may also serve as nesting and sheltering resource to some ant species (Perfecto & Vandermeer 1994; Andrew et al. 2000). Therefore, if these resources are limited, a positive relationship between litter abundance and ant species richness is expected. Furthermore, some resources in litter may be more important than others, such as branches or leaves for ant nesting (Soares & Schoereder 2001), and it is possible that some of litter fraction abundance may be more important than the total litter abundance.

Litter composition may be important because a more homogeneous litter may support less species than a heterogeneous one, since homogeneity offers less different opportunities of resources and conditions. Habitat heterogeneity is defined as the within-habitat variations in resources and conditions, and it is usually considered an important factor determining species richness (Tilman & Pacala 1993). The effects of heterogeneity on species richness is well documented, in scales varying from forest remnants to biogeographic regions (Perfecto & Snelling 1995; Rosenzweig 1995; Bragança et al. 1998; Rojas & Fragoso 2000). In small scales, such as within-habitat patches or microhabitats, there are no studies to our knowledge of the effects of heterogeneity on species richness determination.

In this paper we asked the question why does local biodiversity of litter ants vary, testing the hypotheses of local resource availability and heterogeneity to species richness determination.

Methods

Study site

The sampling design was installed in a forest reserve (Centro de Estudos de Florestas Naturais) with an area of about 300ha, in Viçosa, Minas Gerais, Brazil (20º 45’S, 42º51’W). The climate is moderate subtropical moist with a rainy season from September to April and dry season from May to August (Golfari 1975). The annual rainfall ranges from 1500 to 2000 mm, average air relative humidity of 80% and temperature ranging from 14 to 26.1 ºC (Castro et al. 1983).

This remnant has suffered periodic exploration due to coffee crops, and other disturbances and it is protected from such disturbances since 1966, when a process of natural secondary succession started. The secondary forest occupies presently most of the reserve area, and we arbitrarily have chosen a forested area to carry out the sampling design.

Sampling design

Local species richness was considered the number of ant species occurring in each litter sample. To determine this species richness 88 litter samples were collected using a plastic container with 30cm in diameter. The points were placed at least three meters from each other. The samples were taken to the laboratory and placed for 10 days in modified Berlese funnels to extract the ants. The ants were identified to genus (Bolton 1994) and, whenever possible, to species with the help of Ivan C. do Nascimento (UFV) and Dr. Jacques H. C. Delabie (CEPLAC).

The litter was oven dried, separated into four fractions (leaves, branches, fruits + seeds, and detritus) and each fraction was weighted.

Statistical analyses

The effect of total litter amount on ant species richness was tested through linear regression, using local species richness as response variable and total litter weight as explanatory variable.

The effect of each fraction weight was also tested through multiple linear regression, using local species richness as response variable and the weight of each fraction as explanatory variables. The complete model was adjusted and, if the model was significant, each explanatory variable was removed in turn, verifying significant changes in deviance (Crawley 1993).

Besides the importance of each fraction on species richness determination, local combination of the fractions in the sample may also be important. If there are ant species specialists in each litter fraction, the presence of more fractions with similar weights in the sample would increase local species richness, because there would be resources for each group of litter fraction specialist. Local heterogeneity was estimated by the coefficient of variation (CV) of the fraction weights. Samples with high CV have at least one fraction with more weight than the others, favoring the group of ants specialists in that fraction, and these samples were considered less heterogeneous. Conversely, samples with low CV were considered more heterogeneous, because the fraction weights would be more similar, and all litter resources would occur in similar amounts. The effect of heterogeneity on local species richness was tested through linear regression, using local ant species richness as response variable and CV as explanatory variable.

In all analyses the used models were checked by analyses of residuals and the models were criticized accordingly.

Results

Thirty-four ant species, belonging to four subfamilies, were collected. The subfamily most represented was Myrmicinae, with 21 species, followed by Ponerinae (nine species), Formicinae (three species) and Dolichoderinae (one species) (Table 1). Local species richness varied from zero to 10 species. Table 1 also presents some important biological information on the species sampled.

Total litter amount positively influenced ant local species richness (F(1, 86)=4.104; p=0.046; r^2=0.046; Fig. 1), although the effect of the fractions was not significant (F(4, 83)=1.980; p=0.105). Heterogeneity also did not influence ant local species richness (F(1, 46)=0.003; p=0.957).

Discussion

The results showed a positive statistical significant relationship between local ant species richness and total litter weight (Fig. 1). Other authors have found different results regarding this relationship, and litter abundance usually does not determine ant species richness (Delabie & Fowler 1995; McGlynn et al. in press). Nevertheless, the general rule is that the number of coexisting species is determined by resource availability (Schluter & Ricklefs 1993). Litter amount may be used as a surrogate of resource availability, because ants may use litter directly as nesting sites or refuge (Hölldobler & Wilson 1990; Andrew et al. 2000). Litter may also contain food resources, such as prey (Levings & Windsor 1984), decomposing material, or seeds, and it is expected that larger amounts of litter would cause an increase in these resources. Therefore, litter would affect species richness indirectly by limiting food resource availability. If litter is a limiting resource, or if it is really determinant of local species richness, then we would expect that these communities were structured by interspecific competition. However, there is little evidence on the importance of such interactions on litter ant communities (Yanoviak & Kaspari 2000; Soares & Schoereder 2001; Soares et al. 2001, but see Mercier & Dejean 1996; McGlynn & Kirksey 2000)

Another process to explain the positive relationship between ant species richness and litter weight is that litter amount affects microclimate. Microclimate changes may affect directly species occurrence because species have different condition requirements (Torres 1984). This effect may also be indirect, by affecting species interactions, such as competitive hierarchies (Cerdá et al. 1997; Perfecto & Vandermeer 1996), prey availability (Levings & Windsor 1984; Delabie & Fowler 1993; Collevatti & Schoereder 1995) or predator activity (Levings 1983).

Area effects may also be a causal factor of the relationship between ant species richness and litter weight. We collected a constant area of litter, and variations of weight may be connected to variations in litter composition or in litter volume. Species-area relationships are probably the most frequent pattern in ecology (Rosenzweig 1995) and possibly is interfering in the observed pattern, both direct and indirectly. Larger litter volume may contain more ant individuals, and therefore there would be a higher probability of sampling more species. The same reasoning can be done to the species used as resources by the ants.

We expected that at least the amount of branches in litter would show a positive effect on ant species richness, because most species are known to use this fraction as nesting sites (Carvalho & Vasconcelos, 1999). Nevertheless, these species may also use other litter fractions as nesting and foraging sites (Table 1), showing that these species are generalist regarding nesting sites. Therefore, it is possible that the ants really prefer using branches to nest (Soares & Schoereder 2001), but they seem to be able to substitute the resource to other fraction available (Delabie et al. 2000). Regarding food resources, litter ant species are also able to use different resources, and even though litter composition may affect arthropod community composition, most litter ant species are omnivorous. Litter environment favors omnivory, because it contains several different resource types, ranging from vegetal and animal detritus, to fungi, and to arthropods, and they are supposedly all ephemeral (Delabie et al. 2000).

Even though we did not find effect of local heterogeneity on species richness, other spatial scales have produced significant relationships between these variables (Perfecto & Snelling 1995; Rojas & Fragoso 2000; Ribas et al. unpublished data). The significant relationships between ant species richness and heterogeneity occurred mainly in arboricolous ants. Canopy and litter ants have different resource availability, quality, and predictability (Yanoviak & Kaspari 2000), and therefore their environments exert different evolutionary pressure on the ants. Canopy ants may be more specialists and litter ants more generalists. Litter and resources within it are not as predictable and long-lasting as the resources that occur in the trees, such as extrafloral nectaries or domatia. Therefore, abundance of generalists species in litter ant communities may be responsible for the absence of effect of environmental heterogeneity on these ants.

Heterogeneity, on the other hand, may act in a larger scale than the presently studied (Koltliar & Wiens 1990). Patches of different habitats inside a forest may be caused by the presence of different tree species, or patches of plant communities in different successional stages (Perfecto & Snelling 1995; Rojas & Fragoso 2000), and are probably larger than the spatial scale studied. Schluter & Ricklefs (1993) suggested that local scales are homogeneous, whereas Bell et al. (1993) stated that larger areas are supposed to have more variation than smaller ones. The latter authors measured the environmental condition variations, which was higher in larger distances. The scale we worked with, hence, is ideal to study the local effects on diversity, but it seems not large enough to study the effects of environmental heterogeneity.

According to the obtained results, neither partial resource availability (litter fraction weight) nor the combinations between these parameters (heterogeneity) are conditioning factors of litter ant species richness. Even though total litter weight have produced a significant effect on ant species richness, few variation in local species richness is explained by this factor (r^2=0.046). Litter weight, and the resources associated to it, should not be determinant of local species richness, and other factors should explain this local variation. Litter is so ephemeral and unpredictable that ant community dynamics has to be studied to reach for convincing explanations of the factors conditioning local species richness.

A possible explanation is the occurrence of local disturbance that kills individuals, decreasing local species richness and confounding the effect of resource availability (Kaspari 1996). Strength and frequency of disturbances would determine site species richness, because a disturbed local would gradually recover species richness, and a photograph of local species richness would show differences according to the time elapsed between disturbance and the ant sampling. These disturbances may be the presence of predators, such as army ants, and litterfall or the presence of larger animals, which may disrupt the original structure of litter.

Disturbance studies show the importance of this factor in community structuring, including ant communities (Oliver et al. 2000; Shure & Phillips 1991; Roth et al. 1994; Kaspari 1996; Vasconcelos 1999; York 2000), and in litter ants disturbance seems to be a most important factor in these communities.

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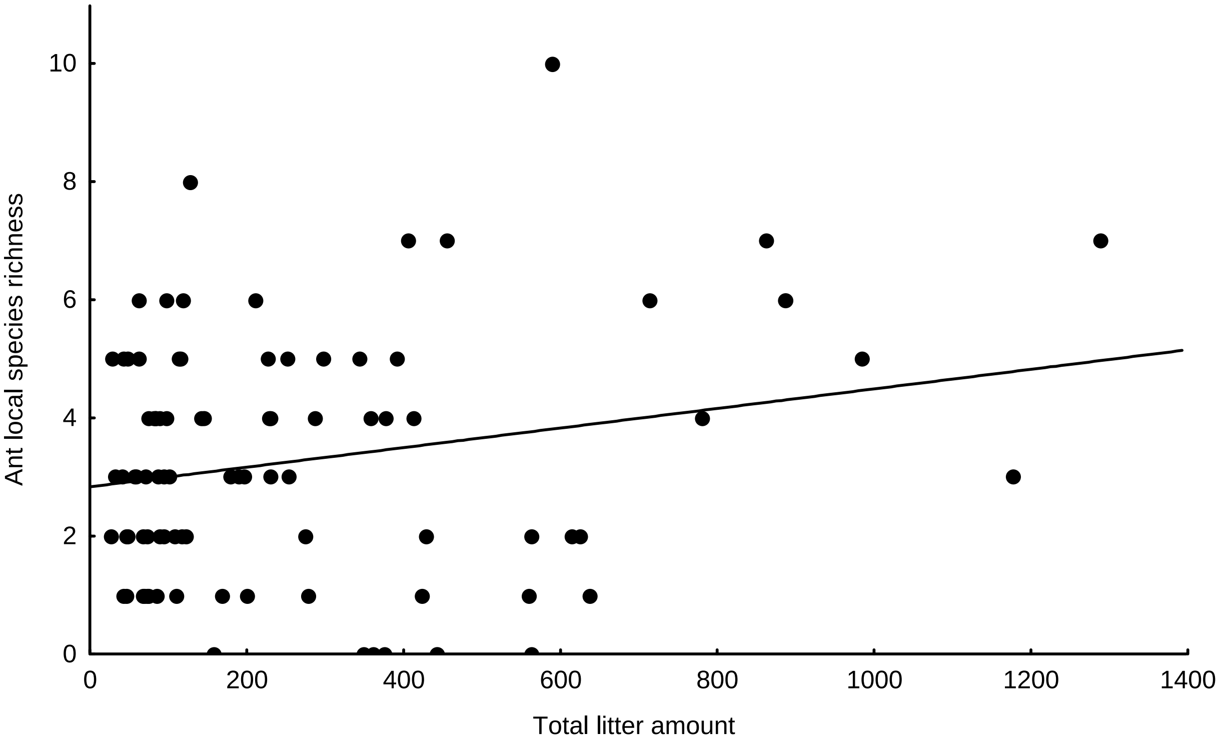
Table 1 – Litter ant species sampled in Viçosa, MG. Nesting sites, and feeding habits, are also presented whenever this data are available. Nesting sites are represented by: b = branches; s = soil; l = litter (detritus) and f = fruits (Data from Delabie & Fowler 1995; Delabie et al. 2000; Soares & Schoereder 2001). Number within parenthesis following genera indicate the number of species sampled in the present paper.

	FEEDING INFORMATION	NESTING INFORMATION
Myrmicinae		
Hylomyrma reitteri		genus characteristic of litter-nest and forage
Megalomyrmex sp1	litter omnivores and scavengers	genus with species characteristic of the litter (nest and forage)
Monomorium floricola	true omnivorous (soil or litter dominants)	
Octostruma jheringhi	possible litter omnivores and scavengers or litter specialist predator	characteristic of the litter (nest and forage)
Octostruma rugifera	possible litter omnivores and scavengers or litter specialist predator	characteristic of the litter (nest and forage) b, s
Oligomyrmex sp	litter specialist predators (preys on eggs of several groups of arthrpods)	genus with species characteristic of the litter (nest and forage)
Pheidole (9 species)	litter omnivores and scavengers	l, b, s
Solenopsis (4 species)	litter omnivores and scavengers	genus with species characteristic of the litter (nest and forage) l, f, b, s
Strumygenys prox. perpava	litter specialist predators	characteristic of the litter (nest and forage)
Wasmannia sp	true omnivorous (soil or litter dominants)	
Ponerinae	generalist predators	characteristic of the litter (nest and forage)
Anochetus sp	litter generalist predator (different species of the genera)	
Discothyrea sexuarticulada	litter specialist predator (possible egg predator)	
Ganmptogenys sp1	litter generalist predators (most of species)	b, s
Gnamptogenys striatula		b
Hypoponera (4 species)	litter generalist predator (different species of the genera)	l, b, s
Pachycondyla harpax		
Formicinae		
Brachymyrmex (2 species)	true omnivorous (soil or litter dominants)	characteristic of the litter (nest and forage) r, l, b, s
Camponotus (myrmobrachys) crassus	true omnivorous (soil or litter dominants)	primarily arboreal
Dolichoderinae		
Linepithema sp		

Figure 1 – Relationship between litter ant species richness and total litter weight (F(1, 86)=4.104; p=0.046; r^2=0.046)



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CAPÍTULO 2

Litter ant community dynamics conditioning local species richness and composition

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Running title. Litter ant dynamics and local richness

Abstract. The determination of local species richness is usually attributed to species interactions and to environmental conditions, although the mechanisms by which these factors act upon biodiversity are poorly studied. This paper experimentally tested the hypothesis that the variation of local species richness of litter ants is caused by the dynamics of local immigration and extinction, and that this dynamics is altered by litter structure. We designed an experiment isolating and removing all ant species from litter plots to study immigration and extinction rates to and from these plots along two months. We also collected these litter samples and evaluated the importance of litter structure on the ant community dynamics. We compared species composition before and after species immigration, to analyze which species re-colonize samples of litter without ants. There was no significant extinction in two months, even though litter samples without ants partially recovered species richness in the same time. However, species composition before and after the induced disturbance were different. Litter structure did not influence the above process. Our results showed that local disturbances decreased species richness and changed species composition. Litter may be disturbed in several ways and species richness restoration by immigration occurs gradually, creating patches of different species richness and composition. Such disturbances effects, causing local extinction, confound interactions and microhabitat effects, and may have an important role in community structuring.

Keywords. Biodiversity; Disturbance; Extinction; Formicidae; Immigration; Local Processes; Succession; Tropical Forest

Biodiversity studies up to the middle of the last century emphasized the search for patterns, even though this approach has been changed due to the interest in conservation and management of species rich sites. Conservation interest has led to the search for biodiversity-rich sites, independently of the spatial and temporal patterns involved, such as latitude or altitude patterns. These attempts of synthesis ultimately led to the definition of hotspots as areas of high biodiversity, and consequently with a great conservation interest (Myers et al. 2000).

Despite the unquestionable importance of studying biodiversity patterns, the study of processes determining these patterns is less frequent. The study of such processes must receive more attention because it is necessary to know not only where biodiversity is higher, but also to understand what mechanisms are responsible by its maintenance (DeSouza et al. 2001).

The mechanisms determining biodiversity may act on different spatial and temporal scales, which are usually divided in local, regional, global and historical scales. Ecological processes such as species interactions and small scale disturbances are considered local processes, which interact with processes acting on larger scales to determine how many species will be present in a given site and time (Schluter & Ricklefs 1993).

Forest litter is presently considered one frontier in biodiversity studies because it represents an enormous biodiversity and is believed to shelter several important processes of the forest, such as nutrient and soil dynamics (Copley 2000). An important and abundant fraction of litter arthropod communities is composed by ants (Levins et al. 1973; York 1999), and considerable attention has recently been given to ground-dwelling ant communities, and to factors determining their biodiversity. Local factors, such as competition (McGlynn & KirKsey 2000), microclimate (Torres 1984; Perfecto & Vandermeer 1996; Kaspari & Weiser 2000), litter abundance (Carvalho & Vasconcelos, 1999; Oliver et al. 2000), local disturbance (Kaspari 1996), and predation (Hirosawa et al. 2000) are usually regarded as key factors determining litter ant biodiversity, even though other authors cite factors acting on larger spatial scales (Roth et al. 1994; Wigley & Roberts 1997; Carvalho & Vasconcelos 1999; Vasconcelos 1999; York 2000; Vasconcelos & Delabie 2000).

There is little evidence for the importance of litter abundance (Delabie & Fowler 1995; McGlynn et al. in press) and competition on litter ant communities (Yanoviak & Kaspari 2000; Soares & Schoereder 2001; Soares et al. 2001). On the other hand, there is a hypothesized importance of the dynamics of local communities on biodiversity, including dynamics of immigration and extinction linked to local processes (Levins et al.1973; Soares et al. 2001; Chapter 1).

Disturbance in litter communities is a frequent event, because this microhabitat receives constantly an input of vegetal and animal detritus, and also because this organic material is constantly subject to decomposition and incorporation into soil (Facelli & Pickett 1991). Other sources of litter disturbance may include the presence of army ants and other predators (Hirosawa et al. 2000). The response of litter ant communities to local disturbances may be local extinction or colony migration, and several litter ant species are known to frequently relocate their nests (Byrne 1994; Herbers 1994; Franks & Sendova Franks 2000), but the influence of such processes on local species richness have not been studied yet.

This paper experimentally tested the hypothesis that the variation of litter ant local species richness is caused by the dynamics of local immigration and extinction, and that this dynamics is altered by litter structure.

Material and Methods

Study site

The sampling design was installed in a forest reserve with an area of about 300ha, in Viçosa, Minas Gerais, Brazil (20º 45’S, 42º51’W). The climate is moderate subtropical moist with a rainy season from September to April and dry season from May to August (Golfari 1975). The annual rainfall ranges from 1500 to 2000 mm, average air relative humidity of 80% and temperature ranging from 14 to 26.1 ºC (Castro et al. 1983).

This remnant has suffered periodic exploration due to coffee crops, and other disturbances and it is protected from such disturbances since 1966, when started a process of natural secondary succession. The secondary forest occupies presently most of the reserve area, and we arbitrarily have chosen a forested area to carry out the sampling design (Fig. 1).

Testing the effect of extinction

Fourty-four litter samples of 30cm diameter were isolated with plastic containers 30cm high. The containers were dug 3cm into soil to maintain it at a fixed place. A strip in the superior edge of the container was treated with Tanglefoot®, which avoided ants to get into and out of the sample. Each site remained isolated for two months (February to April), after which the litter was removed and placed for 10 days in modified Berlese funnels to extract the ants. The isolated litter samples were considered treatment (extinction) and were compared by analysis of variance with 48 control samples. These were non-isolated samples of litter, with the same area of treatment and were removed in the same day of isolated samples. Isolation impeded the transit of ants by litter to and from treatment area, and therefore any difference between treatment and control was attributed to local extinction. We expected that, if local extinction occurred in two months, species richness would be smaller in treatment than in control samples, because there would not occur a rescue effect in isolated samples. Furthermore, isolation distinguished between local extinction and emigration, because the ants could not leave the samples.

The ants were sorted, mounted and identified to genus (Bolton 1994) and, whenever possible, to species with the help of Ivan C. do Nascimento (UFV) and Dr. Jacques H. C. Delabie (CEPLAC).

Testing the effect of immigration

Fourty samples with 30cm diameter of litter were removed in January, receiving a code number relative to their sampling site. These samples were placed in Berlese funnels for three days, and then manually sorted to remove all the ants present (initial species composition). These litter samples were returned to the forest, in the beginning of February, and placed exactly in the same place from where they were taken. After two months the samples were re-collected, and placed for 10 days in Berlese funnels to extract the ants (final species composition). The ants from initial and final samples were sorted, mounted and identified to genus (Bolton 1994) and, whenever possible, to species with the help of Ivan C. do Nascimento (UFV) and Dr. Jacques H. C. Delabie (CEPLAC).

Because number of species in the sample returned to the plots was zero, number of species found after two months was attributed to immigration. The final number of species was compared by analysis of variance with control samples, as described above. To analyze species composition in the initial and final samples we compared the species before and after immigration, dividing the species into three classes: (1) species that were present in the initial samples and absent in the final samples; (2) species that were absent in the initial samples and were found in the final samples; and (3) species present in both samples. Class one brings few information on if re-colonizing species were already present in the initial samples or if re-colonization is based on species that are locally new, and therefore we did not use this class in the analysis. We compared the classes two and three above through analysis of variance with Poisson errors, corrected for overdispersion (Crawley 1993). If species composition in the samples was altered by disturbance, class two would present higher species richness than class three, i.e., most re-colonizing species would be different from the original local set of species.

Litter structure

In all samples the litter was dried, sorted into four fraction (leaves, branches, fruits+seeds and detritus) and weighted. The effect of total litter amount on ant species richness, both for extinction and immigration, was tested through linear regression, using the number of local extinction or immigration as response variable and total litter weight as explanatory variable.

The effect of each fraction weight was also tested through linear regression, using the number of local extinction or immigration as response variable and the weight of each fraction as explanatory variables. The complete model was adjusted and, if the model was significant, each explanatory variable was removed in turn, verifying significant changes in deviance (Crawley 1993).

Besides the importance of each fraction on extinction or immigration, the combination of these fractions in the sample may also be important. If there are ant species specialists in each litter fraction, the presence of more fractions with similar weights in the sample would increase such processes, because there would be resources for each group of litter fraction specialists. Local heterogeneity was estimated by the coefficient of variation (CV) of the fraction weights. Samples with high CV have at least one fraction with more weight than the others, favoring the group of ants that are specialists in that fraction, and these samples were considered less heterogeneous. Conversely, samples with low CV were considered more heterogeneous, because the fraction weights would be more similar, and all litter resources would occur in similar amounts. The effect of heterogeneity on local species richness was tested through linear regression, using the number of local extinction or immigration as response variable and CV as explanatory variable.

In all analyses the used models were checked by analyses of residuals and the models were criticized accordingly.

Results

We collected 63 species in all litter samples, belonging to 6 subfamilies (Table 1). In control plots there were 34 species (mean=3.1; SD=1.77) and in isolated samples, used for testing extinction, 32 species (mean=2.9; SD=1.82). The samples where ants were removed, used for testing immigration, had 34 species and after two months accumulated 28 species (mean=2.3; SD=1.60).

Isolated litter samples did not differ in species richness from the control samples (F(1, 88)=0.414; p=0.52), showing that extinction, if happened, did not affect species richness. After two months, litter samples with all ants removed recovered their species richness only partially, differing from control samples (F(1, 86)=5.157; p=0.026; Fig. 2). The number of species present both in initial and final samples was significantly lower than the number of species that were absent in the initial samples (Poisson errors; χ^2=14.146; df=1; p=0.0002; Fig. 3), showing that species composition was affected by disturbance.

The importance of litter structure was not tested for extinction, because we did not detect significant extinction. Litter structure did not influenced ant local immigration, neither for its total weight (F(1, 38)=0.004; p=0.95), weight of the fractions (F(4, 35)=1.212; p=0.323), nor for heterogeneity (F(1, 38)=1.156; p=0.289).

Discussion

We did not observed changes in species richness between isolated and control plots, and there are several possible explanations for that pattern, in addition to the actual absence of extinction in two months. The first explanation may be linked to migration of litter ants, because to our purposes local extinction may also be nest relocation, or colony movement, which is very common in these ants (Herbers 1994; Byrne 1994; Franks & Sendova Franks 2000). Since we have impeded the ant emigration any colony movement would be restricted by container limits. This restriction did not, however, increased colony mortality in the sample area, probably because this area has resources enough to maintain species richness.

We isolated the litter plots to avoid colony movements to and from the sample. This isolation may also have prevented surface disturbances, such as the effect of predators that would enter the sample in the absence of the treatment, such as army ants and other arthropods, which effect on litter ant communities is high (Hirosawa et al. 2000). The plastic container also avoided disturbances, such as large animals movements, which would also have effects on individuals and species occurrence in the plots. Predation and disturbance prevention may have decreased extinction in the isolated samples, causing therefore the observed pattern.

Litter ants may also move through the soil (J. H. C. Delabie, personal information). There is few information on biology of tropical litter ants, but the information available for some species shows that several species have already been collected in soil and litter. Therefore, our isolation may have prevented movement through litter, but did not avoid the soil movements, allowing rescue effects of the ant fauna inside the plots, even if extinction really has happened. Furthermore, if the ants could move through the soil, they would been able to use resources outside the plot.

The last explanation for the absence of isolation effects on litter ant communities is a change in species composition. Accordingly, it is possible that some ant species went to extinction during the experiment, but these species may have been replaced by other species that came from the soil. If there is a difference in species composition between litter and soil, there would also be a change in species composition inside the plot, which would be occupied more by soil than litter species.

Two months were not time enough for the litter ant communities to reconstitute their species richness (Fig. 2), i.e., immigration occurred but was not sufficient to recover the original community. Furthermore, there were detectable effects on species composition, which was different from the original condition (Fig. 3). Two different processes may lead to the above result. First, the results suggest that species richness restoration did not occur from soil species that were foraging in the litter. If this happened we would have removed only some workers, but the colony would still have remained in the soil. When the litter was replaced the same soil ant species would start to forage in the litter and few changes in species composition would have been noticed. Even though this mechanism may have occurred for some ant species that nest in the soil and forage in the litter (Table 1), probably it is not prevailing for litter ant species. Secondly, it must be considered that litter removal might also affect soil nesting species, impairing re-colonization of litter by soil species.

Litter structure and heterogeneity did not influenced this re-colonization. This result was expected, because we have not noticed a strong relationship between litter parameters and species richness (Chapter 1), which agrees with other authors (Delabie & Fowler 1995; McGlynn et al. in press). Furthermore, if species colonization was dependent on litter parameters we would not find the differences in species composition before and after re-colonization, because the species would search for specific microhabitat conditions. Ant species re-colonization of litter is then independent of litter structure and local heterogeneity, as well as of local soil species.

Species composition in litter ant communities may change along time, following a small scale ecological succession. This succession may be either directional or based on lottery models (Begon et al. 1996). If the succession is directional, then there are some species that depend on disturbance occurrence, because they would be pioneer species that occur only after disturbance and in the absence of dominant species. Along succession these species would be substituted by other species more adapted to the conditions of middle and final succession stages. Pioneer species would have to leave the patch in the presence of dominant species and go to other patches in earlier succession stages. This hypothesized mechanism would also explain the high migration frequency of litter ant species.

However, dominance hierarchies are not necessary to explain species persistence in litter ant communities, which may follow a lottery model of succession. Such models assume that species are both good colonizers and similar competitors. The pattern of litter ant species richness may arise if these species colonize litter patches at random, and the patches are also randomly created by disturbance, such as the passage of predatory ants (Hirosawa et al. 2000), physical perturbations by large animals and tree fall.

To determine which succession model is correct for litter ant communities we would have to compare species composition in treatment and control samples. In a directional succession we would expect that species composition in the treatment plots would be more similar, because all samples were placed in the field at the same time, and suffered equal intensity disturbances. On the other hand, if the succession occurs by lottery models, we would expect that the treatment samples would be as dissimilar among them as with the control plots.

Concluding, our results pointed out that local physical litter parameters are not important conditioning factors influencing the dynamics of litter ant communities. The local species richness and composition are probably determined by a complex dynamics of local disturbances in different time intervals and intensity, which decreases species richness and changes species composition. Immigration to local disturbed sites partially recover ant species richness, but with a change in species composition. Litter ant communities, hence, would be formed by a mosaic of patches in different successional stages, with different local ant communities.

Interestingly, the mechanism we propose to explain species richness variation in litter ant communities also occurs in spatial scales very different than we worked, as is the case of dynamics of forest patches (e.g. Connell 1978). This mechanism needs further experimental tests, such as removal experiments followed daily during extensive periods, to reveal completely the effect of local disturbances on local community structure.

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Table 1 – Species of ants sampled in Viçosa, MG, Brazil, and respective biological information on their nesting and foraging habits. The numbers in parentheses refer to (1) Soares & Schoereder 2001; (2) Fowler & Delabie 1995; (3) Delabie & Fowler 1995; and (4) Delabie et al. 2000.

Myrmicinae	
Acanthognatus stipulosus	Genus of litter predators
Apterostigma grupo complexo pilosus sp	Genus of litter or soil-fungus growers (4)
Crematogaster sp	*C. ellevans*: Soil, genus of arboreal dominants, incidentally foranging the floor and litter (4)
Hylomyrma reitteri	Genus characteristic of litter-nest and forage (4)
Hylomyrma sp1	
Megalomyrmex (3 species)	*M. goeldii:* Rolled leaves, branch and soil (1)
Monomorium floricola	Litter and soil (3), genus characteristic of litter-nest and forage, soil or litter dominants (4)
Octostruma jheringhi	Litter and soil (3)
Octostruma rugifera	Branch and soil (1)
Oligomyrmex sp	Genus characteristic of litter-nest and forage (4)
Pheidole (10 species)	Litter omnivores and scavengers
Pyramica denticulata	
Pyramica subedentata	
Rogeria sp	Genus characteristic of litter-nest and forage (4)
Solenopsis (5 species)	*S. geminata*: Litter and soil (2), genus characteristic of litter-nest and forage, soil or litter dominants (4)
Stegomyrmex vizottoi	Genus characteristic of litter-nest and forage (4)
Strumygenys sp1	*S. louisianae:* Branch (1)
Strumygenys sp prox perpava	Genus characteristic of litter-nest and forage (4)
Wasmannia sp	*W. auropunctata*: Litter and soil (2, 3), Genus characteristic of litter-nest and forage, soil or litter dominants (4)
Formicidae	
Brachymyrmex (4 species)	Genus characteristic of litter-nest and forage, soil or litter dominants (4)
Camponotus sp1	*C. trapezoideus:* Branch, *C. cingulatus:* Litter and soil (2, 3), Genus characteristic of litter-nest and forage, soil or litter dominants (4)
Camponotus sp3	
Camponotus (myrmobrachys) atriceps	
Camponotus (myrmobrachys) crassus	
Camponotus (myrmaphaenus) sp	
Myrmelachista sp	
Cerapachyinae	
Cerapachys splendens	Genus characteristic of litter-nest and forage (4)

Ecitoninae	
Labidus coecus	Litter and soil (3)
Dolichoderinae	
Dolichoderus attelaboides	Soil (3)
Linepithema sp	*L. humile*: Litter and soil (3)
Ponerinae	Genera characteristic of the litter (nest and forage)
Amblyopone lurilabes	Litter (1)
Anochetus sp	*A. mayri*: Litter and soil (3)
Discothyrea sexarticulata	Litter specialist predator-possible egg predator (4)
Gnamptogenys sp1	
Gnamptogenys striatula	Branch (1), litter and soil (3)
Hypoponera foreli	Branch and soil (1, 2)
*Hypoponera (*6 species)	
Odontomachus meinerti	*O. minutus*: litter, O. *haematodus:* litter and soil (3)
Pachycondyla harpax	Litter and soil (3)
Pachycondyla striata	

Figure 1 – Schematic view of the sampling design.

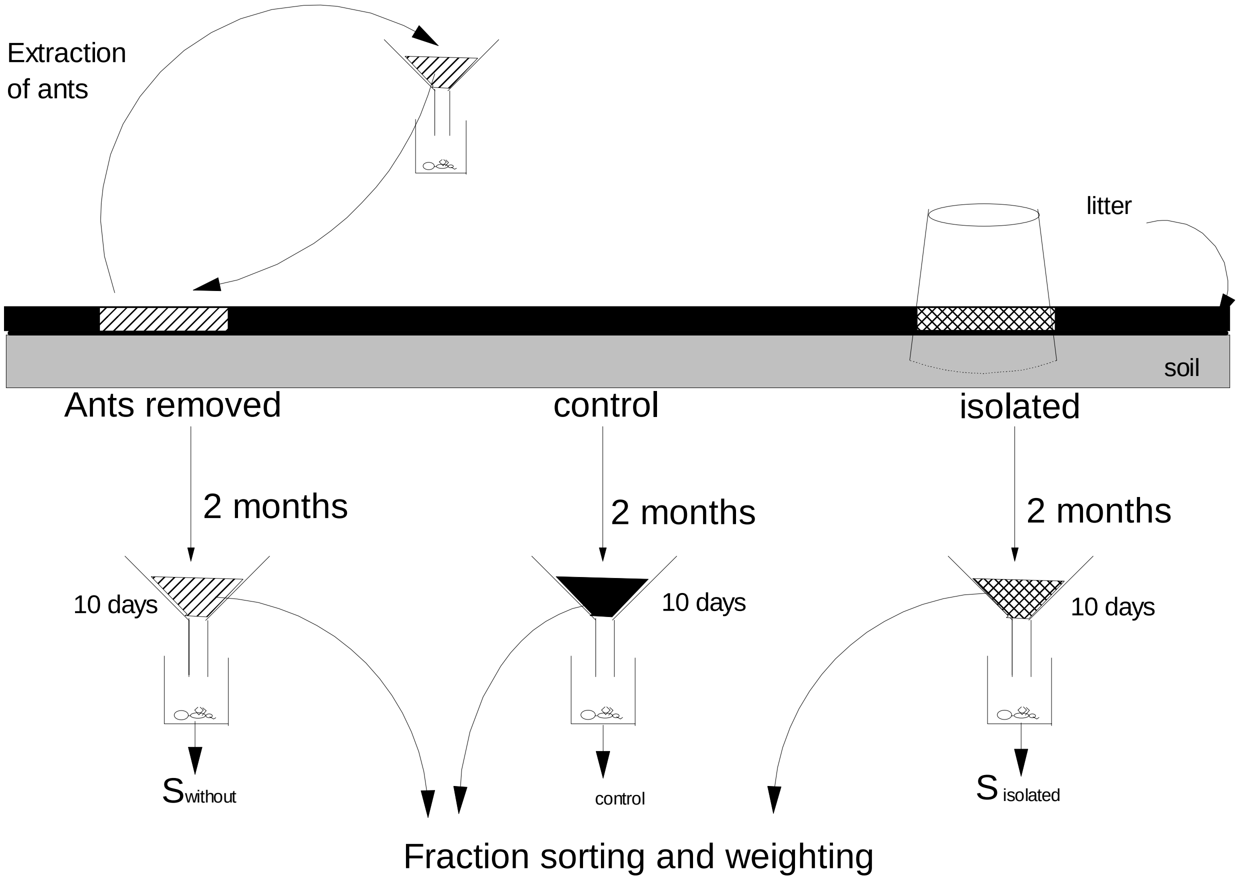

Figure 2 – Local ant species richness in control (litter sample without management) and in immigrants plot (litter sample two months after ant removal). The difference between treatments is significant (ANOVA: F(1, 86)=5.157; p=0.026).

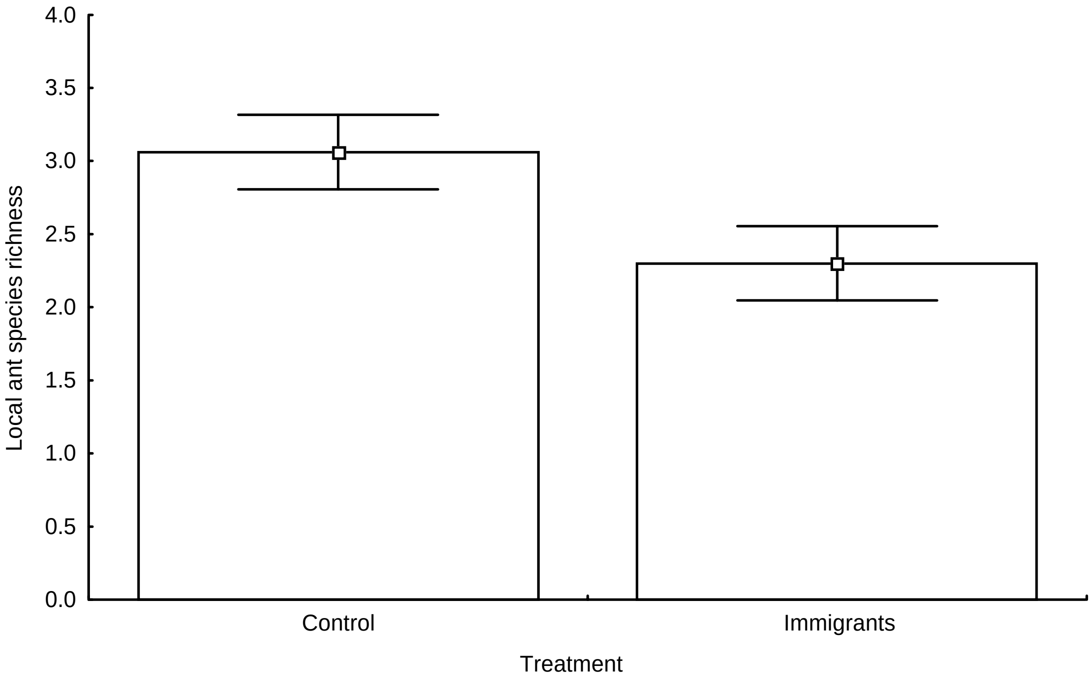

Figure 3 – Changing of local ant species composition in the treatment with ant removal. The ants found after two months may be exclusive of these samples (exclusive) or may have been found before ant removal (common). These numbers were significantly different (ANOVA with Poisson errors; χ^2=14.46; df=1; p=0.0002), showing that ant species composition changed after species re-colonization.

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CONCLUSÕES GERAIS

Os resultados do primeiro capítulo apresentam uma relação positiva estatisticamente significativa entre o peso seco da serapilheira e a riqueza local de espécies de formigas. O peso da serapilheira é uma medida indireta de disponibilidade de recursos, uma vez que pode ser usada diretamente como local para nidificação ou refúgio (Hölldobler & Wilson 1990; Andrew et al. 2000). A abundância de serapilheira pode influir indiretamente sobre a riqueza local de espécies porque maiores quantidades de serapilheira devem conter recursos como fungos, matéria em decomposição, frutos, sementes e artrópodes que servem como presas (Levings & Windsor 1984).

A quantidade de serapilheira altera o microclima e por isso também pode definir a riqueza local estabelecendo condições adequadas ou não para a sobrevivência de determinadas espécies em um local (Torres 1984). Condições microclimáticas também podem alterar as interações entre as espécies (Cerdá et al. 1997; Perfecto & Vandermeer 1996; Levings & Windsor 1984; Delabie & Fowler 1993; Collevatti & Schoereder 1995; Levings 1983) afetando a riqueza local indiretamente.

O chamado “efeito de área” (Rosenzweig 1995), pode ser responsável por este resultado porque a variação encontrada no peso da serapilheira indica diferenças na estrutura e/ou volume da amostra. Assim, maiores volumes de serapilheira podem conter mais indivíduos e consequentemente mais espécies e o mesmo raciocínio pode ser tomado em relação a quantidade de recursos.

Em relação à composição da serapilheira (peso das frações) as análises não mostraram maior importância de nenhuma das frações. Estes resultados podem ser explicados pela capacidade das espécies de formigas de serapilheira utilizarem diferentes recursos (Delabie et al. 2000). Não foram encontrados efeitos da heterogeneidade da serapilheira sobre a riqueza local de espécies de formigas. É possível que a heterogeneidade atue em escalas mais amplas do que abordado nesta tese (Koltliar & Wiens 1990). Entretanto é interessante notar que a ausência do efeito da heterogeneidade é uma evidência de que a escala utilizada nesta tese é apropriada para o estudo de processos locais

O estudo da dinâmica da comunidade não mostrou um efeito significativo das extinções sobre a riqueza local num período de dois meses. Os resultados evidenciaram que a dinâmica das espécies de serapilheira parece ser mais afetada pelos movimentos das espécies do que pela extinção local.

O experimento com recolonização mostrou que há migração para áreas onde houve remoção de espécies, entretanto dois meses não foi um período de tempo suficiente para que tenha sido recuperada a riqueza local encontrada antes do distúrbio. A recolonização foi independeste da abundância, composição e heterogeneidade da serapilheira, reforçando os resultados do primeiro capítulo.

A composição da comunidade após a migração também foi alterada ou seja, as espécies que recolonizam uma área não foram as mesmas que habitavam aquele local antes do distúrbio. Este fato mostra que perturbações em pequena escala podem ser um fator importante para a estrutura desta comunidade. É provável que após um distúrbio a comunidade mude ao longo do tempo. Desta forma é possível que a comunidade de serapilheira seja formada por um mosaico de manchas em diferentes estágios de sucessão. Estudos sobre a composição das espécies que recolonizam uma área após uma perturbação deverão mostrar o padrão de sucessão e fornecerão informações importantes sobre o mecanismo pelo qual a dinâmica destas comunidades determina a riqueza local.

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