TATIANNE GIZELLE MARQUES SILVA

DIVERSIDADE DE FORMICIDAE EM FLORESTAS ESTACIONAIS DECÍDUAS EM DIFERENTES ESCALAS TEMPORAIS E ESPACIAIS

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

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SUMÁRIO

RESUMO

SILVA, Tatianne Gizelle Marques, D.Sc., Universidade Federal de Viçosa, fevereiro de 2011. **Diversidade de formicidae em florestas estacionais decíduas em diferentes escalas temporais e espaciais**. Orientador: José Henrique Schoereder. Coorientadores: Mário Marcos do Espírito Santo, Carlos Frankl Sperber e Ricardo Ildefonso de Campos.

Os processos ecológicos influenciam a diversidade de espécies em diferentes escalas espaciais e temporais. Dentro de cada escala (espacial ou temporal), diferentes fatores atuam sobre a diversidade dependendo da dimensão das escalas. Por exemplo, interações entre espécies (escala espacial local) e sazonalidade (escala temporal ampla). O objetivo dessa tese foi investigar os processos ecológicos que determinam a riqueza de espécies de formigas das Florestas Estacionais Decíduas (FEDs) em diferentes escalas espaciais e temporais. Primeiro identificamos os processos ecológicos que governam a diversidade de formigas em diferentes escalas de tempo (sucessão ecológica e variação estacional), com a finalidade de entender a relação causa-efeito dos padrões de diversidade encontrados no estudo. Nossos resultados indicaram um aumento da riqueza total de espécies de formigas nos estágios mais avançados de sucessão. Na análise de cada microhabitat, a riqueza de formigas arbóreas e epigéicas não mudaram com o avanço da sucessão. Entretanto, a composição da comunidade de formigas destes dois microhabitats diferiu entre estágios sucessionais. Para o microhabitat hipógeico, o número de espécies de formigas foi maior nos estágios intermediário e tardio de sucessão. A porosidade do solo e a riqueza de espécies de plantas explicam este aumento da riqueza de espécies de formigas hipogéicas. Além disso, a composição de formigas hipógeicas também diferiu entre os estágios sucessionais. Adicionalmente, o número total de espécies de formigas foi maior na estação seca e a composição de espécies de formigas não mudou entre as estações. Portanto, tanto a sucessão quanto a sazonalidade influenciam a riqueza de espécies de formigas nas FEDs. Finalmente, o segundo capítulo da tese tem como objetivo determinar se há processos não-aleatórios influenciando o padrão observado de diversidade de formigas, como também determinar em qual escala estes processos podem ser mais influentes. A partição aditiva da diversidade foi usada para separar a diversidade regional de formigas (γ) nos componentes de diversidade dentro (α) e entre (β) amostras. A partição espacial da diversidade de espécies de formigas distribuída entre as regiões do Brasil mostra que cada ponto de coleta (α) retém uma diversidade média maior que o esperado pela hipótese nula. As diversidades β_2 observada (entre fragmentos) e β_3 observada (entre regiões) foram maiores que as esperadas pelo acaso. Aplicando a análise de partição para cada região separadamente, as diversidades β_2 observadas entre os fragmentos (FED e entorno) de todas as regiões do Brasil foram maiores que as esperadas pela hipótese nula. A análise de partição nos ajudou a identificar as fronteiras espaciais onde os processos não-aleatórios devem interagir e diferenciar desproporcionalmente a diversidade de formigas. Portanto, com base na composição de espécies e padrões de diversidade que encontramos em nossos estudos, enfatizamos a importância da preservação de áreas remanescentes e secundárias de FEDs.

ABSTRACT

SILVA, Tatianne Gizelle Marques, D.Sc., Universidade Federal de Viçosa, February 2011. **Diversity of formicidae in tropical dry forest at different temporal and spatial scales**. Advisor: José Henrique Schoereder. Coadvisors: Mário Marcos do Espírito Santo, Carlos Frankl Sperber and Ricardo Ildefonso de Campos.

Ecological processes influence species diversity at different spatial and temporal scales. Within each scale (spatial or temporal) different factors act on diversity depending on the size of the scales. For example, interactions between species (local spatial scale) and seasonality (large time scale). The purpose of this thesis was to investigate the ecological processes that determine the ant species richness in Tropical Dry Forest (TDFs) in different spatial and temporal scales. First we identified the ecological processes that govern the ant diversity in different time scales (ecological succession and seasonal variation), in order to understand the cause-effect patterns of diversity found in the study. Our results indicated an increase in the total richness of ant species in the later stages of succession. In the analysis of each microhabitat, the richness of arboreal and epigaeic ants did not change with the advancing of succession. However, the composition of ant communities of the two microhabitats differed among successional stages. For the hypogaeic microhabitat, the number of ant species was higher in intermediate and late stages of succession. The porosity of the soil and the richness of plant species explain this increase in species richness of hypogaeic ants. Moreover, the composition of hypogaeic ants also differed among the successional stages. Additionally, the total number of ant species was higher in the dry season and the composition of ant species did not change between seasons. Therefore, both the succession and the seasonality influence the ant species and richness in the TDFs. Finally, the second chapter of the thesis aims to determine whether there are nonrandom processes influencing the observed pattern of ant diversity, but also to determine at what scale these processes can be more influential. The additive partitioning of diversity was used to separate the regional ant diversity (γ) into components of diversity within (α) and between (β) samples. The spatial partitioning of ant species diversity distributed among the regions of Brazil shows that each collection point (α) holds a mean diversity larger than the one expected by the null hypothesis. The β_2 diversities observed (between fragments) and β_3 observed (between regions) were higher than expected by chance. Applying the partition analysis for each region separately, the β_2 diversities observed between fragments (TDF and surrounding areas) from all regions of Brazil were higher than the ones expected by the null hypothesis. The partition analysis helped us to identify the spatial boundaries, where the non-random processes must interact and differentiate disproportionately ant diversity. Therefore, based on species composition and diversity patterns that we found in our studies, we emphasize the importance of preserving the remaining and secondary areas of TDFs.

INTRODUÇÃO GERAL

O entendimento das mudanças espaciais e temporais na biodiversidade é um dos temas centrais da ecologia e da biologia da conservação (Magurran, 1988; Ricklefs, 2004), uma vez que os fatores que determinam a diversidade de espécies de uma determinada assembleia são altamente dependentes da escala nos quais são examinados (Ricklefs 1987, Caley & Schluter 1997). De fato, a variação da diversidade nessas diferentes escalas é bem documentada em diferentes grupos de organismos (Wolda 1978, DeVries et al. 1997, 1999; Ribeiro et al. 2008). Dessa forma, estudos de estrutura de comunidades devem levar em conta processos que atuam tanto em pequena escala (*e.g.* interações) quanto em escalas maiores (*e.g.* especiação e extinção) para a determinação da diversidade local de espécies.

A riqueza de espécies pode ser influenciada por processos que agem em diferentes escalas temporais (Ricklefs & Schluter 1993, Godfray & Lawton 2001). Numa escala de tempo ecológico, alguns estudos abordam os efeitos das alterações da paisagem, causados pelos distúrbios antrópicos, sobre a comunidade biológica (e.g. Amaral & Meyer, 1999, Huntingford et al. 2000, Liddel, 2001, Matsinos & Troumbis 2002, Zavala & Zea 2004, Neves et al. 2010). Um método amplamente empregado no estudo de áreas que possuem idades pós-distúrbio diferentes é a cronosequência. Segundo Walker et al. (2010), cronosequência é um conjunto de áreas formadas a partir do mesmo material de origem ou substrato que diferem no tempo desde que foram formadas. Este conceito aplica-se a áreas em processo de sucessão ecológica. Entretanto, algumas críticas têm sido formuladas sobre o uso da cronosequência, uma vez que cada área de uma cronosequência deve ter a mesma história de componentes bióticos e abióticos. A premissa anterior é quase impossível de ser alcançada e provada, especialmente nos trópicos, onde existe um elevado grau de heterogeneidade ambiental. Muitos estudos que utilizam cronosequências são apoiados por considerarem locais com características similares de tipo de solo, topografia e/ou história do uso da terra (Lebrija-Trejos et al. 2008, Vargas et al. 2008). Portanto, com o auxílio deste método, podemos elucidar padrões de diversidade e analisar os processos que determinam a riqueza de espécies em uma ampla escala de tempo (a sucessão ecológica).

Numa escala de tempo mais fina, as mudanças sazonais na vegetação podem causar respostas mais drásticas nas comunidades animais associadas do que mudanças de longo-prazo (Lambin 1996), como a sucessão ecológica. Os efeitos da sazonalidade sobre a floresta, como por exemplo, mudança na disponibilidade de recursos, umidade e temperatura, afetam os padrões fenológicos das plantas e, consequentemente, a abundância, riqueza e composição de espécies da fauna (Janzen 1984, Basset et al. 2003, Cuevas-Reyes et al. 2006). O padrão encontrado comumente em estudos realizados em florestas tropicais úmidas é o aumento do número de espécies na estação chuvosa, devido à maior disponibilidade de recursos e heterogeneidade do habitat, além de melhores condições microclimáticas (Tauber et al. 1998, Guedes et al. 2000, Neves et al. 2010). Entretanto, alguns estudos encontraram resultados diferentes para florestas sazonais, evidenciando uma maior riqueza de espécies na estação seca (Gove et al. 2005, Delsinne et al. 2008).

Além da influência dos processos ecológicos nas diferentes escalas temporais, a diversidade também pode ser influenciada por processos que agem em diferentes escalas espaciais. Whittaker (1960) foi um dos primeiros pesquisadores a reconhecer a relação entre a diversidade e a escala espacial, propondo o conceito de partição da diversidade em componentes alfa, beta e gama. Tal estudo propôs uma relação multiplicativa entre os três componentes da diversidade, na qual a diversidade regional (γ) seria obtida pela multiplicação dos componentes α e β ($\gamma = \alpha*\beta$). Para riqueza de espécies deste modelo, o número de espécies é a unidade de α, enquanto a diversidade β teve seu cálculo proposto através de diferentes equações, inclusive podendo ser expresso pelo índice de similaridade entre as diversidades α. Já na partição aditiva, demonstrada analiticamente por Lande (1996), a diversidade α em uma dada escala é a soma da diversidade alfa e beta da escala imediatamente inferior (ou seja, $\alpha_2 = \alpha_1 + \beta_1$). Tanto a diversidade α quanto a β possuem a mesma unidade, número de espécies. A partição aditiva da diversidade tem sido amplamente utilizada em estudos que visam elucidar os padrões de distribuição da biodiversidade em escalas espaciais múltiplas. Com esta análise é possível determinar o nível espacial que apresenta a principal fonte de diversidade, o que auxilia a direcionar esforços para a conservação ambiental (Veech et al. 2002, Gering et al. 2003).

Entre as florestas sazonais está a Floresta Estacional Decídua (FED), que mantém um alto nível de diversidade de espécies e endemismo (Sánchez-Azofeifa et al. 2005, Gillespie 2005). Atualmente, muito deste tipo de vegetação consiste de fragmentos, considerados refúgios da flora e fauna, que se encontram em diferentes localizações da região Neotropical (Prado & Gibbs 1993, Prado 2000). Nas Américas, as FEDs já perderam 66% da sua extensão (Portillo-Quintero & Sánchez-Azofeifa 2010). Esta perda de área pode ser devido a estas florestas serem historicamente exploradas para a prática da agricultura e ocupação humana (Ewel 1999; Sánchez-Azofeifa et al. 2005; Pennington et al. 2006). Além disso, existem poucas áreas protegidas de FED (Portillo-Quintero & Sánchez-Azofeifa 2010), o que evidencia a necessidade de se conhecer a diversidade biológica presente nestas florestas, assim como os fatores que estão estruturando as comunidades.

Entre os vários organismos que podem ser usados em estudos de diversidade, as formigas são consideradas um excelente modelo, pois ocupam vários níveis tróficos e contribuem substancialmente no funcionamento do ecossistema. Além disso, a diversidade de formigas de uma região pode ser estruturada por fatores que agem em diferentes escalas espaciais e temporais (Ribas et al. 2003, Neves et al. 2010). Sendo assim, as formigas são uma ferramenta de enorme potencial para a identificação de processos que estão governando a riqueza de espécies em diferentes escalas.

Desta forma, a presente tese investigou os processos ecológicos que determinam a riqueza de espécies de formigas das Florestas Estacionais Decíduas em diferentes escalas temporais e espaciais. A tese se encontra dividida em dois capítulos, que foram escritos na forma de artigos. No primeiro capítulo pretendemos identificar os processos que governam a diversidade de formigas em diferentes escalas de tempo (sucessão ecológica e variação estacional), com a finalidade de entender a relação causa-efeito dos padrões de diversidade encontrados no estudo. O segundo capítulo teve como objetivo identificar em qual escala espacial processos não-aleatórios determinam a maior diversidade de formigas, o que nos permite apontar os possíveis processos reguladores da diversidade biológica e traçar estratégias de conservação.

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CAPÍTULO 1

Ant community structure in a secondary Tropical Dry Forest: the role of ecological succession and seasonality

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ABSTRACT

This study identified the main biological mechanisms that govern the diversity of ants on different time scales (ecological succession and seasonal variation) to understand the dynamics and the structure of ant communities. Ants were sampled in 15 permanent plots distributed in to early, intermediate and late stages of succession (five plots per stage) at the Parque Estadual da Mata Seca, Minas Gerais, Brazil. In each of the five plots, five sampling points were selected from each other. At each sample point, unbaited pitfall traps were installed in hypogaeic, epigaeic and arboreal microhabitats. We collected 95 ant species from 26 genera. Our results indicated that there was an increase in the total ant species richness in advanced (intermediate and late) stages of succession. We also observed that the ant communities were segregated between successional stages. For the arboreal and epigaeic microhabitat, the ant species richness did not change with succession progression, but the composition these two microhabitats differed among successional stages. Differently from the arboreal and epigaeic ants, the hypogaiec ant species richness was higher in the intermediate and late stages of succession and the composition of hypogaeic ants differed among the successional stages. Additionally, the total number of ant species was higher in the dry season, whereas the composition of ant species did not change between seasons. A considerable fraction of the ant community was observed only during advanced stages of succession, demonstrating the importance of secondary habitats in maintaining biodiversity.

Key-words: dry forest; seasonal variation; species composition; species richness; successional change.

SPECIES DIVERSITY COULD BE INFLUENCED BY PROCESSES ACTING AT DIFFERENT SPATIAL AND TEMPORAL SCALES (Ricklefs & Schluter 1993, Godfray & Lawton 2001). Spatial scales have received increased attention in the analysis of the relationship between biodiversity and changes in landscape structure (Ribas *et al.* 2003, Kalacska *et al.* 2004) rather than the effects of time scales. This shift in focus occurred because the variation in the number of species in a landscape depends on the ecological processes that operate on multiple time scales (Lambin 1996). Ecological succession and seasonality are processes that occur in different time scales and can influence the species diversity of a forest in different ways.

Tropical Dry Forests (TDFs) have been subject to intense and constant depletion because they are historically targeted for agriculture and human occupation (Sánchez-Azofeifa *et al.* 2005, Pennington *et al.* 2006). These factors can increase the area of TDFs that is in the ecological succession process. Two basic models of ecological succession have been described: communities controlled by dominance and communities controlled by foundation. In the model where communities are controlled by dominance, the altered habitat will initially be colonised by pioneer species that are later replaced by intermediate and climax species due to the niche requirements of the species or through competition, which is altered throughout the succession. In this model, there is directional succession, and the species composition in the final stage is predictable (Dauber & Wolters 2004, 2005). In communities governed by the foundation model, some species may colonise the altered environment while inhibiting, facilitating, or tolerating the establishment of other species. If the early colonisers inhibit the establishment of other species, the community composition will remain the same throughout the succession process. This model is typically called the lottery model (Yu *et al.* 2001). Conversely, if the initial species facilitate or tolerate the replacement of species, there will be a change in the composition of species in the area.

The seasonal changes that occur in the structure of TDFs influence different groups of animals and constitute another important temporal process (Tauber *et al.* 1998, Vâlcu 2006). The main structural change of this ecosystem results from high foliar deciduousness, which is caused by a prolonged dry season and restricts the productivity of plants to the 3-5 months per year when rainfall is highly concentrated (Sánchez-Azofeifa *et al.* 2005). The seasonality of this forest affects the phenological patterns of plants as well as the abundance, richness and composition of the fauna species (Janzen 1984, Cuevas-Reyes *et al.* 2006). According to Gove *et al.* (2005), who studied a Mexican TDF, the arboreal ant richness increased in the wet season. In studies conducted in a Brazilian TDF, the arboreal ant species richness did not differ between seasons, but the abundance and richness of beetle species in the Scarabaeidae family were higher in the wet season, and the composition of ant and beetle species changed between the seasons (Neves *et al.* 2010a, b).

Among the various organisms that could be used in diversity studies, ants are considered an excellent model because they are highly abundant, diverse and have a wide geographical distribution (Underwood & Fischer 2006). Moreover, ants occupy multiple trophic levels and contribute substantially to the ecosystem functioning (Hölldobler & Wilson 1990, Jouquet *et al.* 2006). In addition, the diversity of ants has been positively related to habitat complexity because the ant species richness increases with habitat heterogeneity and the availability of resources in tropical forests (Ribas *et al.* 2003, Armbrecht *et al.* 2004, Ribas & Schoereder 2007). Furthermore, the composition of the arboreal ant community changes along successional stages (Neves *et al.* 2010b). For these reasons, ants can be used as indicators of the natural regeneration of the forest after disturbances (Neves *et al.* 2010b).

In this study, we intended to understand the dynamics and the structure of the ant communities on different time scales (ecological succession and seasonal variation). On the time scale for ecological succession, we tested the following hypotheses:

(1) The succession dynamics are controlled by dominance. Thus, the ant species richness is higher in more advanced stages of succession, possibly due to the competitive exclusion of pioneer species by specialist species, leading to a shift in community composition.

(2) The succession dynamics are controlled by the foundation. In this model, the ant species richness would remain constant, species would only be replaced, and the composition of ant species may or may not change during the successional stages.

We measured variables that could estimate the availability of resources and habitat conditions for the ant communities in order to identify factors that could explain the diversity patterns found within the succession models.

On the time scale of seasonal variation, we tested the following hypothesis:

(3) The ant species richness is higher during the dry season, and the composition of ant species changes between seasons.

METHODS

STUDY AREA AND SAMPLING DESIGN.—The study was carried out at the Parque Estadual da Mata Seca (PEMS), a fully protected conservation area that was established by the expropriation of four farms in 2000. The park is currently managed by the Instituto Estadual de Florestas (IEF). The PEMS has an area of 15,466.44-ha and is located in the middle São Francisco valley in the municipality of Manga, Minas Gerais (14°48'36" – 14°56'59"S and 43°55'12" – 44°04'12"W). The original vegetation of the park is TDF, which is dominated during the dry season by trees that are 90-95% deciduous (May-October) (Pezzini *et al.* 2008) and grow on flat, nutrient-rich soil (IEF 2000). The climate is considered tropical semi-arid (Köppen classification) and is characterised by a pronounced dry season during the winter. The region's average temperature is 24.4ºC

(Antunes 1994), and the mean annual precipitation is 818 ± 242 mm (Madeira *et al.* 2009). The main economic activities in the PEMS area before the expropriation of the farms were the cultivation of beans and maize as well as keeping livestock. Approximately 1525-ha (15%) of the PEMS are abandoned pastures in different stages of succession (IEF 2000).

In January 2006, 15 plots, each with an area of 20 x 50 m (0.1-ha each), were installed in forest patches inside the PEMS. These plots were undergoing early, intermediate or late successional stages (five plots for each stage), as classified by the history of the land use (*i.e.*, the time since the land was abandoned) and by the vertical (tree height, number of forest strata) and horizontal (density of trees) structures in the vegetation areas (see Madeira *et al.* 2009, Neves *et al.* 2010a, b for detailed descriptions of these stages). Plots from the same regeneration stage were located in a sequence and ranged 0.2-1.0 km from each other. All of the plots were located along a 7 km transect encompassing all stages, and were placed inside an old farm in areas where the land was managed similarly over the past 30 years, when the property belonged to the same owner. The plots had similar topographical, soil and microclimate characteristics, which reduced the variation in physical conditions that could affect the succession process and chronosequence studies (Vargas *et al.* 2008).

ANT COLLECTION.—The ants were collected twice: in September 2008 (13.6 mm of rain), during the late dry season, and in February 2009 (247.5 mm of rain) at the onset of the rainy season. In each of the five plots, five sampling points were selected for each successional stage that were 10 m apart from each other, for a total of 25 points per stage and 75 points overall. Because different microhabitats may have different compositions (Schmidt & Solar 2010), pitfall traps without baits were installed at each sample point in hypogaeic (underground), epigaeic (ground level) and arboreal microhabitats. The arboreal pitfall was designed based on the description in Ribas *et al.* (2003), and the epigaeic pitfall was similar to the arboreal pitfall but was buried so that the opening of the container was located at ground level. The hypogaeic pitfall was built according to methods described by Schmidt and Solar (2010).

The traps in the epigaeic and arboreal microhabitats were kept in the field for 48 h, and the pitfalls for the hypogaeic microhabitat were kept in the field for 72 h. The impact caused by soil disturbance and the lack of attraction bait could hinder the access of subterranean ants to the traps. For this reason, we increased the amount of time the pitfall was placed in this microhabitat because the increased time would be sufficient for the ants to reconstruct their tunnels (Schmidt & Solar 2010). After this period, the ants were removed from the traps and taken to the laboratory, where they were mounted and identified. Ants were sorted to genus and then to species or morphospecies. Ant nomenclature follows Bolton *et al.* (2007). Voucher specimens are deposited at the reference collection at the Laboratório de Ecologia de Comunidades at the Universidade Federal de Viçosa (UFV), in Viçosa, Brazil.

EXPLANATORY VARIABLES COLLECTION.—In September 2008, we measured variables that could estimate the availability of resources as well as the local conditions for the resident ants in each type of microhabitat that was sampled. For the arboreal ants, we measured the basal circumferences of all trees found in a two-meter radius around each sample point. Trees with higher basal circumferences occupied a larger area and could provide a higher number of nesting places for ants. Thus, these data yielded an estimate of the available resources for arboreal ants. Also, we also obtained a digital image next to the tree where the arboreal pitfall of each sample point was installed. The images were taken using a Nikon Coolpix 4500 camera with a fish-eye lens attached. The camera was mounted on a levelled tripod at 1.5 m above the soil, with the fish eye focus setting into infinity (Mitchell & Whitmore 1993). The black and white images were taken in the late afternoon to avoid over-exposure from the midday sun. We used the software Gap Light Analyser (GLA) to measure the percentage of canopy cover from the resulting photos (Frazer *et al.* 1999). Because the photos have been taken in the late dry season, the canopy cover is estimated by the wood area that shades the forest floor. This measure was used as an estimate of the climatic conditions of the microhabitat because the canopy cover can affect the availability of light and humidity in the understory. Areas with greater canopy cover may maintain a microclimate that is more suitable for arboreal ant species (Wielgoss *et al.* 2010).

For the epigaeic ants, we collected three samples of leaf-litter one meter away from each of the epigaeic traps, each within an area of 20 x 20 cm. These samples were mixed, packed in plastic bags and transported to the Laboratório de Ecologia de Comunidades at the UFV. After this, the sampled leaf-litter was stored in paper bags and oven-dried at 60ºC until a constant litter weight. The dry weight was used to estimate the availability of resources for epigaeic ants because the leaf-litter serves as a source of food and provides possible nesting sites for ants (Kaspari 1996, Muscardi *et al.* 2008). The percentage of canopy cover was also used as an estimate of abiotic conditions for epigaeic ants. The methodology was similar to the procedures conducted for the arboreal microhabitat, but the digital photographs were taken with the camera positioned at ground level and near the epigaeic pitfall.

Regarding hypogaeic ants, a soil sample was removed with a metal ring of known volume (91.61 cm^3) to determine the moisture content as well as the density and porosity of the soil at each collection point. These measurements served to characterise the soil structure and the condition of this microhabitat for resident ants. The analyses were performed at the Laboratório de Física do Solo at the UFV.

We measured the tree species richness assisted by experts. We counted the number of tree species with a circumference at breast height (CBH) of less than 10 cm present in each plot of the successional stages in the TDF that was studied. The richness of trees was used as an estimate of the soil condition for ants in all of the microhabitats because the physical structure of soil is modified by the establishment of plant species in the area (Sagar & Verma 2010).

DATA ANALYSES.—The data on the ants sampled in the first year (2008) were used to test the first two hypotheses, linked to the study of ecological succession. The sampling carried out during the wet season did not include the estimation of explanatory variables, was used only to compare the ant communities in two different seasons.

We verified the response of ant species richness to successional stages and to seasons with an analysis of variance (ANOVA). We used the Poisson distribution of errors. All levels (stages) were compared by using a contrast analysis for the aggregation levels and comparing the changes in deviations (Crawley 2007). When the level of aggregation did not significantly alter the deviance explained by the model, the levels were aggregated and the model was simplified. All of the models were subjected to residual analysis to assess the adequacy of the distribution of errors (Crawley 2007).

The responses of ant species richness to variables measured in the arboreal (richness of tree species, basal circumference and canopy cover), epigaeic (richness of tree species, leaf-litter dry weight and canopy cover) and hypogaeic (richness of tree species, moisture, density and porosity of the soil) microhabitats were verified through analyses of covariance (ANCOVA) using the Poisson distribution of errors. The stages of succession were added to the models as a covariate. The variables sampled as estimates of resources and conditions were used as explanatory variables, and the ant species richness in each microhabitat was considered to be the response variable in each model. Non-significant explanatory variables were withdrawn from the complete models, which were subjected to residual analyses to assess the adequacy of the distribution of errors (Crawley 2007).

We used a nonparametric multidimensional scaling (NMDS) to test for differences in the compositions of ant communities between the successional stages and between seasons. The ordination was performed using Jaccard index, calculated from a presence/absence matrix. The stress value indicates how much the axes produced by the analysis explain the variations of the raw data. According to Sturrock and Rocha (2000), matrices with 45 objects (in this case, the objects were pitfalls) with bi-dimensional stress up to 0.360 present non-random distributions. Stress results higher than 0.360 indicated poor explanatory power, and further analysis was not performed. We used analyses of similarity (ANOSIM, Clarke 1993) to determine whether the composition of ants differs between the successional stages and between seasons. The R-value indicated the dissimilarity between the groups formed by the ANOSIM. We used the similarity percentage (SIMPER, Clarke 1993) to determine the contributions of individual species to the dissimilarity between the groups. The analyses were performed using the program PAST (PAlaeontological STatistics) version 1.81 (Hammer *et al.* 2008).

RESULTS

We collected 95 ant species from 26 genera. The subfamily with the highest diversity was the Myrmicinae (55 species), followed by Formicinae (21 species), Pseudomyrmecinae (six species), Dolichoderinae (five species), Ecitoninae and Ponerinae (two species each). Amblyoponinae, Cerapachyinae, Ectatomminae and Heteroponerinae were each only represented by a single species (Table S1). Only four species of ants were found in all three successional stages and in both seasons: *Camponotus blandus, Cyphomyrmex transversus, Pheidole* sp. 01 and *Pheidole* sp. 07. The species *Camponotus substitutus* was found in all three stages of succession only in the rainy season, and *Ectatomma edentatum,* *Camponotus* pr. *lespesii, Cephalotes grandinosus, Solenopsis* sp. 01, *Solenopsis* sp. 11 and *Solenopsis saevissima* were found in all three stages only in the dry season (Table S1).

The total ant species richness was significantly higher in the intermediate and late stages of succession (χ^2=9.36; P=0.005; Fig. 1A). The ant communities were segregated between successional stages (Fig. 1B) according to NMDS. This analysis showed that the early stage provided an ant community that was distinct from the more advanced stages of succession (Stress=0.2645; R=0.299; P<0.0001). The species that primarily contributed to the difference between the stages of succession were *Camponotus blandus, Camponotus* pr. *lespesii, Pheidole* sp. 01, *Camponotus atriceps* and *Ectatomma edentatum*. These ant species were found in the intermediate and late stages of succession.

Regarding the microhabitat, the arboreal and epigaeic ant richness did not change with the progress of ecological succession (P>0.05). The variables that were measured to explain the diversity of the arboreal (richness of tree species, basal circumference and canopy cover) and epigaeic (richness of tree species, leaf-litter dry weight and canopy cover) microhabitats did not affect the ant species richness (P>0.05). However, the compositions of the arboreal (Stress=0.1887; R=0.843; P<0.0001; Fig. 2A) and the epigaeic (Stress=0.1862; R=0.396; P=0.0006; Fig. 2B) ant communities differed between the successional stages. The arboreal ant species that primarily contributed to the dissimilarity of the successional stages were *Camponotus atriceps, Camponotus blandus, Camponotus renggeri, Camponotus* sp. 01 and *Camponotus arboreus*. These species were collected in the early and intermediate stages. The epigaeic species *Camponotus renggeri, Camponotus* sp. 02, *Camponotus vitattus, Pheidole* sp. 07 and *Pheidole* sp. 08 that occurred in the late stage contributed to the segregation of the community among the TDF successional stages.

The hypogaeic ant species richness was higher in the intermediate and late stages of succession (χ^2=8.37; P=0.008; Fig. 3A). The community composition of hypogaeic ants was distinct between successional stages (Stress=0.2513; *R*=0.679; *P*<0.0001; Fig. 3B). The factors that explained the increase in the species richness of hypogaeic ants were soil porosity (χ^2=8.74; *P*=0.01; Fig. 4A) and plant species richness (χ^2=8.92; *P*=0.01; Fig. 4B). Soil moisture did not explain the species richness of hypogaeic ants (*P*>0.05), and the soil density was negatively correlated with porosity (*r*=95.1%). Four morphospecies of *Solenopsis* (*S*. sp. 01, 03, 09, and 10), *Pheidole* sp. 01 and *Prionopelta punctulata* were found in the intermediate and late stages. These species primarily contributed to the differences in the community between the successional stages.

The ant species richness was higher in the dry season than in the rainy season (χ^2=85.57; *P*<0.0001; Fig. 5). However, the general composition of ant species did not change between the seasons (Stress=0.4751).

DISCUSSION

BIOLOGICAL MECHANISMS DRIVING SUCCESSION.—The variation on species richness found in the ant communities in the studied TDF is consistent with the model of a community controlled by dominance (see Dauber & Wolters 2004, 2005). This model predicts that ant diversity will be lower in the early stages of succession (Fig. 1A) and that the area will be colonised by generalist species that are common in open and modified environments such as *Acromyrmex landolti, Brachymyrmex patagonicus, Cyphomyrmex* gr. Rimosus sp. 01, *Pheidole* sp. 03 and *Solenopsis* spp. (Table S1). The early stage revealed a differentiated composition of species (Table S1), and most species can tolerate extreme conditions such as low humidity and high temperatures caused by high solar irradiation from the discontinuous canopy of the forest. Throughout the succession process, other species colonised the plots, which caused an increase in the diversity of ants in the advanced stages of succession. The following mechanisms might explain the response of ant communities to ecological succession: (1) competition-colonisation balance, in which competing species exclude species that are competitively inferior when both occupy the same area, and (2) the availability of adequate environmental conditions and resources to colonising species.

The first mechanism is centred on the processes of interaction between the species, and it assumes that interspecific competition is a limiting factor for the species richness of ant communities. Although competitive interactions are usually considered important in the structure of ant communities (Deslippe & Savolainen 1995), some authors have reservations about the widespread importance of competition as a structuring force in the ant communities in the Neotropical region (*e.g.* Soares & Schoereder 2001, Ribas & Schoereder 2002).

The second mechanism is grounded in the changes in physical structures in the environment that occur during the successional process. In tropical forests, plant succession after a disturbance is often characterised by an increase in the structural complexity of the habitat along with an increase in the quantity and diversity of resources (Kalácska *et al.* 2004, Madeira *et al.* 2009), which are important factors for the structure of ant communities (Ribas *et al.* 2003, Armbrecht *et al.* 2004, Ribas & Schoereder 2007). With increasing environmental heterogeneity, a higher number of ant species can coexist in the same area because they occupy different spatial niches. This mechanism is the most acceptable explanation for the variation in total diversity between ant communities in the studied TDF. Much of this diversity variation occurred due to subterranean ant fauna, because only the ant community of the hypogaeic microhabitat responded to ecological succession in the studied TDF (Fig. 3A).

During natural regeneration, soil goes through physical changes due to the establishment of different plant species in the disturbed area. The areas in the early successional stage are characterised by bush vegetation and highly compacted soil because they were previously used as pasture until 2000. In the intermediate and late stages, there is a higher diversity of plant communities, and the soil is more porous. The hypogaeic microhabitat presents different ant fauna (Rabeling *et al.* 2008, Schmidt & Solar 2010) that is closely linked to processes occurring in this forest stratum, which could also contribute to the movement of water and soil as well as nutrient cycling (Lobry de Bruyn 1999, Sousa-Souto *et al.* 2007). Thus, the soil changes caused by a disturbance exert pressure on the ant community in this microhabitat, which results in a decrease in diversity. In the studied TDF, the colonisation of new ant species parallels the physical structure of the soil (Fig. 4A) as well as the increase of plant diversity (Fig. 4B) along the successional process. Moreover, these environmental changes were reflected not only in the richness but also in the composition of the hypogaeic ant community (Fig. 3B), which was sensitive to changes that occur in its microhabitat.

Differently from the hypogaeic ants, the arboreal and epigaeic ant communities are consistent with the model of a community controlled by foundation. This model predicted that diversity would not vary throughout successional process. The inhibition, facilitation and tolerance are the three mechanisms involved in the diversity regulation this community model (Connell & Slayer 1977). The dynamics of each mechanism is based on different kind of the interactions between species. These mechanisms are more commonly observed in plant communities that are undergoing succession (Clements 1916, Connell & Slayer 1977, Pickett *et al.* 1987, DelMoral & Wood 1993). For arboreal and epigaeic ant communities of our study, we hypothesize that habitat conditions influence more strongly the ant species richness than the mechanisms that involve intraspecific interactions (inhibition, facilitation or tolerance).

We found some evidence to show that habitat condition is an important regulator of ant species richness in arboreal and epigaeic microhabitats. *Crematogaster obscurata* is found in dry forests and nests in the dead portions of live trees (Longino 2003). Species of this genus, and other members of the *Azteca* and *Cephalotes* genera, are usually very aggressive and dominate the resources that are exploited by their communities. Despite being dominant and found in dry habitats, *C. obscurata* was collected only in intermediate and late stages of succession along with the *Azteca* species and *Cephalotes atratus* (Table S1). Therefore, the occurrence of these species in advanced successional habitats may be due to the presence of specific resources for structuring large nests, such as trees that have larger CBH, and not because some early ant species inhibits, tolerate or environment prepare for the installation these ant species.

SEASONAL VARIATION.—In the tropics, some insect populations are influenced by seasonal changes in temperature and moisture (Tauber *et al.* 1998, Guedes *et al.* 2000), and ant populations are generally more diverse during the rainy season (Torchote *et al.* 2010). Contrary to most studies in humid tropical forests, we found a higher ant species richness during the drought season (Fig. 5), demonstrating that such information is not adequate to the studies conducted on TDFs. This pattern of seasonal variation has been found in other TDFs. For example, a community of leaf-litter and epigaeic ants in the Argentinean Chaco (Delsinne *et al.* 2008) and a community of arboreal and terrestrial ants in a Mexican TDF (Gove *et al.* 2005) also showed higher species richness in the dry season. However, Neves *et al.* (2010b), using baited pitfall traps, found no seasonal differences in the arboreal ants species richness in the same TDF investigated in this study. The presence of baits could induce distinct foraging patterns and alter the natural feeding pattern because a high-protein and high-calorie resource is being offered. Furthermore, we believe that the presence of bait provided an even distribution of resources, which made the areas more equivalent in terms of resources. Thus, the results of our study show a natural increase in the ant species number foraging in the dry season during different successional stages.

Unlike diversity, the composition of ant communities did not change between the seasons, indicating that these species ultimately support the seasonal abiotic and environmental changes that occur in the TDF. Therefore, if an ant community present in the forest was the same in the dry and rainy seasons, and if there was an increase in ant species richness in the dry season, then a specific process is controlling local diversity. The mechanism proposed by Lassau and Hochuli (2004) for the diversity of ants in less complex habitats might also explain the higher ant species number collected in the TDF during the dry season. The foliar deciduousness of the trees could have simplified the physical environment by reducing the moisture and shade levels, which could have facilitated nest building and foraging by the ants, especially because most species are thermophilic (Hölldobler & Wilson 1990). Moreover, as the availability of resources decreased in the dry season, the ants needed to increase their foraging area to find food, thereby increasing the chances that they would fall into the traps. During the rainy season, the opposite process would occur.

SECONDARY TDFS CONSERVATION.—Although the history of TDFs is marked by human exploitation, the future of this unique and diverse ecosystem depends on conservation, management and restoration. Our results showed that environments with a simple physical structure (*e.g.*, degraded forests and plantations) did not support species from the forest. A considerable fraction of the ant community only appeared in the advanced stages of succession, which reinforced the importance of secondary habitats in maintaining the ecosystem biodiversity.

We hypothesize that the restoration of the ant diversity in TDFs is faster than in rainforests. Bihn *et al.* (2008) found that even after 35-50 years of regeneration in an Atlantic forest, the ant community did not show the species richness and community composition of a mature forest. Based on the pattern of succession in TDF, it is likely that 25 years of regeneration in this forest would be sufficient to restore the richness and community composition of ants, as also showed in the estimates made by Neves *et al.*

(2010b). Tropical rain forests usually have a high level of alpha diversity (Lopez & Zambrana-Torrelio 2006), and when interactions are disrupted by habitat disturbance, species recolonisation and the establishment of inter and intraspecific interactions can take longer than the same processes in TDFs, which explains the difference in the resilience times for these different areas.

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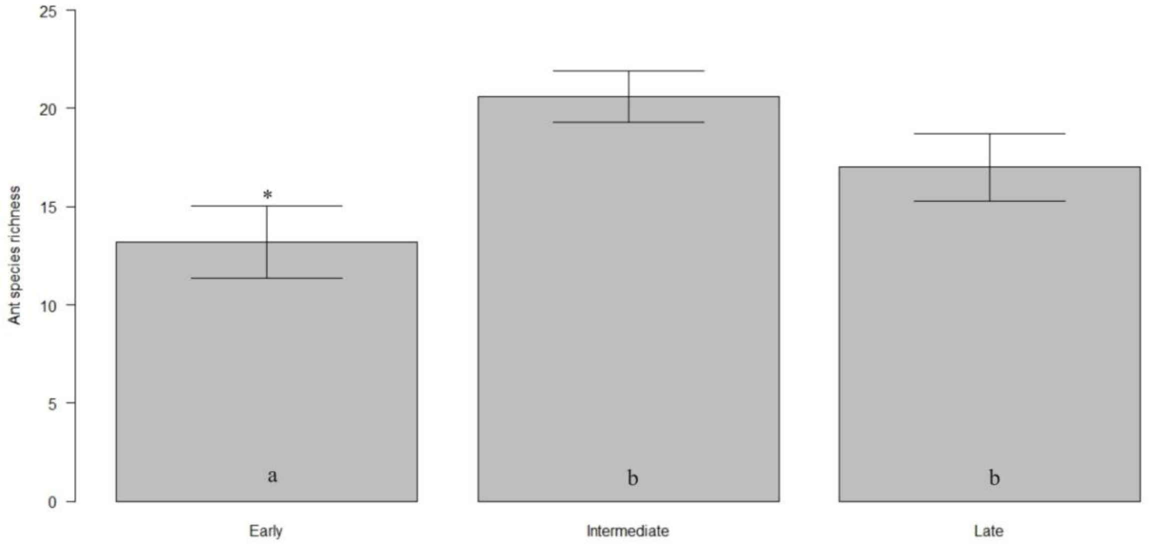
FIGURE 1. Ant species richness (mean±SE) in the successional stages (A). Different letters and asterisks on the bars represent statistically significant differences between successional stages as determined by contrast analysis (*P*=0.005). Ant species composition (B) of the early (square), intermediate (circle) and late (triangle) stages of succession in a Tropical Dry Forest (*P*<0.0001).

FIGURE 2. NMDS of ant species in the (A) arboreal (*P*<0.0001) and (B) epigaeic (*P*=0.0006) microhabitats for the early (E), intermediate (I) and late (L) successional stages of a Tropical Dry Forest.

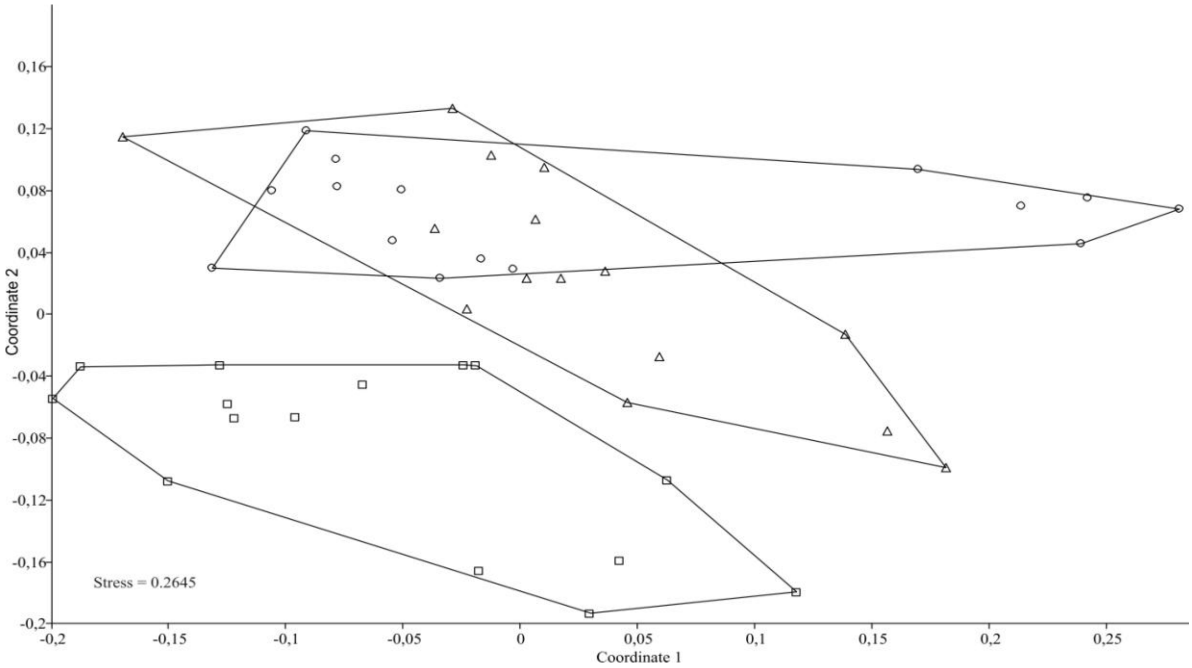
FIGURE 3. Hypogaeic ant species richness (mean±SE) (A). Different letters and asterisks on the bars represent the statistical differences between successional stages as determined by contrast analysis (*P*=0.008). NMDS of hypogaeic ant species (B) in the different successional stages: early (E), intermediate (I) and late (L) (*P*<0.0001).

FIGURE 4. Responses of the hypogaeic ant species richness to soil porosity (A) and tree species richness (B) in a Tropical Dry Forest (*P*=0.01).

FIGURE 5. Seasonal variation of ant species richness in a Tropical Dry Forest (*P*<0.0001).


25
20
15
10
5
0
Ant species richness
*
a
b
b
Early
Intermediate
Late

A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0,12
0,08
0,04
0
-0,04
-0,08
-0,12
-0,16
-0,2
Coordinate 2
-0,2
-0,15
-0,1
-0,05
0
0,05
0,1
0,15
0,2
0,25
Coordinate 1
Stress = 0.2645

B

FIGURE 1

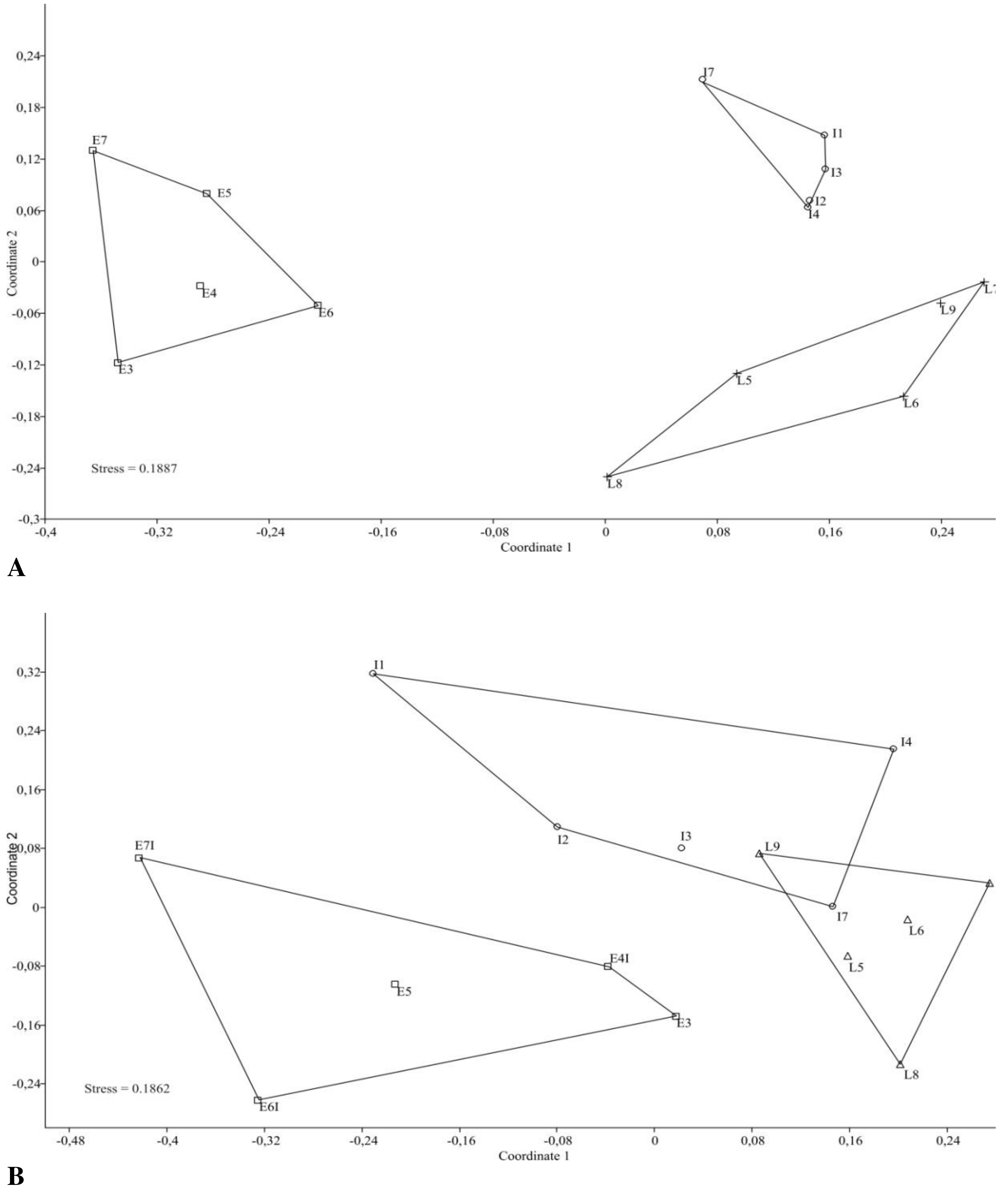
I7
I1
I3
I2
I4
E7
E5
E4
E6
E3
L5
L6
L8
L9
Stress = 0.1887
Coordinate 2
Coordinate 1
0,24
0,18
0,12
0,06
0
-0,06
-0,12
-0,18
-0,24
-0,3
-0,4
-0,32
-0,24
-0,16
-0,08
0
0,08
0,16
0,24
A
I1
I4
I2
I3
L9
I7
L6
L5
L8
E7I
E4I
E5
E3
E6I
Stress = 0.1862
Coordinate 2
Coordinate 1
0,32
0,24
0,16
0,08
0
-0,08
-0,16
-0,24
-0,48
-0,4
-0,32
-0,24
-0,16
-0,08
0
0,08
0,16
0,24
B

FIGURE 2

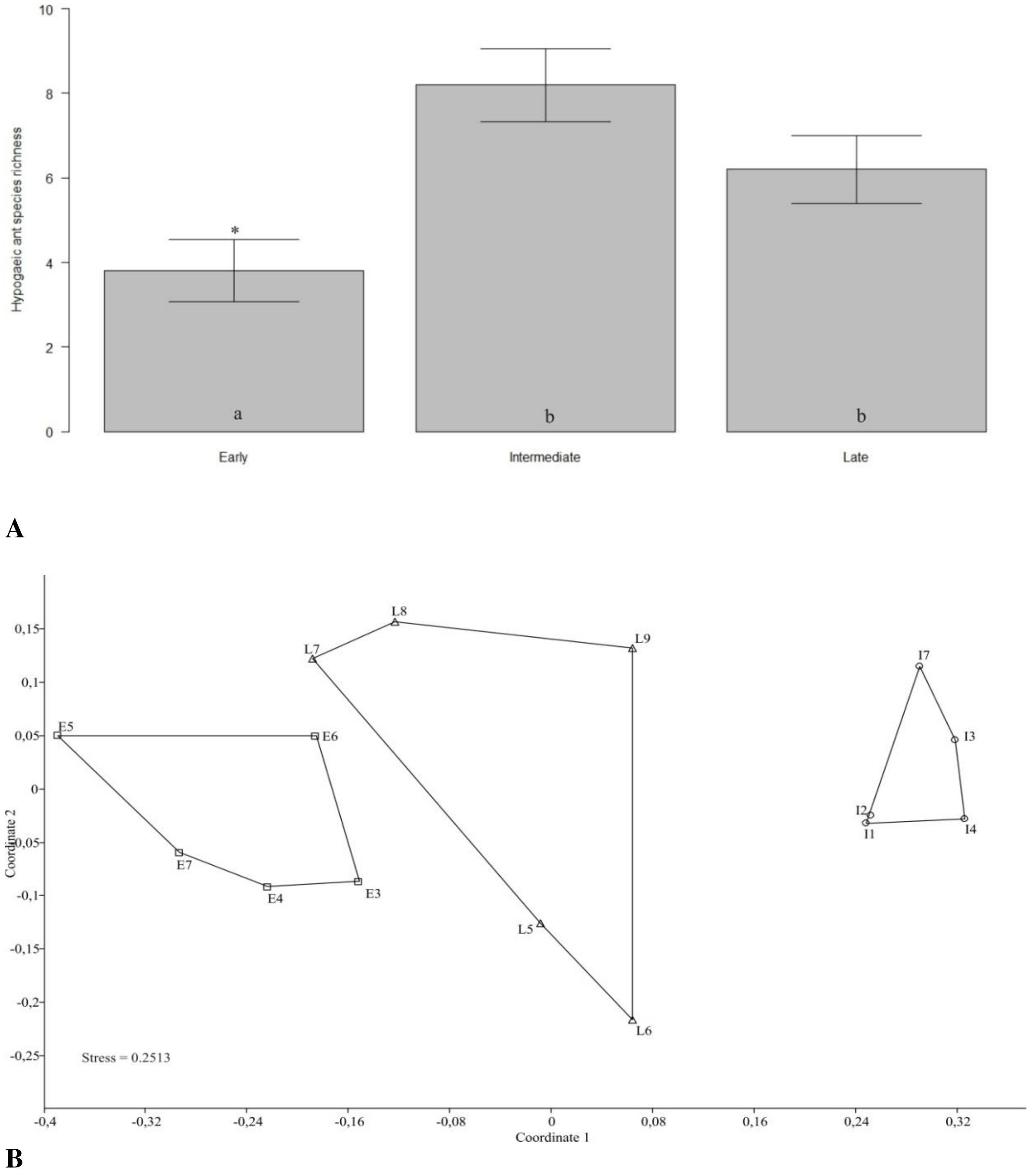
10
8
6
4
2
0
Hypogaeic ant species richness
*
a
b
b
Early
Intermediate
Late
A
0,15
0,1
0,05
0
-0,05
-0,1
-0,15
-0,2
-0,25
Coordinate 2
L8
L9
L7
I7
E5
E6
I3
I2
I1
I4
E7
E4
E3
L5
L6
Stress = 0.2513
-0,4
-0,32
-0,24
-0,16
-0,08
0
0,08
0,16
0,24
0,32
Coordinate 1
B

FIGURE 3

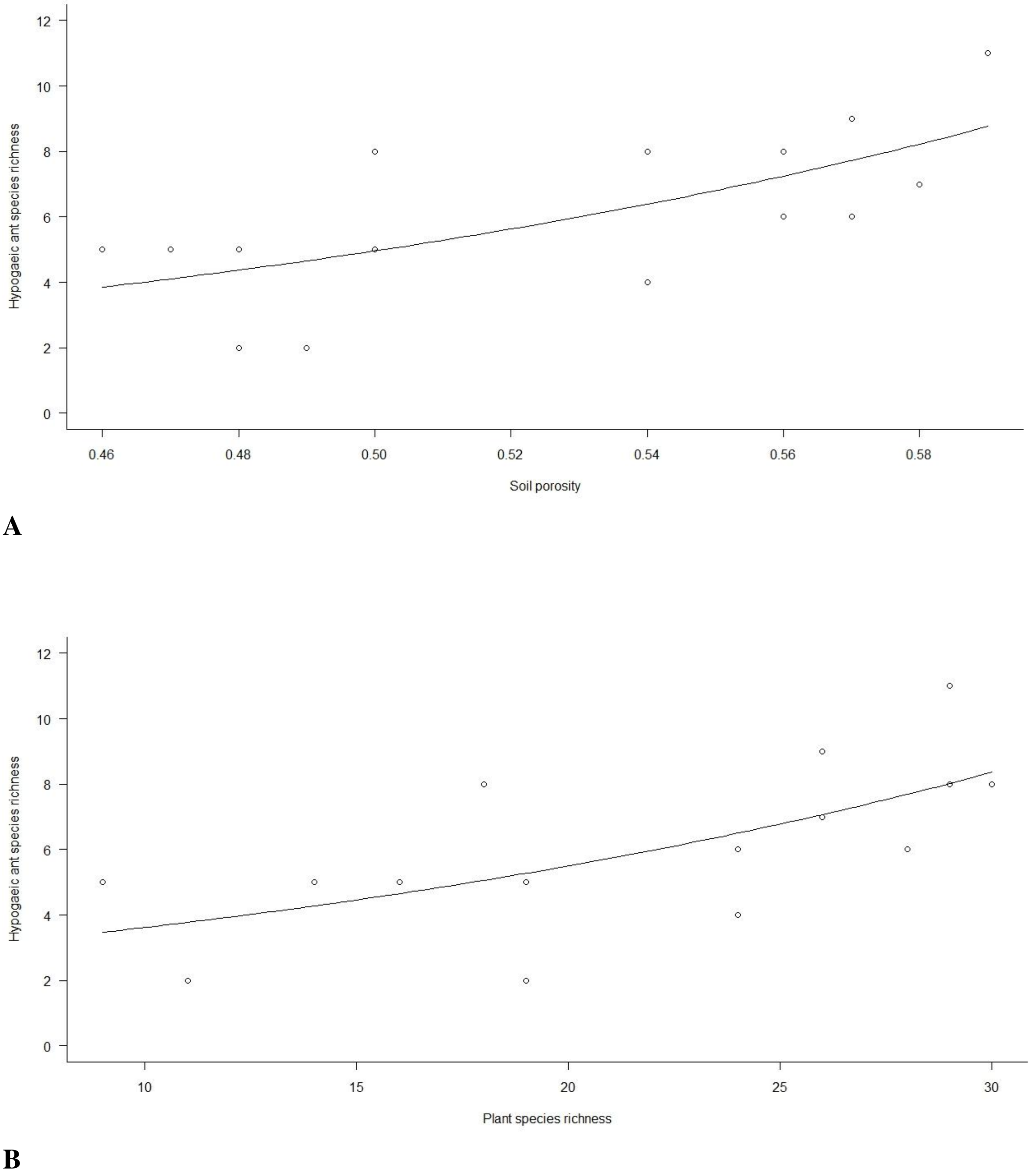
Hypogaeic ant species richness
0
2
4
6
8
10
12
0.46
0.48
0.50
0.52
0.54
0.56
0.58
Soil porosity
A
Hypogaeic ant species richness
0
2
4
6
8
10
12
10
15
20
25
30
Plant species richness
B

FIGURE 4

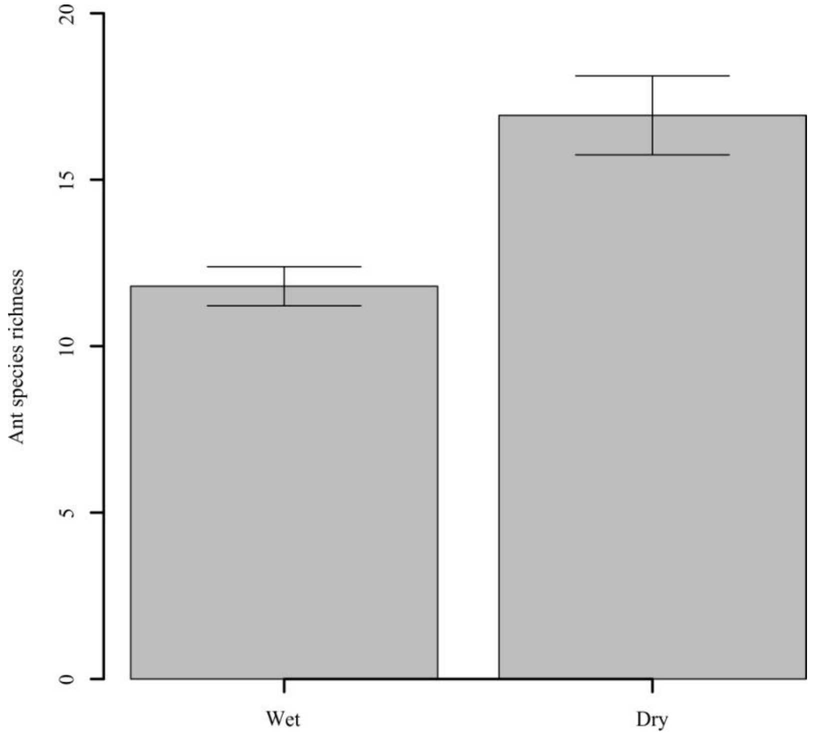

FIGURE 5

Table S1. Ant species collected in a Tropical Dry Forest fragment from different successional stages in Parque Estadual da Mata Seca during the dry and rainy seasons. A = arboreal microhabitat, E = epigaeic microhabitat and H =hypogaeic microhabitat.

	Stages of Succession / Seasons					
	Initial		Intermediate		Late	
Taxa	Dry	Rainy	Dry	Rainy	Dry	Rainy
Amblyoponinae						
Prionopelta punctulata Mayr, 1866				H	H	H
Cerapachyinae						
Acanthostichus serratulus (Smith, 1858)		H		H		
Dolichoderinae						
Azteca sp. 01					A	
Azteca (gr. Alfari) sp. 02						A
Dorymyrmex sp. 01			E			
Forelius brasiliensis Forel, 1908		E	E			E
Tapinoma melanocephalum (Fabricius, 1793)	A				H	
Ecitoninae						
Cheliomyrmex morosus (Smith, 1859)				H		
Labidus coecus (Latreille, 1802)				H	H	
Ectatomminae						
Ectatomma edentatum Roger, 1863	E		AEH		E	
Formicinae						
Brachymyrmex sp. 01					H	
Brachymyrmex sp. 02					E	

Brachymyrmex coactus (Mayr, 1887)				EH		H
Brachymyrmex pr. *coactus*			H		E	
Brachymyrmex pr. *longicornis*				H	H	
Brachymyrmex patagonicus Mayr, 1868	AEH					
Camponotus sp. 01			A			
Camponotus sp. 02			AE		AE	
Camponotus arboreus (Smith, 1858)			AE	AE	A	AE
Camponotus atriceps (Smith, 1858)			AE		AE	
Camponotus blandus Forel, 1901	AE	AE	AE	AE	E	E
Camponotus cingulatus Mayr, 1862				AE		AE
Camponotus crassus Mayr, 1862	A		AE	AE		
Camponotus germaini Emery, 1903				AEH		E
Camponotus pr. *lespesii*	AE		AE		AEH	
Camponotus melanoticus Emery, 1894		E				
Camponotus renggeri Emery, 1894	AE	AE			A	
Camponotus substitutus Emery, 1894		AEH		AE		AE
Camponotus pr. *westermanni*					A	
Camponotus vittatus Forel, 1904			AE	A	AE	A
Nylanderia pr. *guatemalensis*						H
Heteroponerinae						
Acanthoponera mucronata (Roger, 1860)						A
Myrmicinae						
Acromyrmex landolti (Forel, 1885)	E	E				
Acromyrmex octospinosus (Reich, 1793)	E		A			
Acromyrmex rugosus (Smith, 1858)		EH		E		

Atta sexdens Forel, 1908				E		
Cephalotes atratus (Linnaeus,1758)				A	A	A
Cephalotes betoi De Andrade, 1999			A			
Cephalotes christopherseni (Forel, 1912)	A					
Cephalotes grandinosus (Smith, 1860)	A		AE		AEH	
Cephalotes minutus (Fabricius, 1804)	A					
Cephalotes pavonii Latreille, 1809		A				E
Cephalotes pusillus (Klug, 1824)	A	A			AE	A
Crematogaster abstinens Forel, 1899	E					
Crematogaster ampla Forel, 1912			AE	A		A
Crematogaster pr. *bruchi*	E		E			
Crematogaster evallans (Forel, 1907)		A				
Crematogaster obscurata (Emery, 1895c)					A	
Crematogaster torosa Mayr, 1870				AE		A
Crematogaster pr. *torosa*			A		A	
Crematogaster victima Smith, 1858						A
Cyphomyrmex gr. *rimosus* sp. 01	H					
Cyphomyrmex transversus Emery, 1884	E	H	H	EH	E	E
Pheidole sp. 01	EH	AEH	AE	AEH	AEH	AEH
Pheidole sp. 02			E	E	E	EH
Pheidole sp. 03	E					
Pheidole sp. 04	E	EH			E	
Pheidole sp. 05	EH	A		H		H
Pheidole sp. 06	AEH	EH				
Pheidole sp. 07	E	E	EH	EH	AEH	AEH

Pheidole sp. 08	AEH	E	EH	EH	AEH	
Pheidole sp. 09			H	EH		
Pheidole sp. 10			H			
Pheidole sp. 11				H		
Pheidole sp. 12				E		
Pyramica lilloana (Brown, 1950)					H	
Rogeria blanda (Smith,1858)			H		H	
Solenopsis (gr. Globularia) sp. 01	H		H		H	
Solenopsis sp. 02			H		E	
Solenopsis sp. 03			H		H	
Solenopsis sp. 04					H	
Solenopsis sp. 05			H			
Solenopsis (gp.Globularia) sp.06		H			EH	
Solenopsis sp. 07		EH	H	H		H
Solenopsis geminata (Fabricius, 1804)	H	E				
Solenopsis sp. 09	EH				EH	
Solenopsis sp. 10			H		H	
Solenopsis sp. 11	E		AH		H	
Solenopsis sp. 12			H		H	
Solenopsis sp. 13			EH			
Solenopsis sp.14			H			
Solenopsis sp.15	H				H	
Solenopsis sp.16						H
Solenopsis sp.17						E-H
Solenopsis saevissima (Smith, 1855)	E		AH		H	

Wasmannia auropunctata (Roger, 1863)		E			EH	E
Wasmannia lutzi Forel, 1908	A				E	
Ponerinae						
Odontomachus bauri Emery, 1892		E	E	H	E	E
Pachycondyla villosa (Fabricius, 1804)			E		A	
Pseudomyrmecinae						
Pseudomyrmex flavidulus (Smith, 1858)		A				
Pseudomyrmex gracilis (Fabricius, 1804)	A			A		
Pseudomyrmex (gr. Pallidus) sp. 03	A					
Pseudomyrmex (gr. Pallidus) sp. 04	A					
Pseudomyrmex schuppi (Forel, 1901)			A	A		A
Pseudomyrmex termitarius (Smith, 1855)	AE	E	E			E

CAPÍTULO 2

Ant diversity partitioning at multiple spatial scales: ecological processes and implications for the conservation of Tropical Dry Forests

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Running head: Ant diversity partitioning in Tropical Dry Forests

ABSTRACT

The aim of this study was to determine whether there are nonrandom processes influencing the observed pattern of ant diversity, and to determine at what scale these processes can be more influential. To examine the patterns of ant diversity, a nested hierarchical design was used in three spatial scales, ranging from sample points (pitfalls), fragments (Tropical Dry Forests - TDF and surroundings) and regions of Brazil. We used a total of 150 sampling units (15 sampling points x two fragments x five regions = 150). The additive partitioning of diversity was used to split the regional diversity of ants (γ) into the diversity components within (α) and among (β) samples. A null model based on the sample was used to identify variations in the random distribution among the three spatial scales. The spatial partitioning of species diversity of ants distributed across regions of Brazil showed that each sampling point (α) holds a mean diversity larger than expected by the null hypothesis. The observed β2 (between fragments) and β3 diversities (among regions) were higher than the expected by chance. Applying the analysis of partition separately in each region, the observed β2 diversity between fragments (TDF and surrounding areas) was higher than expected by the null hypothesis, to all regions of Brazil. The partition analysis helped us to identify the scales of sampling points inside (α1), between fragments (β2), and among regions (β3), as the spatial boundaries where non-random processes must interact and disproportionately differentiate the ant diversity. Based on species composition and diversity patterns we stressed the importance of creating more protected areas throughout the TDF coverage area.

Keywords: Diversity partitioning, β-diversity, spatial scale, Formicidae, Tropical Dry Forest, local-regional richness, species composition.

INTRODUCTION

Biodiversity might not be evenly distributed among habitats, landscapes and regions. Elucidating the pattern of diversity and knowing why spatial distribution of species diversity varies between spatial scales are among the main concernings of ecological theory (Ricklefs, 2004) and of the ecology of tropical forests in particular (Ribeiro *et al.*, 2008; Pennington *et al.*, 2009). From a long time, studies undertaken within the ecology of communities considered that the local community would be ruled only by local processes (see review in: Tilman & Pacala, 1993; Chesson, 2000; Loreau, 2000). However, different processes can disproportionately determine the regional diversity among the multiple spatial scales. Therefore, to elect only one spatial scale as the main focus of study may lead to biased conclusions with low explanatory power, as distinct patterns may result from studies in other scales (Summerville *et al.*, 2003).

A given observed local species richness may, in theory, result from the transition of species through a series of "filters" (Hillebrand & Blenckner, 2002; Fig. 1). Such filters are representing ecological processes that regulate diversity in different scales, which can influence the arrival and maintenance of the species in a given location (Lawton, 1999). In the local spatial scale, ecological constraints, such as herbivory, competition and abiotic environmental factors can be considered an important filter in determining diversity. Otherwise, on a larger spatial scale, the filter can be represented by historical events, such as evolution for example. Mechanisms such as speciation and migration can regulate the number of species in a region. In tropical ecosystems, both processes acting on a local scale (Ribas *et al.*, 2003; Ribas & Schoereder, 2007) and on broader spatial scales (Harcourt, 2000; Ribas *et al.*, 2003) contribute to regional pool of species.

The additive partitioning of diversity has been considered a promising methodological approach to better understand diversity patterns at multiple spatial scales (Allan, 1975; Wagner *et al.*, 2000; Crist *et al.*, 2003; Gering *et al.*, 2003; Ribeiro *et al.*, 2008; Ligeiro *et al.*, 2010). Lande (1996) showed analytically that the regional species diversity (γ) can be partitioned into additive components, represented by the diversity within the community (α) and among communities (β). Diversity can be estimated using the species richness or diversity indices (e.g. Simpson and Shannon). Hence, the overall diversity of a community may be partitioned as: $\gamma = \alpha + \beta_1 + \beta_2 + \beta_3 + ... \beta_n$, where n is the number of scales adopted by the study (Veech *et al.*, 2002).

One of the main characteristics of the additive partitioning is the proportional differentiation of the total diversity found at each hierarchical level, which allows the researcher to identify which scale contributes more to total biodiversity. It is possible, hence, to obtain more robust evidence of which processes (filters) are more important in structuring the community. For instance, if the diversity observed at the local scale is smaller than that calculated by the null model, hypotheses about the role of inter- and intraspecific interactions as factors limiting species diversity can be put forward. However, before conclusions can be reached, it is imperative to keep in mind that diversity patterns do not determine ecological processes (Gering & Crist, 2002), as they have not been experimentally tested. When the focus is biological conservation, determining the spatial level that presents the major source of biodiversity will help conservationists and policy makers to direct efforts and finances towards environmental conservation (Veech *et al.*, 2002; Gering *et al.*, 2003).

The Tropical Dry Forest (TDF) harbours a high level of species diversity and endemism (Sánchez-Azofeifa *et al.*, 2005). Much of this vegetation consists of fragments located in different regions of South America (Prado & Gibbs, 1993; Prado, 2000). This disjoint distribution of TDFs is the result of repeated fragmentation events (i.e., vicariance) during the last glacial-Holocene transition (marked by increases in temperature and in precipitation). Given this scenario, some core regions of the forest acted as refuges (Prado & Gibbs, 1993), preserving the original species composition of a preceding large and continuous extension of the TDF existing in the Pleistocene (the ‘Pleistocene Arc Hypothesis’ – PAH, see Prado & Gibbs, 1993; Pennington *et al.*, 2000; Prado, 2000).

The area under coverage of the TDFs is nowadays decreasing, which in turn might cause a decline in diversity within it. In the Americas, 66% of these forests have been already destroyed mainly by logging, agriculture and livestock activities, while 60% of its area was lost in South America (Portillo-Quintero & Sánchez-Azofeifa, 2010). The intense and constant depletion of TDFs may have occurred as this ecosystem concentrates a high density of human population, as soil characteristics and amenable climate are attractive to the practice of agriculture and human occupancy (Sánchez-Azofeifa *et al.*, 2005; Pennington *et al.*, 2006).

In areas with a high degree of human disturbances, as TDFs, conservation strategies should be directed to the protection of the still remaining habitats, considering the patterns of distribution of organisms along the region (Brown & Freitas, 2000; Fahrig, 2003). This conservation approach requires a sophisticated knowledge on dynamics of biodiversity distribution throughout different spatial scales (Summerville *et al.*, 2003).

Among the various organisms that can be used in diversity studies, ants are considered an excellent model because they are highly abundant, diverse and with a relatively well-known taxonomy (Alonso & Agosti, 2000; Fernández, 2003). Moreover, regional ant diversity may be determined by factors acting on different spatial scales. Ribas *et al.* (2003) found that factors that act on a local scale (tree density and species richness) determine the arboreal ant species richness in the Cerrado. The authors also inferred that processes acting on a larger scale (evolutionary history, altitude and disturbance) may also be important in determining the ant species richness. This combination of attributes makes the ant community a prospective powerful tool for identifying the spatial scale that contributes most to the regional pool of species, and assists in allocating resources for the conservation of species and habitats.

In this sense, the additive partitioning will help us to identify the spatial scale that contributes most to the regional diversity of ant species in TDFs. These forests are located in different geographical locations of the Neotropics (see Prado, 2000; Pennington *et al.*, 2006, 2009; Werneck *et al.*, 2010). This may cause the local filters, such as climate and species interactions, to be "second order" factors (Lawton, 1982). Second order factors are those that influence species richness, but are not the main factor responsible for determining the species richness in different geographical regions (see also Srivastava, 1999). Based on the evolutionary history of TDFs (PAH), we think that processes acting on a larger spatial scale, such as biogeographic and evolutionary filters, may be the factors that contribute most to determining the species richness of TDFs. Therefore, we tested two hypotheses to identify in which spatial scale non-random processes determine the greatest diversity of ants, allowing us to pinpoint the regulator "filters" and to map biodiversity conservation strategies.

In this study, we characterize the spatial distribution of ants among hierarchical spatial scales, testing the following hypotheses:

(i) Ant diversity is not evenly distributed across the spatial scales investigated. We compared the partitioning of diversity observed with that expected by the null hypothesis (species richness is not uniformly distributed among the scales);

(ii) Ant species composition differs among the fragments sampled. Based on the PAH, it is expected that the species composition of TDFs would be more similar to each other than with their neighbouring surroundings.

MATERIALS AND METHODS

Study area and sampling design

TDFs are defined as a vegetation type typically dominated by deciduous trees (at least 50% of these trees are deciduous). The high leaf deciduousness occurs due to the long dry season (precipitation <100 mm), which constrain the productivity of plants within 3-5 months a year when rainfall is highly concentrated (Sánchez-Azofeifa *et al.*, 2005). The average annual temperature of these forests is greater than 25 °C and annual rainfall varies between 700 and 2000 mm (Sánchez-Azofeifa *et al.*, 2005).

The dry forests are formed by a large group of plant communities that inhabit warm climates, with a marked climatic seasonality (Murphy & Lugo, 1986). The current distribution of TDFs in South America is discontinuous, with large areas located from the Caatinga of northeastern Brazil, to the Valley of the Uruguay River (Fig. 2). The TDFs are in northeastern Brazil (Caatinga core), along the Paraguay-Parana River (Missions core), in southeastern Bolivia and northwestern Argentina ("Subandean Piedmont" core). These forests are also present in areas of favorable soil conditions in the Cerrado biome, in the plateau of central Brazil (Werneck *et al.*, 2010).

We used a hierarchical nested design to sample ants in the studied fragments. Three hierarchical levels were represented in this design, ranging from the regional to the local scale: regions of Brazil, fragments (each TDF and surroundings) and sample points. The largest spatial scale was represented by different regions of Brazil (Fig. 2). The regions studied are located in the States of Bahia (BA), Minas Gerais (MG), Goiás (GO), Mato Grosso do Sul (MS) and Rio Grande do Sul (RS). The fragments studied in each region are inserted into different biomes in Brazil: Atlantic Forest (BA), Caatinga (MG), Cerrado (GO), Pantanal (MS) and Southern Plains, the Pampas (RS).

In each studied region two fragments were sampled (the second largest scale). In each region we selected a TDF fragment and a fragment consisting of the surrounding vegetation. These two fragments are located at the following locations. (1) Independence Farm, Itambé, BA (15º42'39"S, 39º34'08"W, alt. 245 m, area: 100 ha). (2) Parque Estadual Mata Seca - PEMS, Manga, MG (14°48'36"-14°56'59"S, 43°55'12"-44°04'12"W, alt. 493 m, area: 15,466.44 ha). (3) Sabonete Farm, Posse, GO (14°03'53"S, 46°29'15"W, alt. 677

m, area: 100 ha); (4) Parque Nacional da Serra Bodoquena, Bodoquena, MS (20°46'56"S, 56°44'31"W, alt. 413 m, area: 77,232 ha). (5) Parque Estadual do Turvo, Derrubadas, RS (27°14'06"S, 53°58'36"W, alt. 200 m, area: 17,491.40 ha).

In each fragment we distributed 15 sampling points, which represent the spatial scale of the study site. At each point, we installed pitfall traps to collect the ants. We obtained a total of 150 sampling units (15 sampling points x two fragments x five regions = 150).

Ant sampling

Ant sampling was carried out once in each fragment, between the months of January and May of 2008 and 2009, always near to the rainy season in each region. We distributed 15 sampling points in each fragment, apart 15 m from each other. In each sample point, we installed pitfall traps baited with sardine and honey, in the microhabitats hypogaeic (underground), epigaeic (ground level) and arboreal. Sampling ants in different strata of the forest results in a better estimative of the total diversity of ant communities of the fragments studied. The arboreal pitfall follows the description by Ribas *et al.* (2003), the epigaeic is similar to the arboreal, but is buried with the opening of the container at the ground level, and the hypogaeic is as described by Schmidt & Solar (2010).

The traps remained in the field for 48 h and were subsequently removed and taken to the laboratory for sorting, mounting and identification of ants. Ants were sorted to genus and then to species or morphospecies. Ant nomenclature follows Bolton *et al.* (2007). Voucher specimens are deposited at the reference collection at the Laboratory of Community Ecology at the Universidade Federal de Viçosa (UFV), in Viçosa, Brazil.

Data analyses

We used the additive partitioning as a tool to decompose the total ant diversity into the alpha and beta components. The diversity is aggregated into hierarchical levels that have

150 (sample points), 10 (fragments) and five (regions of Brazil) units. The total species richness (γ) found in a collection of samples of any spatial scale can be partitioned in the average number of species occurring within a sample (α) and the average number of species absent from a sample, but present in other sample (β; Veech *et al.*, 2002). Then, $\gamma = \alpha + \beta$, and beta diversity can be estimated by $\beta = \gamma - \alpha$ (Wagner *et al.*, 2000). The diversity components are calculated as $\beta_m = \gamma - \alpha_m$ for the largest spatial scale studied and $\beta_i = \alpha_{i+1} - \alpha_i$ for each inferior spatial scale, considering a hierarchical design with $i = 1, 2, 3, \ldots m$ sampling levels.

In this hierarchical study, a value of beta diversity is associated with each spatial scale. The first beta diversity (β_1) is the difference between the mean diversity within the fragments and the mean diversity of the sample points. Similarly, the β_2 is the difference between the average diversity within regions and the mean diversity within the fragments and β_3 is the difference between the total diversity (γ) and the average diversity within regions. In additive partitioning, the alpha and beta components have the same unit, the number of species. For species richness, for example, alpha diversity is the average number of species in a given level, and beta diversity is the average number of species added to the next hierarchical level (Veech *et al.*, 2002). In this study, the total species richness was partitioned into: $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3$.

We can compare the relative importance of each value of beta diversity using a null model. Crist *et al.* (2003) described two types of null model for the additive partitioning of diversity. The model I ("individual-based randomization") randomizes individuals among samples from all hierarchical levels of study. In model II ("sample-based randomization”), samples of the L-1 level are randomized into the L level, keeping the number of individuals and species present in each sample unit. This form of data randomization preserves the pattern of intraspecific aggregation at each scale, unlike the model I. In model II, the statistical significance of each component of diversity is tested using a separate set of randomizations for each level L of the study. This procedure is performed because each hierarchical level presents a different number of samples. As a result of this form of data randomization, the expected values of α_1 and β_i are not additive to the total diversity (Crist *et al.*, 2003). We decided to use the model II, because part of beta diversity may result from sampling variation, i.e., the partition observed may be the result of hierarchical sampling design (Crist *et al.*, 2003).

Data were randomized 1000 times to generate the expected distribution of the components of diversity under the null model. The observed component of diversity in a given spatial scale was compared with their expected distribution to determine whether this value was lower or higher than expected in the absence of aggregation (null model). The null hypothesis was tested by determining the frequency (fr-value) of expected values higher than observed values in the randomizations. If the fr-value was low ($fr_{exp>obs} < 0.05$), the pattern indicates that the observed diversity is significantly higher than expected, with $p < 0.05$. Conversely, if the fr-value is high ($fr_{exp>obs} > 0.95$), it indicates that the observed diversity is significantly lower than expected, with $p < 0.05$ (Gotelli & Graves, 1996).

The differentiation of diversity components estimated from observed indicates that the spatial distribution of species diversity is heterogeneous. If the mean observed diversity is greater than expected among the study sites, this may be the result of a strong variation within some of the sites, while other sites may show a pattern of diversity similar to the null model. Alternatively, if the mean observed diversity is equal to that expected by the null model, this result may be due to considerable negative deviations at some sites, which are counterbalanced by high and positive deviations from other sites. Therefore, besides carrying out the partition of the whole ant community, we also calculated the components of diversity at each hierarchical level of each separate region of Brazil. In these five independent analyses, the gamma diversity was defined as the total number of species sampled in each region. All tests were performed using R 2.11.1 software (R Development Core Team, 2010) with the package *boot 1.2-42* (Canty & Ripley, 2006). The routine for data analysis were developed by Ribeiro *et al.* (2008).

We used a nonparametric multidimensional scaling analysis (NMDS) to determine differences in ant community composition between the fragments of the five regions studied. The ordination was performed using Euclidean distance, calculated from a presence/absence matrix. The stress value indicates how much the axes produced by the analysis explain the variations of the raw data. According to Sturrock & Rocha (2000), matrices with more than 100 objects (150 sampling points) with a two-dimensional stress up to 0.396 are acceptable. Similarly, matrices of 30 objects (15 sampling points x two fragments) with a two-dimensional stress up to 0.328 and matrices of 75 objects (15 sampling points x five TDF fragments) with a two-dimensional stress of up to 0.386 have non-random distribution. Stress values higher than these indicate a low explanation, and it is not necessary to carry out the subsequent analyses. We used analyses of similarity (ANOSIM; Clarke, 1993) to determine whether the composition of ants differs between the fragments. The R-value indicates the dissimilarity between the groups formed by ANOSIM. We used the similarity percentage analyses (SIMPER; Clarke, 1993) to determine the contribution of individual species to the dissimilarity of the groups. All composition analyses were performed in the software PAST (PAlaeontological STatistics) 1.81 (Hammer *et al.*, 2001).

RESULTS

We collected 163 ant species, from 42 genera. The subfamily with the highest diversity was Myrmicinae (75 species), followed by Formicinae (39 species), Ponerinae (15 species), Dolichoderinae (12 species), Pseudomyrmecinae (nine species), Ectatomminae (five species), Ecitoninae (four species) and Cerapachyinae with two ant species.

Regarding the diversity of ants in different regions of Brazil, we collected 49 species of ants in MG (11 species in common in both forest fragments), 84 species in MS (22 species occurred in the two fragments), 44 species in GO (with 10 species common to both fragments), 46 species in RS (14 species being common to the two environments sampled) and 56 ant species listed for the fragments studied in Bahia, where 14 species occurred in both forest fragments studied. We collected 41 ant species unique to the TDFs and 29 species exclusive to the surrounding environments.

The spatial partitioning of species diversity distributed among regions of Brazil [Fig. 3 (Mean)] shows that each sampling point (α) holds an average diversity (6.10 species) greater than expected by the null hypothesis (5.43 species) ($p < 0.01$). The beta diversity between the points of a same forest ($\beta_1 = 28.89$) was not different from the expected by the null hypothesis (mean estimate with 1000 randomizations $\beta_1 = 29.56$). The contribution of β_2 observed diversity (diversity between fragments) to the total diversity was higher than expected by the null hypothesis ($p < 0.01$). In the largest spatial scale examined (regions of Brazil), beta diversity observed (β_3) was higher than expected by chance ($p = 0.01$).

With the additive partitioning of diversity and null models for each region separately [Fig. 3 (Sites)], the observed alpha diversity was higher than expected from the null hypothesis in all regions ($p < 0.01$). Moreover, the observed β_2 diversity between fragments (TDF and surrounding areas) from all regions of Brazil was higher than expected by the null hypothesis ($p < 0.01$).

The NMDS showed that the ant community composition changes between the five regions of Brazil (Stress = 0.231, ANOSIM R = 0.665, p = 0.001, Fig. 4). According to the SIMPER analysis, the ant species that contributed most to the dissimilarity of the fragments distributed in Brazil were *Pheidole* sp.08 (sampled in the MS, RS and BA), *Camponotus melanoticus* (present in MG, MS and RS), *Camponotus atriceps* (occurred in GO and RS) and *Camponotus arboreus* (found in MG and MS).

The difference in species composition of ants among the studied regions was more evident when we analyzed only the ant community of TDFs. We found that the species composition of these forests differed among regions of Brazil (Stress = 0.219, ANOSIM R = 0.455, $p < 0.0001$, Fig. 5). *Camponotus arboreus*, *Pheidole* sp. 10, *Camponotus atriceps* and *Pheidole* sp. 5 were the species that contributed most to the differences in ant communities among these forests. *C. arboreus* occurred in the TDFs of MG and GO, *Pheidole* sp. 10 occurred in MG and BA, *C. atriceps* occurred in GO and RS, and *Pheidole* sp. 5 GO and MG.

Furthermore, there was dissimilarity in species composition of ants between the fragments of each region. The ants of the TDF were different from the surrounding vegetation community located in MG (Stress = 0.257, ANOSIM R = 0.334, $p < 0.0001$, Fig. 6a), MS (Stress = 0.258, ANOSIM R = 0.468, $p < 0.0001$, Fig. 6b), GO (Stress = 0.284, ANOSIM R = 0.507, $p < 0.0001$, Fig. 6c), RS (Stress = 0.244, ANOSIM R = 0.315, $p < 0.0001$, Fig. 6d) and BA (Stress = 0.305, ANOSIM R = 0.338, $p < 0.0001$, Fig. 6e). The species that contributed most to the dissimilarity of fragments of TDF and arboreal Caatinga (surrounding environment) in MG were *Ectatomma edentatum*, which occurred in the surrounding, and *Crematogaster* pr. *carinata* collected in the TDF. *Pheidole* sp. 19 and *Solenopsis* sp. 08 were the species that contributed most to the differences among the fragments of MS, and these two species were collected in the TDF. *Pheidole* sp. 03 and *Dolichoderus diversus* occurred in the pasture (surrounding environment) in GO and were the species that contributed most to the differentiation of the fragments in this state. The species that contributed most to the difference in species composition between the fragments of RS were *Linepithema micans* and *Camponotus melanoticus*. The first species occurred in the Semideciduous Seasonal Forest (surrounding environment) and the second in the TDF. In the state of Bahia, two *Solenopsis* species (*S*. sp. 04 and *S*. sp. 10) and *Simopelta curvata* were the species that contributed most to the dissimilarity of the fragments. *Solenopsis* sp. 04 and *Simopelta curvata* occurred in the Atlantic Forest (surrounding environment) and *Solenopsis* sp. 10 in the TDF.

DISCUSSION

Ecological processes *x* spatial scales

Components of the ant diversity partition in the different studied spatial scales were higher (α, β_2 and β_3) or equal (β_1) than expected by chance (Fig. 3). These deviations from the null model suggested that the only stochastic processes from the neutral theory (Hubbell, 2001), as the ecological drift, are not enough to explain the pattern of ant diversity in the studied sites, indicating that deterministic processes might also influence ant diversity at different spatial scales.

Several ecological and evolutionary processes can drive the change in diversity at different spatial scales (Messier *et al.*, 2010). On a finer scale, the biological community can be regulated by local factors (Tilman & Pacala, 1993; Chesson, 2000), such as the type and quality of habitat (Weibull *et al.*, 2003), disturbance (Klein *et al.*, 2002) and intra- and interspecific interactions (Veech *et al.*, 2003). Among these factors, we suggest that the lack of negative interspecific interactions may be the mechanism that allowed a higher mean ant diversity per sampling point (α_1) than expected by chance (Fig. 3). This high local diversity was probably because the interactions between species were minimized by the spatial organization of ant communities within the fragments, as the sampled strata of the forest (tree, epigaeic and hypogaeic) maintain distinct ant communities (see Brühl *et al.*, 1998; Bihn *et al.*, 2008). The ant fauna of these microhabitats is adapted to exploit different resources, relaxing the competitive interactions and allowing the coexistence of a higher number of species at each sampling point (Tobin, 1997).

Besides the ecological processes, the forces predicted in the neutral theory are also important in regulating the local community of ants. According to the theory by Hubbell (2001), all species have similar ecological properties, regardless of the ecological interactions involved in community dynamics. The ant species found within each studied fragment may have a similar potential of dispersal and colonization, since the average diversity between sampling sites (β_1) is not different from random (Fig. 3), indicating that species are homogeneously distributed within the forest fragments.

The pitfall trap is a widely used methodology to sample arthropods (Olson, 1991; Ribas *et al.*, 2003; Schmidt & Solar, 2010). Nevertheless, the spatial design of the sampling sites within a fragment may influence the results, since the proximity of the pitfalls can result in spatial similarity of species (Sanderson *et al.*, 1995; Niemela *et al.*, 1996) or the depletion of the local invertebrate fauna (Digweed *et al.*, 1995; Ward *et al.*, 2001). Ward *et al.* (2001) found no differences in richness, abundance and species composition of ants among pitfalls installed 1, 5 and 10 m apart. Moreover, there was no difference in beetle species richness among pitfalls spaced 10, 25 and 50 m (Digweed *et al.*, 1995). These null responses of species richness at different distance intervals among samplings may be due to the homogenous spatial distribution of fauna in the habitat, as hypothesized for the fauna of ants in this study of the fragments.

The spatial distribution of organisms within the environment can be classified in random, uniform or aggregated (Begon *et al.*, 2006). These patterns are the result of ecological relationships among species, such as competition (Duncan, 1991) and dispersion (Collins & Klahr, 1991), in addition to a response to abiotic factors (microclimate). If the distribution of species within the environment is random or aggregated, the distance of the traps must be larger than 25 meters, so that different populations can be sampled, avoiding the depletion of species richness (Digweed *et al.*, 1995). When species are homogeneously distributed within the forest, we believe that the distance between traps does not limit species richness accessed, as there is a high similarity of fauna between sampling points (Fig. 3: β_1). However, as this method of capture of the organisms is passive, we recommend the installation of a considerable number of traps in the area, so to increase the chance of capturing rare or underrepresented species.

Following the above reasoning, we have evidence of the action of the forces provided in the neutral theory in structuring local species richness of ants. These forces are determining a uniform distribution of ant species within the fragments studied. As posed by PAH, the discontinuous TDFs fragments maintain a the original biological diversity of existing continuous area in the Pleistocene, due to the evolutionary history of these forests (see Prado & Gibbs, 1993; Pennington *et al.*, 2000; Prado, 2000). As local factors do not influence the species richness in TDFs, we believe that non-random processes acting on a broad spatial scale may be the determinants of regional diversity in these forests.

In this study we found that the TDFs have diversity [Fig. 3 (β_2)] and ant species composition distinct from their surroundings (Fig. 6), which could indicate that these ant communities were structured by their evolutionary history. However, the ant species composition changes between patches of TDF (Fig. 5), which would be expected by the PAH. Based only on our results, we do not have evidence enough to say that the ant community cannot support this hypothesis, as more information is needed on, for example, the phylogeography of the most representative ant species that occur in these forests, to know the mechanisms that generated the actual geographical distribution of species. Among the ants exclusive to TDFs, *Crematogaster crinosa* would be a species with high potential to clarify the evolutionary history of these forests. This is a common species in dry forests and uncommon in other habitats (Longino, 2003), since it was not found in samples from the surrounding environments, ranging from dry forests to grasslands and wetlands. With this information aggregated to the pattern of diversity elucidated by this study, we would have enough evidence to support or refute the PAH.

Although some studies agree with the PAH (López *et al.*, 2006; Werneck & Colli, 2006; Caetano *et al.*, 2008), recent studies refuted this hypothesis (Mayle, 2004; Werneck *et al.*, 2010). According to Werneck *et al.* (2010), palynological evidence and modeling of the FEDs paleodistribution show that these forests are now more extensive than during the Pleistocene glaciations, as they expanded during the Holocene, following the same model of the historical distribution of the Atlantic Forest (see Carnaval & Moritz, 2008). Also according to this study, during the Pleistocene an east-west corridor linked two large TDF patches located in northeastern Brazil and in the extreme southwest of South America, which could serve as a dispersal route to plants and animals. Thus, the hypothesis of long-distance dispersal proposed by Mayle (2004) is the process that best explains the pattern of diversity of ants found in the fragments of current TDF. During the historical events, populations of species of ants may have migrated among TDF fragments through the dispersal corridor and, after the isolation of the areas, the ant community may have been suffered from external pressures of the biome in which was embedded, leading to different evolutionary histories that consequently led to different diversity (Fig. 3, β_2 and β_3) and ant species composition (Figs 4 and 5).

According to Hubbell (2001), the species composition of a local community would be more influenced by the composition of the surrounding metacommunity and by the dispersal rates of species that occur in the region, than by the evolutionary history of habitat. If the ant community was governed by the neutral theory, then the composition of ant species of TDFs would be similar to their surroundings (as opposed to that found in our study: Fig. 6). Moreover, the differences in composition should be based solely on dispersal limitations, which would increase with distance. We believe that dispersal is not a limiting factor for the species of ants, since 25% (41) of the sampled species occurred in all TDF fragments studied. Moreover, most of these species have wide distribution, since they are generalist species, such as species of *Crematogaster*, *Pheidole* and *Solenopsis*.

According to neutral theory, the divergence of TDFs (Fig. 5) would be solely due to the geographical distance between areas. However, we found that historical and biogeographical factors may also influence the species diversity of TDFs inserted in different biomes. Therefore, this evidence does not fully support the predictions of neutral theory in the determination of diversity, but reinforce the influence of non-random processes (TDF evolutionary history) on ant communities in a larger spatial scale.

We found scale-dependent differences in the spatial patterns of ant diversity, such as those detected for the community of canopy beetles in a deciduous forest in the U.S. (Crist *et al.*, 2003; Gering *et al.*, 2003). With the help of beta diversity in local and regional scales, it was possible to identify the processes (filters) that keep the spatial pattern of diversity found in TDFs. We hypothesize that the filter exerting a greater influence on ant community is the historic, which is determining a distinct community of ants at the landscape level (forest fragments) [Fig. 3: Sites (β_2) and Fig. 6] and regions of Brazil [Fig. 3: Mean (β_3) and Figs 4 and 5]. Similar results were found in the study by Gering *et al.* (2003). This spatial differentiation of diversity makes the Brazilian regions [(largest spatial scale examined), Fig. 3: Mean (β_3)], the hierarchical scale that contributes most to ant species regional diversity (γ).

TDF conservation

Communities may seem to be more or less diverse than expected by chance, depending on the scale of observation. Conservation efforts should consider the importance and magnitude of beta diversity at different spatial scales, in proposing the creation of new parks and protected areas. The partition of diversity can help in this determination, assisting in the selection of areas where ecological processes determine a significantly higher diversity than the random distribution of species. Furthermore, identification of critical scale is the crucial for pinpointing the appropriate spatial scale for habitat management and ecological restoration.

Our results suggest that different fragments of TDFs, distributed in various biomes of Brazil, should be protected and preserved, since each landscape maintain distinct ant communities. Creating multiple protected areas throughout the range of extension of TDFs prioritizes the preservation of both α and β diversities. In our data on the Brazilian TDFs, the β diversity of these forests appears to be related to processes acting on a large spatial scale (TDF evolutionary history). This process determines differences in ant species diversity and composition in the studied forest fragments. In this scenario, the non-governmental organizations (NGOs) and government institutions that finance the creation of new protected areas, should understand that a conservation area created to preserve the diversity in one site may not be sufficient to preserve all species of a region, as evidenced by our study of the area covered by TDFs.

In the Neotropics, the frontier of deforestation occurs mostly in a landscape dominated by TDFs, which has a high rate of human occupation (Portillo-Quintero & Sánchez-Azofeifa, 2010). It is needed to promote the creation of new protected areas and ecological corridors in fragmented landscape of TDF and in addition, involve local communities in sustainable management of TDFs. To do that, is necessary to create alternative sources of income, such as rural tourism and sustainable exploitation of natural resources. These points should be more seriously considered as a high priority measure for conservation of remaining habitats and species that occur in TDFs.

We conclude that, despite the additive partitioning only elucidate the pattern of diversity of a region at different spatial scales (Gering & Crist, 2002), this analysis helps to identify possible non-random processes that govern the diversity. Thus, this technique has helped us to identify the scales where ecological processes differed disproportionately the total diversity of ants, indicating the spatial scale that contributes most to regional diversity, which becomes the primary target for conservation efforts. Furthermore, the partition of diversity also allowed us to highlight the appropriate spatial boundary (between sampling points) to study the processes of the neutral theory, which generated a homogeneous distribution of ants within the fragments. Thus, we suggest that further work should be carried out to understand the processes that interact at the local level to maintain the homogeneous distribution of ants within the fragments of TDF.

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BIOSKETCHES

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FIGURE LEGENDS

Figure 1 Schematic model of the passage of species through selective "filters", spatial scale dependent. Each filter represents the action of ecological processes in determining the biological diversity of a community. Adapted from Blenckner & Hillebrand (2002).

Figure 2 Distribution of main vegetation types in Brazil, in particular, the Tropical Dry Forest (TDF), indicating the study sites located in five regions of Brazil: Bahia (BA) (1), Minas Gerais (MG) (2), Goiás (GO) (3), Mato Grosso do Sul (MS) (4) and Rio Grande do Sul (RS) (5). Modified from Espírito-Santo *et al.* (2009), with permission.

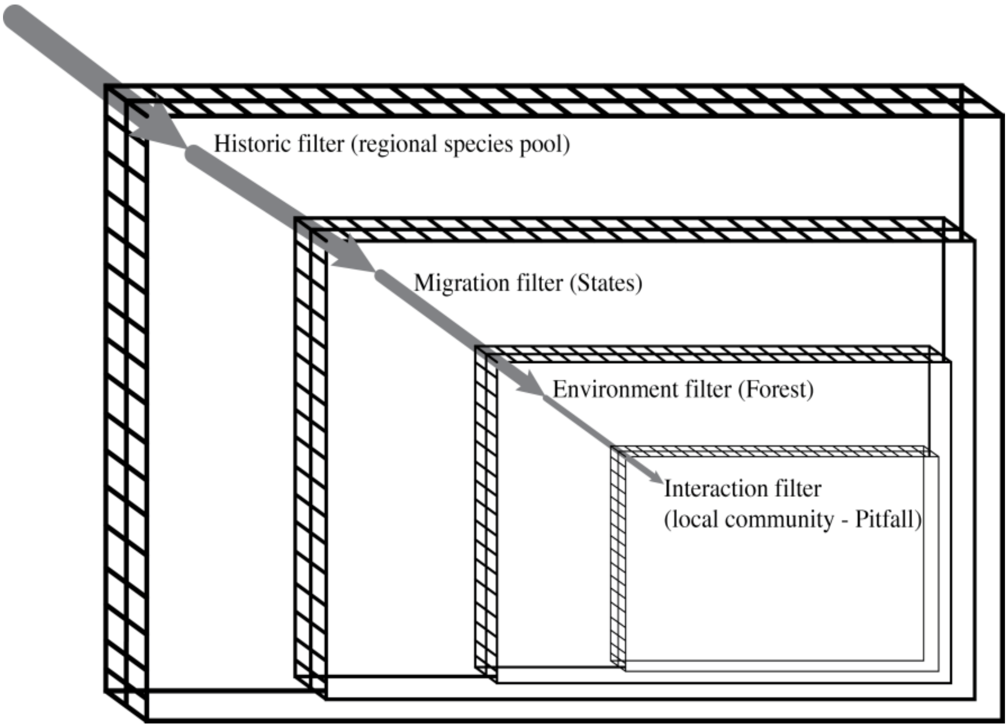
Figure 3 Diversity additive partitioning of ants among hierarchical spatial scales [sampling points, fragments (Tropical Dry Forests and surrounding areas) and regions of Brazil]. The partition observed (Obs) was compared with expected values (Exp) calculated by the null model for the average among the five regions of Brazil (Mean) and for each region separately, located in Bahia (Site 1), Minas Gerais (Site 2), Goiás (Site 3), Mato Grosso do Sul (Site 4) and Rio Grande do Sul (Site 5). Asterisks indicate cases where the observed components of diversity differed from the expected ($p < 0.05$).

Figure 4 Ant species composition of the fragments (Tropical Dry Forests and surroundings) located in different regions of Brazil: Minas Gerais (■), Mato Grosso do Sul (▲), Goiás (Δ), Rio Grande do Sul (+) and Bahia (□). The analysis of nonparametric multidimensional scaling (NMDS) was based on Euclidean distance of the data ($p = 0.001$).

Figure 5 Ant species composition Tropical Dry Forests located in different regions of Brazil: Minas Gerais (■), Mato Grosso do Sul (▲), Goiás (Δ), Rio Grande do Sul (+) and Bahia (□). The analysis of nonparametric multidimensional scaling (NMDS) was based on Euclidean distance of the data ($p < 0.0001$).

Figure 6 Composition of ant species of Tropical Dry Forests (■) and their surroundings (□) located in Minas Gerais (a) and Mato Grosso do Sul (b), Goiás (c), Rio Grande do Sul (d) and Bahia (e). The analysis of nonparametric multidimensional scaling (NMDS) was based on Euclidean distance of the data ($p < 0.0001$).

FIGURES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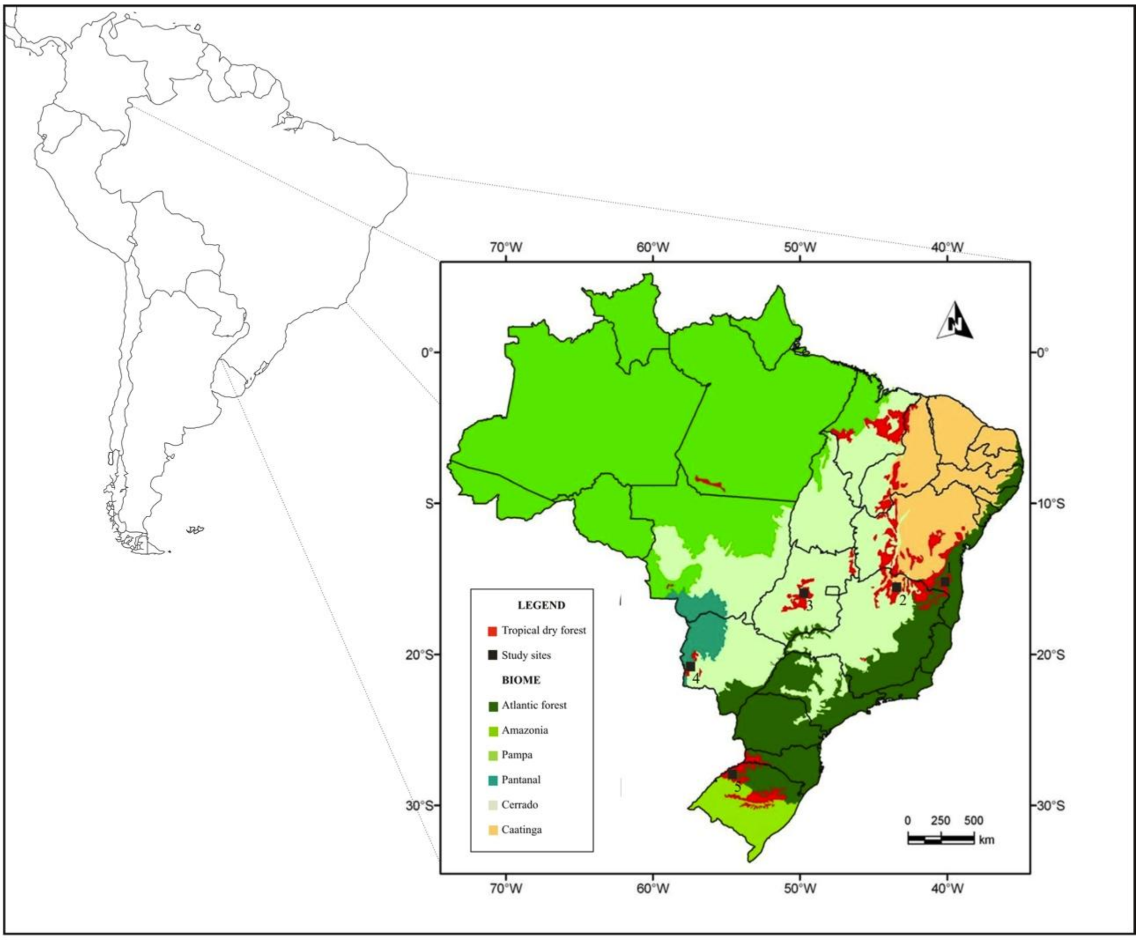
Migration filter (States)
Environment filter (Forest)
Interaction filter
(local community - Pitfall)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LEGEND
Tropical dry forest
Study sites
BIOME
Atlantic forest
Amazonia
Pampa
Pantanal
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0 250 500
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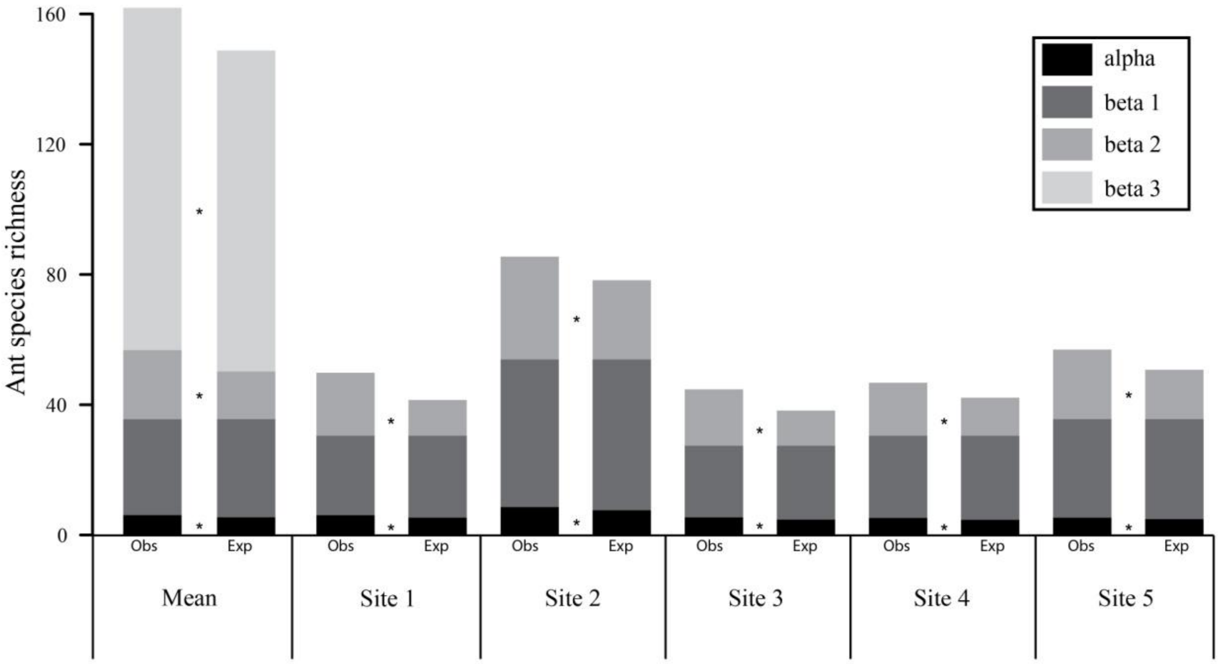
Ant species richness
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80
120
160
alpha
beta 1
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Site 1
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Site 4
Site 5
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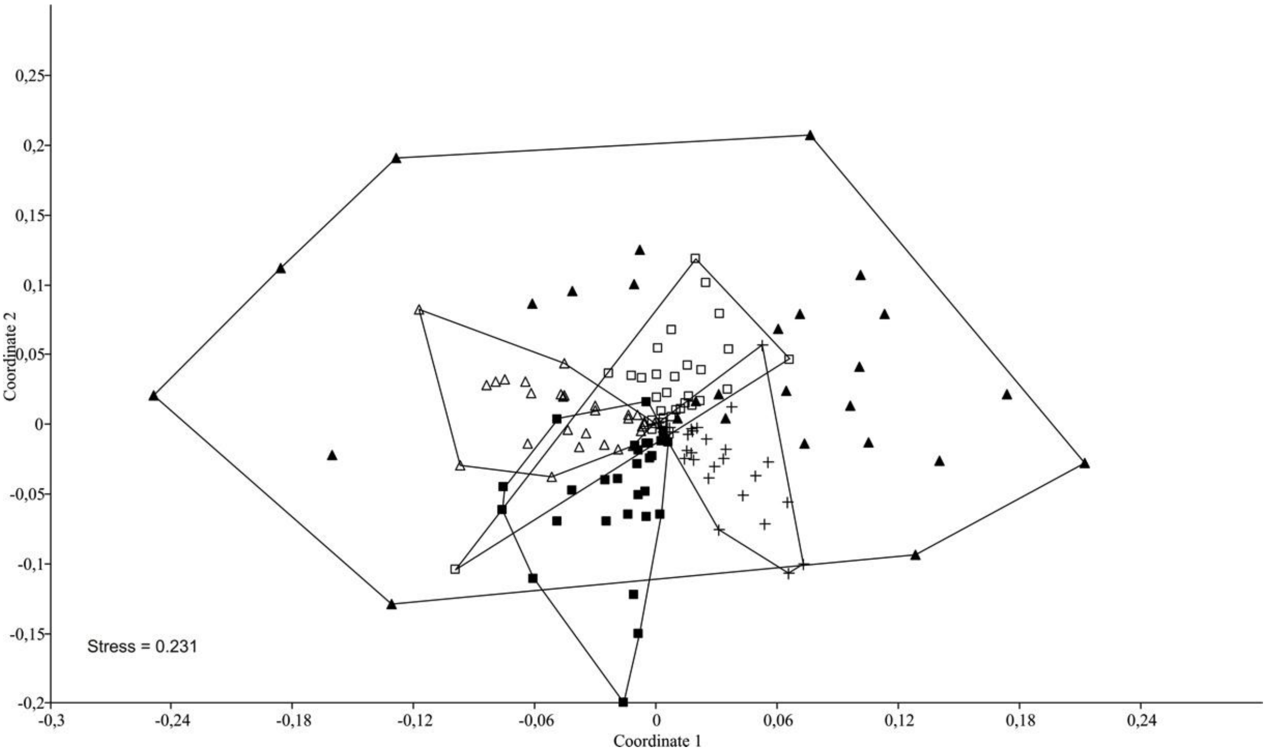
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Coordinate 1
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0,15
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0
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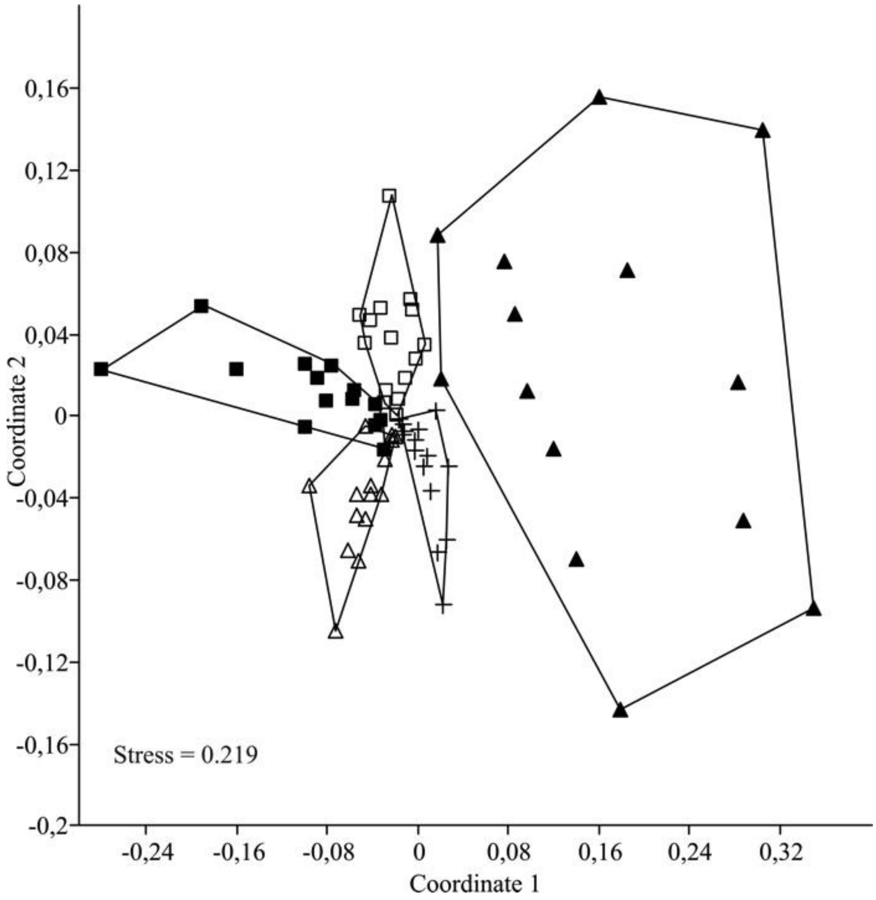
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Coordinate 1
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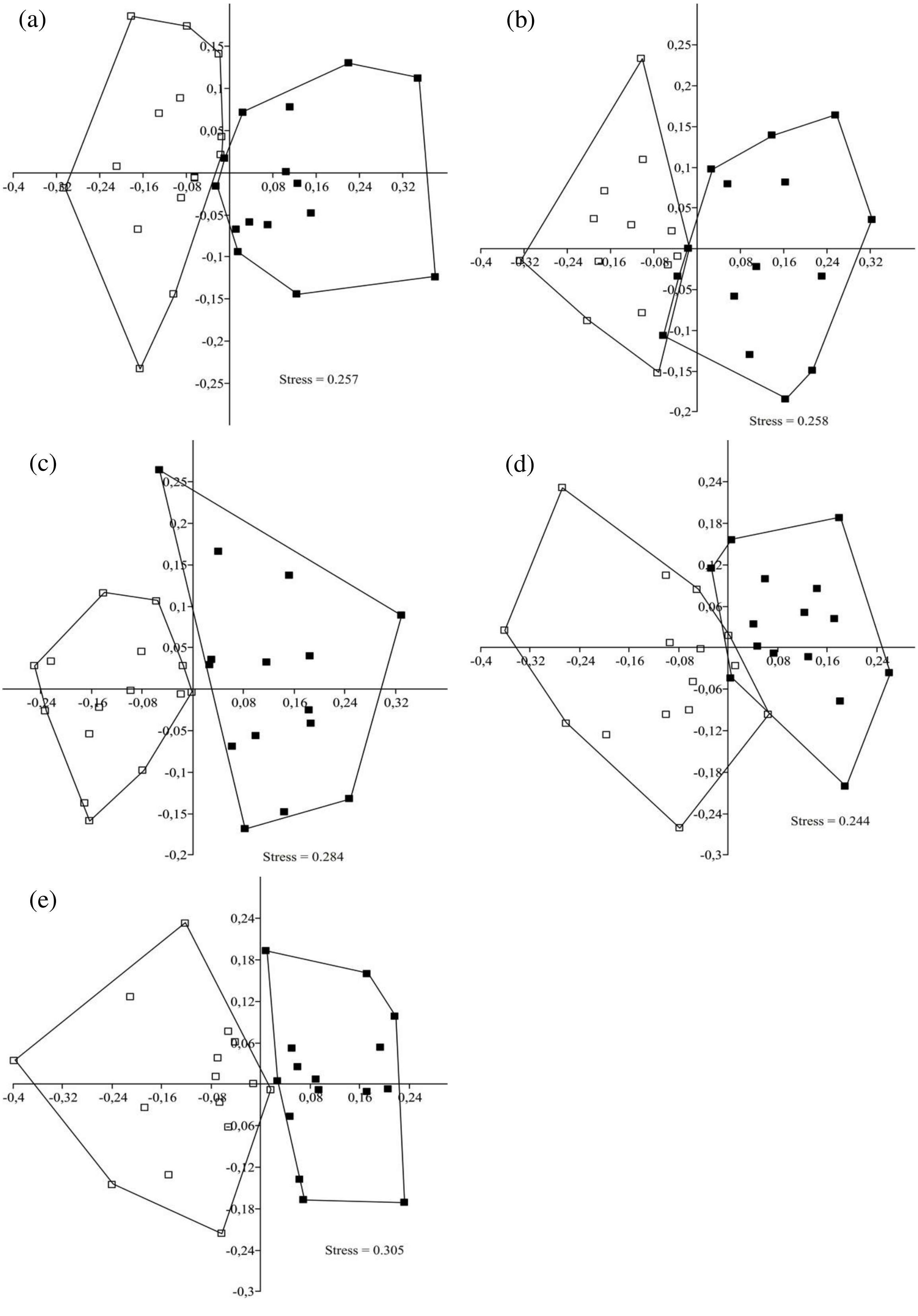
(a)
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(b)
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(c)
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(d)
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(e)
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CONCLUSÃO GERAL

Os resultados da presente tese evidenciam que o estudo da influência relativa das diferentes escalas espaciais e temporais sobre a riqueza de espécies, pode produzir uma série de evidências a respeito dos fatores causadores da diversidade local.

Com relação ao estudo realizado em diferentes escalas de tempo na Floresta Estacional Decídua (FED) (Capítulo 1), vimos que a variação da riqueza de espécies de formigas é mais abrupta em uma menor escala de tempo (sazonalidade) do que numa escala de tempo mais ampla (sucessão). Analisando cada escala separadamente, vimos que o número de espécies de formigas aumenta durante o processo sucessional, como previsto pelo modelo de comunidade controlada por dominância (veja Dauber & Wolters 2004, 2005). Este padrão é sustentando pela fauna de formigas do microhabitat hipogéico, pois os estágios sucessionais não influenciaram a riqueza de formigas arbóreas e epigéicas. Isto pode ser devido às formigas hipogéicas estarem intimamente ligadas aos processos que ocorrem neste estrato da floresta (e.g. ciclagem de nutrientes) (Lobry de Bruyn 1999; Sousa-Souto et al. 2007). Sendo assim, pode-se considerar as formigas hipógeicas mais sensíveis às alterações que ocorrem na floresta durante o processo de sucessão ecológica do que as formigas dos outros microhabitats. Em conclusão, as comunidades de formigas de cada microhabitat da FED em sucessão, apresentam diferentes padrões de diversidade e consequentemente, diferentes processos regulam a diversidade de espécies. Portanto, a fauna de formigas hipogéicas pode indicar com maior precisão as consequências da modificação do habitat sobre a diversidade biológica.

Na escala de tempo menor, a riqueza de espécies de formigas da FED é maior na estação seca do que na estação úmida. Este padrão é diferente dos resultados tradicionalmente encontrados nos estudos realizados em florestas úmidas (veja Lindsey & Skinner 2001, Torchote et al. 2010). No entanto, este padrão é cada vez mais consistente para estudos realizados em FEDs. Este fato faz com que as extrapolações dos padrões encontrados nas florestas úmidas não são sejam corretamente aplicadas às FEDs, já que são florestas que apresentam características estruturais e fisiológicas bastante diferentes.

Com relação às escalas espaciais, encontramos resultados bastante interessantes sobre a diversidade de formigas das FEDs em múltiplas escalas (Capítulo 2). Primeiro, acreditamos que o uso da partição aditiva da diversidade para o teste de modelos nulos foi bastante inovador e contribuiu de maneira significativa para o impacto do estudo. Encontramos que a diversidade de formigas está distribuída desproporcionalmente entre as escalas espaciais analisadas. A maior escala espacial de estudo (regiões do Brasil) foi a que mais contribuiu para diversidade regional de formigas das FEDs. Apesar desta variação da riqueza de espécies entre as escalas ser resultado da ação de diferentes processos não-aleatórios, temos evidências suficientes para indicar a história evolutiva das FEDs como o principal processo estruturador da riqueza e composição de espécies de formigas destas florestas. Com este estudo, estamos contribuindo para o entendimento dos processos determinantes da distribuição das espécies de formigas nas múltiplas escalas espaciais. Além disso, foi possível apontar o limite espacial adequado para a conservação e manejo do habitat (maior escala analisada: regiões do Brasil).

Em conclusão, os estudos desenvolvidos na presente tese contribuem de maneira significativa no conhecimento dos processos ecológicos reguladores da diversidade de formigas em diferentes escalas espaciais e temporais nas FEDs. Além disso, e não menos importante, com os nossos estudos expandimos o conhecimento sobre a ecologia e dinâmica das FEDs. Por este ecossistema ainda ser negligenciado por organizações não governamentais e instituições federais na obtenção de recursos para sua conservação e restauração ambiental (Portillo-Quintero & Sánchez-Azofeifa 2010), com os nossos resultados constatamos e enfatizamos de maneira categórica a importância da preservação das áreas remanescentes e secundárias de FEDs. Tal preservação auxiliará na conservação das espécies e do ecossistema. Além disso, com uma orientação adequada, a população que reside perto de uma área de proteção ambiental de FED, poderá desfrutar dos recursos que a floresta oferece, criando uma fonte alternativa de renda para as populações carentes.

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