

Habitat structure
in the composition of leaf-litter insects
in mosaic environment ¹

Estrutura do habitat
na composição de insetos de serapilheira
em ambiente de mosaico ¹

RENAN DA SILVA OLIVIER²

RODRIGO ARANDA³

MAURÍCIO NEVES GODOI³

ANA GABRIELLA LOBO VILALVA²

According to “habitat heterogeneity hypothesis”, proposed by MACARTHUR AND MACARTHUR (1961), heterogeneous environments offer greater amount of niches and resources resulting in greater species richness (BAZZAZ, 1975; HASTINGS, 1990; MCINTYRE *ET AL.*, 2001). The heterogeneity is an important characteristic and affect many ecological systems (LI & REYNOLDS, 1995; VINATIER *ET AL.*, 2011). In most ecosystems, plants are largely responsible for environment physical structure and, therefore, influences habitat complexity and distribution and interactions between species in multiples scales (LAWTON, 1983; MCCOY & BELL, 1991; HU *ET AL.*, 2014). Deposition patterns of leaf-litter can also promote environmental heterogeneity, while influencing the dynamics of plant and animal communities (FACELLI & PICKETT, 1991; MOLOFSKY AND AUGSPURGER, 1992). The leaf-litter is an important component in forests and wooded savannas, consisting of dead organic matter composed mostly of flowers, fruits and decaying leaves (DIAS & OLIVEIRA-FILHO, 1997). Indeed, the accumulation of fallen leaves forms

¹ Universidade Federal de Mato Grosso do Sul (UFMS) — CEP 79090-900, Campo Grande (Mato Grosso do Sul). ² Laboratório de Sistemática, Ecologia e evolução, Centro de Ciências Biológicas e da Saúde. ³ Programa de Pós-Graduação em Ecologia e Conservação.

an important soil microenvironment of these environments, maintaining a stable temperature with high humidity, which supports the existence of many organisms, especially arthropods and the characteristics of local leaf-litter can affect the communities (BASSET, 1996; BAR-MASSADA *ET AL.*, 2014).

Insects are a diverse and abundant group in terrestrial environments which assume significant roles in ecosystems (HUGHES *ET AL.*, 2000), participating in nutrient cycling and soil formation processes. Through nests, galleries and acorns, fecal arthropods cause soil aggregation by acting on hydraulic properties and dynamics of organic material (LAVELLE & SPAIN, 2001; HUNTER, 2002). Herbivorous insects also regulate plant populations, while in general serve as a food source for many animals (YORK, 1999; ANDERSEN *ET AL.*, 2003). Performing these functions, insects act as important components in ecosystems (KREMEN *ET AL.*, 1993). Insects that comprise soil fauna can be diggers, decomposers, transporters of mineral material, predators, fungal feeders and consumers of roots (GULLAN & CRANSTON, 1994; LAVELLE & SPAIN, 2001). Moreover, these animals can spread passively several microbial species at different levels in soil by their vertical movements (SEASTEDT, 1984; MOORE *ET AL.*, 1988; GULLAN & CRANSTON, 1994) which affect the decomposition rate of leaf-litter (SEASTEDT, 1984). In addition, soil insects can assist humus fragmentation and enable complex interactions between organisms in terrestrial ecosystems (BUTCHER, 1971).

Leaf-litter insect communities are influenced by various environmental factors such as humidity, vegetation type, mass, and leaf-litter depth (MENEZES *ET AL.*, 2002; MCINTYRE *ET AL.*, 2001). These factors can be influenced by openings or reduced clearing of tree cover as part of managed forestry (DIAS-FILHO, 1998; MENEZES *ET AL.*, 2002) and this configuration as an ecological filter for species (DUFLOT *ET AL.*, 2014). These changes profoundly affect the structure and dynamics of the forest, and, thus also affect leaf-litter insect communities (MENEZES *ET AL.*, 2002). While are sensitive to such changes, arthropods also serve as indicators of ecosystem functioning (LINDEN *ET AL.*, 1994; ILLIG *ET AL.*, 2010), therefore, studies which seek to measure and characterize the diversity of soil insect communities can contribute to various ecological problem solutions (GOLDEN & CRIST, 1999; FAHRIG, 2003; RUBBO & KIESECKER, 2004; GOMES *ET AL.*, 2007; SOUZA *ET AL.*, 2008).

The aim of this study is to evaluate the effect of habitat heterogeneity on richness, abundance and composition of insect's leaf-litter community. We tested the hypothesis that heterogeneous environments have higher abundance and richness of insects, and species composition is different between environments.

MATERIAL AND METHODS

STUDY AREA

The study was conducted at *Estancia Mimosa Ecoturismo (EME)* ($20^{\circ}58'57.70''\text{S}$ - $56^{\circ}30'58.40''\text{W}$) (Fig. 1), a farm in Bonito city, Mato Grosso do Sul, approximately 20 km from Bodoquena Range National Park (BRNP). This property has approximately 400 ha and bounded by the Mimoso River along its southern portion. The region substrate is rocky and covered by one of the last remaining areas of plateau vegetation, characterized by a predominance of deciduous and semideciduous forest (BOGGIANI *ET AL.*, 1999), but the substrate also contains savanna formations and gallery forest (FARIA & ARAÚJO, 2010) and areas of active and abandoned pastures.

SAMPLES

We collected samples from September 2011 to June 2012. 103 samples were randomly selected with each plot spaced 200 meters apart, overlapping samples. These plots were distributed in five distinct vegetation types: Deciduous forest (DF), Riparian forest (RP), Savanna (S), Cerradão (CC) and Dirty pastures (DP) (Table 1). Vegetation type

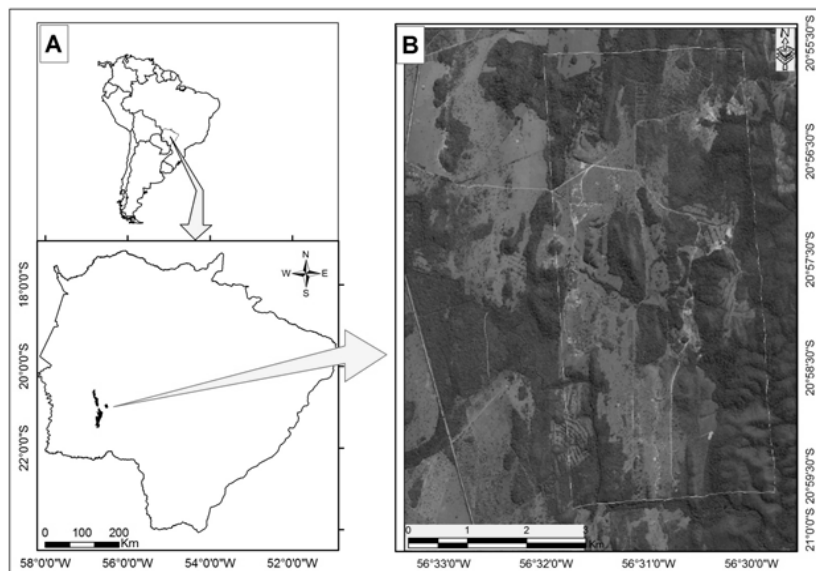


Fig. 1. Location of Bodoquena Mountains (A) and *Estância Mimosa Ecoturismo* (B) in the municipality of Bonito, Mato Grosso do Sul (Brazil).

Table 1. Description of vegetation types found in the study area, Bodoquena Mountains, state of Mato Grosso do Sul. Number of sample in each vegetation type (n). [Adapted from RIBEIRO & WALTER (1998); CIRELLI & PENTEADO-DIAS (2003)].

DECIDUOUS FOREST (47)	Predominance of large woody individuals, 10 to 25 meters, with a dense canopy and understory continuous and well developed.
RIPARIAN FOREST (8)	Forest vegetation accompanying rivers of medium and large size of the Cerrado region, where woody vegetation does not form galleries.
CERRADÃO (15)	Characterized by the presence of species that occur in the Cerrado and also by species of woods (xeromorphic aspect). It provides predominantly a continuous canopy and tree cover which can oscillate 50 to 90 %. The average height of the tree stratum varies from 8 to 15 meters, which provides lighting conditions that favor the formation of differentiated shrub and herbaceous.
SAVANNA (23)	Characterized by the presence of low, very rigid trees with characteristics such as sloping and winding, with branches twisted and irregular, often with evidence of burnt leaves. Some species presenting underground organs of resistance (xilopodes), allowing regrowth.
DIRTY PASTURES (10)	Brachiaria pastures and other exotic grasses with high cover bushes and trees.

DESCRIPTION

For each plot we harvested four subplot of leaf-litter samples which were distributed cardinally (north, south, east and west) ten meters from the center of the plot. Each subplot sample was removed from an area of 400 cm² (20 x 20 cm) totalizing 1600 cm² per plot and immediately stored in plastic bag, properly labeled, and subsequently taken to the Laboratory of Zoology at the Universidade Federal de Mato Grosso do Sul, for triage and identification of specimens. All insects were identified based on: COSTA *ET AL.* (2006), TRIPLEHORN & JOHNSON (2011) and RAFAEL *ET AL.* (2012).

We classified the environments according to the following variables: number of trees (dbh 10 cm), number of dead trees, number of shrubs (dbh<10 cm), canopy height (m), canopy cover (%), herbaceous height (cm), herbaceous cover (%) and leaf-litter cover (%). All these variables were measured at four locations in each plot, in the same locations where the leaf-litter was collected and subsequently tabulated according to mean values.

DATA ANALYSIS

Descriptive analysis of community is based on taxonomic level until family. We also present values associated with richness and abundance. Analysis of Variance (Anova) and Kruskal-Wallis analyses were realized to verify differences in richness and abundance between environments. Non-Metric Multidimensional Scaling (NMDS)(Bray-Curtis similarity) were performed to analyze the insect community, simple linear regression correlates the data on the insect community (NMDS) against the environmental variables (Principal Components Analysis — PCA). The percentage of similarity between the groups was calculated for environments using measures of Bray-Curtis similarity. Non-parametric multivariate analysis of variance (NPMANOVA) with 10.000 permutations was realized to test for differences in community composition between vegetation types. Canonical correspondence analysis (CCA) was used to verify the effect of environmental variables on species composition.

RESULTS

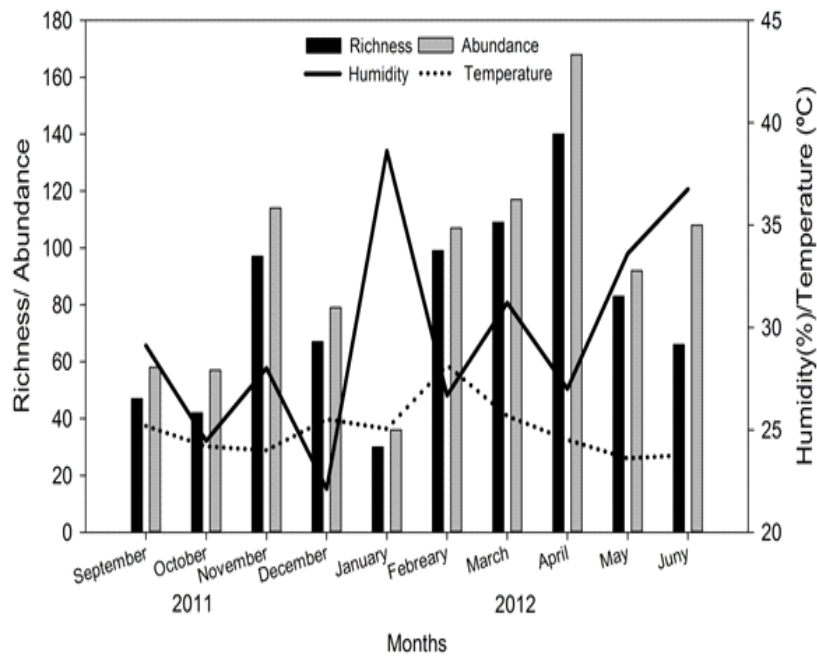
Was sampled 630 insects belonging to 32 families were collected, which Blattidae (76), Formicidae (63, just presence and absence), Carabidae (52), Blatellidae (37), Staphylinidae (19), Tenebrionidae (12), Reduviidae (11), Mogoplistidae e Termitidae (10), Scarabaeidae (eight), Cicadellidae (seven) and Curculionidae (six) were the most representative. The remaining 24 taxa showed an abundance less than or equal to five. Among larvae, the most abundant group was Lepidoptera (241), followed by Diptera (30) and Coleoptera (20) (Table 2). We could observe the monthly variation of richness and abundance in the rainy season (Figure 2). There was not a statistically significant difference in richness (Anova, $F=0.297$, $p = 0.879$) and abundance (Kruskal-Wallis, $H= 0.215$, $d.f.=4$, $p= 0.995$) between environments. An analysis of insect community (NMDS, Stress = 0.26) (Fig. 3) revealed a correlation with vegetation types and difference in the composition related to vegetation type (NPMANOVA, $F= 2.553$, $p= 0.0003$). The vegetation types had different values than the composition similarity (Table 3).

Table 2. Insects sampled in leaf-litter at *Ecotourism Estancia Mimosa*. Occurrence in habitats: 1, Savannah; 2, Cerradão; 3, Decidua forest; 4, Dirty pasture; 5, Riparian forest.

Order	Family	Environment
Blattaria	Blatellidae	1,2,3,4,5
	Blattidae	1,2,3,5
Coleoptera	Anobiidae	1
	Buprestidae	3
	Carabidae	1,2,3,5
	Curculonidae	1,3
	Immature	1,3
	Nitidulidae	3
	Ptylodactilidae	3
	Rhysodidae	1
	Scarabaeidae	1,2,3,5
	Staphylinidae	1,2,3
	Tenebrionidae	2,3
	Zopheridae	1
Dermaptera	Anisolabididae	5
Diptera	Immature	1,2,3,5
	Phoridae	1
	Psychodidae	1
	Sciaridae	2
Hemiptera	Cicadellidae	2,3,5
	Cicadidae	1
	Pentatomidae	1,2
	Reduviidae	1,2,3,4
Hymenoptera	Ampulicidae	3
	Braconidae	4
	Formicidae	1,2,3,4,5
	Mutillidae	1
Isoptera	Termitidae	1
Lepidoptera	Immature	1,3,5
Neuroptera	Myrmeleontidae	2,3
Orthoptera	Acrididae	1,3,5
	Proscopiidae	1
Psocoptera	Lachesillidae	3
Trichoptera	Phryganeidae	3

Table 3. Percentage of similarity between environments and values of non-parametric multivariate analysis of variance (NPMANOVA). *statistical significance ($p \leq 0,05$).

Similarity between environments	%	NPMANOVA (p)
Dirty pasture vs Riparian forest	73,33	0,003*
Deciduous forest vs Dirty parture	65,65	0,0015*
Riparian forest vs Savanna	64,07	0,0104*
Cerradão vs Riparian forest	62,18	0,0209*
Deciduous forest vs Riparian forest	61,24	0,108
Deciduous forest vs Savanna	59,61	0,0401*
Dirty pasture vs Savanna	59,12	0,0514*
Cerradão vs Deciduous forest	59,06	0,0081*
Cerradão vs Dirty parture	58,35	0,0345*
Cerradão vs Savanna	55,43	0,706
Total similarity	60,15	

Fig. 2. Monthly variation in species richness and abundance of individuals in leaf litter due to changes in temperature ($^{\circ}$ C) and humidity (%) between the months of September 2011 to June 2012.

There was also a positive relationship between evaluated community composition (NMDS) and environmental variables (PCA) (linear regression, $R^2=0.195$, $p<0.001$) (Fig. 4).

Through CCA we saw that many variations were explained by canopy height (27.40%), shrub height (20.08%), dead tree (18.09%), canopy cover (11.49%) and herbaceous cover (9.40%) variables. However, only leaf-litter cover was the variable with a significant influence (8.42%, $p=0.003$) (Fig. 5). We could see that even without significance, the most explanatory values were related to leaf-litter formation.

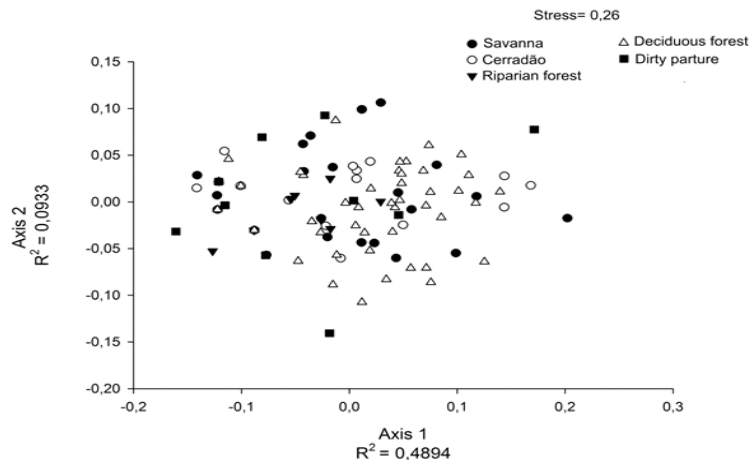


Fig. 3. Non-Metric Multidimensional Scaling (NMDS) of the insects leaf-litter community in different phytophysionomies.

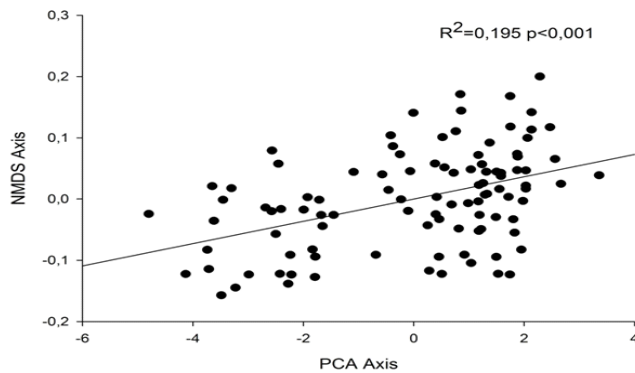


Fig. 4. Linear regression between Non-Metric Multidimensional Scaling (NMDS) (insect community) and Principal Component Analysis (PCA) (environmental variables).

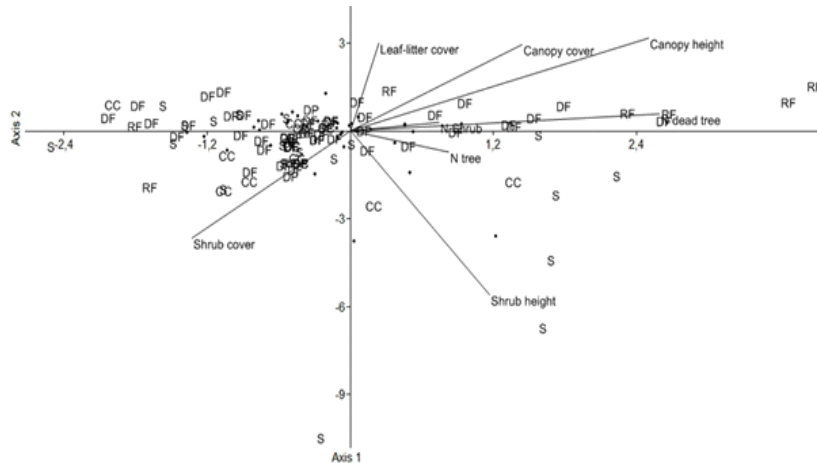


Fig. 5. Canonical correspondence analysis (CCA) of environmental variables on community composition of leaf litter insects. CC, Cerradão; DF, Deciduous forest; DP, Dirty pasture; RF, Riparian forest; S, Savanna. Black dots morphotypes.

DISCUSSION

In contrast with literature (GOLDEN & CRIST, 1999; CAGNOLO *ET AL.*, 2002; TEWS *ET AL.*, 2004; MENEZES *ET AL.*, 2009), our study did not find greater abundance or richness of arthropods in heterogeneous edaphic habitats. Instead, low microclimatic variation, and the variation of heterogeneity within vegetation types, probably explains the lack of a positive relationship between abundance or richness and environmental heterogeneity gradient, what would be expected. Indeed, MENEZES *ET AL.*, (2009) found greater richness of insect species in better structured edaphic environments with higher heterogeneity, since these environments provide better trophic conditions and a less variable microclimate. GOLDEN & CRIST (1999) and CAGNOLO *ET AL.* (2002) observed that soil arthropods have low species richness in altered environments instead of greater homogeneity. Similar results exhibiting lesser abundance of insects in more homogeneous areas formed by *Pinus* species (ALCARAZ & AVILA, 2000; GANHO & MARINONI, 2006). Moreover, savannah formations have naturally lower humidity keeping insect populations with low abundance.

Environments with distinct phytophysiological characteristics present an insect community composition significantly different indicating that community structure is more influenced by environmental characteristics than richness or abundance. Metrics as richness and abundance do not

respond effectively the structural variations of the environment. Depending on the group, we have patterns of higher abundance of individuals in open areas, but belonging to few species, for example Orthoptera (PFADT, 1984) and general herbivorous (FAHRIG & JONSEN, 1988).

Habitat provides little explanations about the observed insect community structure (19.5 %). This may be related with the choice of variables used as predictors of vegetation complexity. Microclimate and microhabitat variation, in each plot, may be the most important factor which influences the community structure, as an issue pointed by other studies (ROCHA *ET AL.*, 2010; VASCONCELLOS *ET AL.*, 2010). For Coleoptera, the ground-dwelling community is highly influenced by local variables (JANSSEN *ET AL.*, 2009), which directly responds the micro-variation of community structure metrics (*e.g.*, leaf-litter depth and quality). Furthermore, larger-scale habitat variables, as chosen in this study, correlate only partially with the structure of the arthropod community (BARTON *ET AL.*, 2010).

The direct relationship among arthropods and different gradients of environmental complexity is undoubtedly linked to arthropods nutritional needs. WARREN & ZOU (2002), for example, examining the distribution of millipedes related to soil in three different fields, found that distribution of such groups was strongly influenced by quality of the leaf-litter, as well as the availability of nutrients. Also CAGNOLO *ET AL.*, (2002), observed a correlation between taxonomic composition changes and guilds formation in native grasslands. Trophic guild groups composition indicates that more generalist species colonize multiple habitats, while the presence of more specialist species is related to a greater or lesser degree of environmental heterogeneity, depending on biological needs of each constituent group.

In addition, we have the presence of disturbed areas, such as dirty pasture, and alteration of native vegetation by exotic pasture, which can be an important factor on species occupation. We can observe high similarity between groups composition and environments, as riparian, deciduous forest and dirty pasture. This high similarity between different environments is mainly a physical space issue. The dirty pasture permeates the riparian areas and deciduous forest, being spatially closer, facilitating dispersion and allowing highest similarity between areas.

Thus, we observe that community metrics like richness and abundance, analyzed separately, do not respond to changes in community structure. However, when considering the composition of arthropod community, we observe a relationship between the arthropod leaf-litter community and environmental predictor variables. Though microclimate and microhabitat variables on a small scale correlate robustly with community structure, composition is directly related to habitat structure.

SUMÁRIO

Os padrões de recrutamento da serapilheira são determinantes importantes da comunidade de artrópodes do solo, que são fundamentais para a manutenção dos ecossistemas. Comunidades de insetos são influenciadas por vários fatores ambientais da serapilheira. Esses fatores podem ser afetados por aberturas ou reduzido desmatamento de cobertura de árvores, e o nível de complexidade ambiental influencia diretamente nesta dinâmica. Este estudo tem como objetivo analisar a relação entre a estrutura do habitat e da riqueza, abundância e composição da comunidade de insetos de serapilheira. Nós testamos a hipótese de que ambientes mais heterogêneos teriam valores mais elevados relacionados com as métricas da comunidade de insetos. Foram analisados 103 lotes de cinco tipos de vegetação distintas. De cada parcela, foram coletadas quatro amostras de 20cm² de serapilheira e, posteriormente, submetidas à triagem e identificação dos espécimes. A classificação ambiental foi realizada de acordo com as seguintes variáveis ambientais: número de árvores (DAP > 10 cm), número de árvores mortas, número de arbustos (DAP < 10 cm), altura do dossel (m), cobertura do dossel (%), herbácea altura (cm), cobertura herbácea (%), cobertura de serapilheira (%). Foram coletados 630 indivíduos distribuídas em 32 famílias. Não há nenhuma relação entre a riqueza ou abundância e heterogeneidade. Apesar da comunidade como um todo não mostrar relação, no entanto, existe uma relação positiva entre a estrutura do habitat e grupos específicos apresentaram preferência por determinadas áreas. Embora a comunidade responda a variações de habitat, as variações de microclima e microhabitat possivelmente também afetam a heterogeneidade da mesofauna do solo.

PALAVRAS-CHAVE: fauna edáfica; complexidade do habitat; Insecta, distribuição espacial

SUMMARY

Patterns of leaf-litter training are important determiners of soil arthropod communities, which are fundamental for the maintenance of ecosystems. Insects communities are influenced by various leaf-litter environmental factors. These factors can be affected by openings or reduced clearing of tree cover, and the level of environmental complexity directly influences this dynamic. This study aims to analyze the relationship between habitat structure and the richness, abundance and composition of the leaf-litter insect community. We test the hypothesis that more heterogeneous environments produce higher values related to the metrics of insect community. We analyzed 103 plots from five distinct vegetation types. From each plot, we collected four samples of 20cm² leaf-litter,

and subsequently submitted for the screening and identification of the specimens. The environmental classification was performed according to the following environmental variables: number of trees (dbh >10 cm), number of dead trees, number of shrubs (dbh <10 cm), canopy height (m), canopy cover (%), herbaceous height (cm), herbaceous cover (%), leaf-leaf-litter cover (%). We collected 630 individuals of Insecta distributed in 32 families. There is no relationship between richness or abundance and heterogeneity. Despite community as a whole, however, there is a positive relationship between habitat structure and specific groups preference for certain areas. Though the community responds to variations in habitat, variations in microclimate and microhabitat possibly also affect the soil mesofauna heterogeneity.

KEY WORDS: edafic fauna; habitat complexity; Insecta; Spatial distribution

RÉSUMÉ

Les modes de recrutement en litière de feuilles sont déterminants importants de la communauté des arthropodes du sol qui sont fondamentales pour la maintenance des écosystèmes. Les communautés d'insectes sont influencés par plusieurs facteurs environnementaux des litières de feuilles. Ces facteurs peuvent être affectés par des ouvertures ou par la réduction de la déforestation des canopées, et le niveau de la complexité 'environnemental influe directement sur cette dynamique. L'objectif de cette étude est d'analyser la relation entre la structure de l'habitat et de la richesse, l'abondance et la composition de la communauté des insectes de la litière de feuilles. Nous avons testé l'hypothèse de que des environnements plus hétérogènes ont des valeurs plus élevées liées aux mesures de la communauté d'insectes. Nous avons analysé 103 lots de cinq types distincts de végétation. Pour chaque parcelle, quatre échantillons de 20cm² de litière de feuilles ont été collectées, et par la suite a été prise le dépistage et l'identification des spécimens. La classification de l'environnement a été faite en fonction des variables environnementales suivantes: nombre d'arbres (DHP > 10 cm), le nombre d'arbres morts, le nombre des arbustes (DHP <10 cm), taille de la canopée (m), la couverture de la canopée (%), la taille des herbacées (cm), couverture herbacée (%), couverture de litière (%). Nous avons collecté 630 individus réparties dans 32 familles. Il n'y pas aucune relation entre la richesse ou l'abondance et la variété. Bien que la communauté comme un ensemble, cependant, il y a une relation positive entre la structure de l'habitat et des groupes spécifiques ont montré de la préférence pour certaines zones. Bien que la communauté de répondre aux changements d'habitat, les changements dans le microclimat

et microhabitat éventuellement affectent également l'hétérogénéité de la mésofaune du sol.

MOTS CLÉS: faune edafic, complexité du habitat, Insecta, distribution Spatiale

BIBLIOGRAFIA

- ALCARAZ, R. E. & J. M. ÁVILA. 2000. Landscape heterogeneity in relation to variations in epigeic beetle diversity of a Mediterranean ecosystem. Implications for conservation. *Biodiversity Conservation*, 9 (7): 985-1005.
- ANDERSEN, A. N.; J. ORGEAS; R. D. BLANCHE & L. M. LOWE. 2003. *Terrestrial insects*. In: *Fire in tropical savannas*, Andersen, A.N., G.D. Cook & R.J. Williams, (Eds.). Springer-Verlag. Pp: 107-125.
- BAR-MASSADA, A.; R. KENT, & Y. CARMEL. 2014. Environmental heterogeneity affects the location of modelled communities along the niche neutrality continuum. *Proceeding of Biological Science*. 281:20133249.
- BARTON, P. S.; A. D. MANNING; H. GIBB; D. B. LINDENMAYER & S. A. CUNNINGHAM. 2010. Fine-scale heterogeneity in beetle assemblage under co-occurring Eucalyptus in the same subgenus. *Journal of Biogeography*, 37 (10): 1927-1937.
- BASSET, Y. 1996. The seasonality of arboreal arthropods foraging within an australian rainforest tree. *Ecological Entomology*, 16 (3): 265-278.
- Bazzaz, F. A., 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, 56 (2): 485-488.
- BOGGIANI, P. C.; A. M. COIMBRA; A. L. GESICKI; A. N. SIAL; V. P. FERREIRA; F. B. RIBEIRO & J. FLEXOR. 2000. *Tufas calcárias da Serra da Bodoquena*. In: *Sítios Geológicos e Paleontológicos do Brasil*, in Schobbenhaus C., D.A. Campos, E.T. Queiroz, M. Winge & M. Berbert-Born (Eds.). Editora Brasília., pp: 249-259.
- BUTCHER, J. W.; R. SNIDER & R. J. SNIDER. 1971. Bioecology of edaphic Collembola and Acarina. *Annual Review of Entomology*, 16 (1): 249-288.
- CAGNOLO, L.; S. I. MOLINA & G. R. VALLADARES. 2002. Diversity and guild structure of insects assemblages under grazing and exclusion regimes in a montane grassland from Central Argentina. *Biodiversity Conservation*, 11 (3): 407-420.
- COSTA, C.; S. IDE & C.E. SIMONKA. 2006. *Insetos imaturos: Metamorfose e identificação*. Editora Holos.
- DIAS, H. C. T. & A. T. OLIVEIRA-FILHO. 1997. Variação temporal e espacial da produção de serapilheira em uma área de floresta estacional semidecídua montana em Lavras-MG. *Revista Árvore*, 21 (1): 11-26.

- DIAS FILHO, M. B. 1998. *Alguns aspectos da ecologia de sementes de duas espécies de plantas invasoras da Amazônia Brasileira: implicações para o recrutamento de plântulas em áreas manejadas*. In: Floresta amazônica: dinâmica, regeneração e manejo, Gascon C. and P. Moutinho (Eds.). Instituto Nacional de Pesquisas da Amazônia, pp: 233-248.
- DUFLOT, R.; R. GEORGES; A. ERNOULT; S. AVIRON & F. BUREL. 2014. Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica*, 56: 19–26. DOI:10.1016/j.actao. 2014.01.004.
- FACELLI, J. M & S. T. A. PICKETT. 1991. Plant litter: Its dynamics and effects on plant community structure. *Botanical Review*, 57 (1): 1-32.
- FARIA, R. R. & A. C. ARAÚJO. 2010. Flowering phenology and pollination of ornithophilous species in two habitats of Serra da Bodoquena, Mato Grosso do Sul, Brazil. *Anais da Academia Brasileira de Ciências*, 82 (4): 843-855.
- FAHRIG, L. & I. JONSEN. 1988. Effect of habitat patch characteristics on abundance and diversity of insects in a agricultural landscape. *Ecosystem*, 1: 197-205.
- FAHRIG, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematic*, 34 (1): 487-515.
- GANHO, N. G. & R. C. MARINONI. 2006. A variabilidade espacial das famílias de Coleoptera (Insecta) entre fragmentos de Floresta Ombrófila Mista Montana (Bioma Araucária) e plantação de *Pinus elliotii* Engelmann, no Parque Ecológico Vivat Floresta, Tijuca do Sul, Paraná, Brasil. *Revista Brasileira de Zoologia*, 23 (4): 1159-1167.
- GOLDEN, D. M. & T. O. CRIST. 1999. Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. *Oecology*, 118 (3): 371-380.
- GOMES, A. A.; R. M. MUSSURY; S. P. Q. SCALON; F. WATTHIER; K. A. A. CUNHA & H. S. FILHO. 2007. Avaliação do impacto da fragmentação de florestas nativas sobre a mesofauna edáfica na região de Dourados-MS. *Ciência Agrotecnológica*, 31 (3): 612-618.
- GULLAN, P. J. & P. S. CRANSTON. 1994. *The insects: an outline of entomology*. Chapman and Hall.
- HASTINGS, A. 1990. Spatial Heterogeneity and Ecological Models. *Ecology*, 71 (2): 426-428.
- HU, G.; Y. JIN; J. LIU & M. YU. 2014. Functional diversity versus species diversity: relationships with habitat heterogeneity at multiple scales in a subtropical evergreen broad-leaved forest. *Ecological Restoration*, 29: 897-903. DOI:10.1007/s11284-014-1178-6.

- HUGHES, J. B.; G. D. DAILY & P. R. EHRLICH. 2000. Conservation of insects Diversity: a habitat approach. *Conservation Biology*, 14 (6): 1788-1797.
- HUNTER, M. D. 2002. Landscape structure, habitat fragmentation and the ecology of insects. *Agricultural and Forest Entomology*, 4 (1): 159-166.
- ILLIG, J.; R. A. NORTON, S. SCHEU, & M. MARAUN. 2010. Density and community structure of soil-and bark-dwelling microarthropods along an altitudinal gradient in a tropical montane rainforest. *Experimental and Applied Acarology*, 52 (1): 49-62.
- KREMEN, C.; R. K. COLWELL; T. L. ERWIN; D. D. MURPHY; R. F. NOSS & M.A. SANJAYAN. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, 7 (4): 796-808.
- LAVELLE, P. & A.V. SPAIN, 2001. *Soil ecology*. Kluwer Academic Pub.
- LAWTON, J. H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, 28 (1): 23-29.
- LI, H., & J. F. REYNOLDS. 1995. On definition and quantification of Heterogeneity. *Oikos*, 73 (2): 280-284.
- LINDEN, D.R.; P.F. HENDRIX & D.C. COLEMAN, 1994. *Faunal indicators of soil quality*. In: *Defining soil quality for a sustainable environment*. J.W Doran, D.C. Coleman, D.F. Bezdicek and B.A. Stewart (Eds.). ed. Soil Science Society of America. pp: 91-106.
- MACARTHUR, R. H. & J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42 (3): 594-598.
- MCCOY, E. D. & S. S. BELL. 1991. *Habitat structure: the evolution and diversification of a complex topic*. In: *Habitat structure: the physical arrangement of objects in space*. Bell, S S., E.D. McCoy & H.R. Mushinsky (Eds.). Vol. 8. 1 ed. Chapman and Hall. pp: 3-27.
- MCINTYRE, N.E.; J. RANGO; W. F. FAGAN & S. H. FAETH. 2001. Ground arthropod community structure in a heterogeneous urban environment. *Landscape Urban Planning*, 52 (4): 257-274.
- MENEZES, C. E. G.; M. E. F. CORREIA; M. G. PEREIRA; I. BATISTA; K. M. RODRIGUES; W. H. COUTO; L. H. C. ANJOS & I. P. OLIVEIRA. 2009. *Macrofauna edáfica em estádios sucessionais de Floresta Estacional Semidecidual e pastagem mista em Pinheiral (RJ)*. *Revista Brasileira de Ciência do Solo*, 33 (6): 1647-1656.
- MENEZES, S.; F. PIMENTEL; K. MORKROSS; G. Q. ROMERO & E. M. L. GONSALES. 2002. *Danos e mortalidade em árvores em floresta manejada e não-manejadas na Amazônia Central*. In: *Ecologia da Floresta Amazônica*. Curso de campo da floresta Amazônica. Venticinque E. and J. Zuanon (Eds) ed. Instituto Nacional de Pesquisas da Amazônia pp:19-21.

- MOLOFSKY, J. & C. K. AUGSPURGER. 1992. The effect of litter on early seedling establishment in a tropical forest. *Ecology*, 73 (1): 68-77.
- Moore, J. C.; D. E. Walter & H. W. Hunt. 1988. Arthropod regulation of microbiota and mesobiota in belowground detrital food webs. *Annual Review of Entomology*, 33 (1): 419-439.
- PFADT, R. E., 1984. Species richness, density and diversity of grasshoppers (Orthoptera: Acrididae) in a habitat of mixed grass prairie. *Canadian Entomology*, 116: 703-709
- RAFAEL, J. A.; G. A. R. MELO; C. J. B. CARVALHO; A. S. CASARI & R. CONSTANTINO. 2012. *Insetos do Brasil: Diversidade e taxonomia*. Editora Holos.
- ROCHA, P. L. B.; T. S. SÁ; R. P. DAMASCENO & R. XAVIER. 2010. Do litter arthropods respond to microhabitat? A case study from Brazilian sand dunes in semi-arid Caatinga. *Revista Brasileira de Zoociência*, 12 (3): 257-271.
- RUBBO, M. J. & J. M. KIESECKER. 2004. Leaf litter composition and community structure: Translating Regional species changes into local dynamics. *Ecology*, 85 (9): 2519-2525.
- SOUZA, R. C.; M. E. F. CORREIA; M. G. PEREIRA; E. M. R. SILVA; R. R. PAULA & L. F. T. MENEZES. 2008. Estrutura da comunidade da fauna edáfica em fragmentos florestais na Restinga de Marambaia, RJ. *Revista Brasileira de Ciência Agrária*, 3 (1): 49-57.
- SEASTEDT, T. R. 1984. The role of microarthropods in the decomposition and mineralization processes. *Annual Review of Entomology*, 29 (1): 25-46.
- TEWS, J.; U. BROSE; V. GRIMM; K. TIELBÖRGER; M. C. WICHMANN; M. SCHWAGER & F. JELTSCH. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31: 79-92.
- TRIPLEHORN, C. A. & N. F. JOHNSON, 2011. *Borrer and Delong's introduction to the study of insects*. Editora CENGAGE LearningTM.
- VASCONCELLOS, A.; A. G. BANDEIRA; F. M. S. MOURA; V. F. P. ARAÚJO; M. A. B. GUSMÃO & R. CONSTANTINO. 2010. Termite assemblages in three habitats under different disturbance regimes in the semi-arid Caatinga of NE Brazil. *Journal of Arid Environment*, 74 (2): 298-302.
- VINATIER, F.; P. TIXIER; P. F. DUYCK & F. LESCOURRET. 2011. Factors and mechanisms explaining spatial heterogeneity: a review of methods for insect populations. *Methods Ecology and Evolution*, 2 (1): 11-22. DOI:10.1111/j.2041-210X.2010.00059.x.
- WARREN, M. W. & X. ZOU. 2002. Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico. *Forest Ecology Management*, 170 (1): 161-171.

YORK, A. 1999. Long term effects of frequent low intensity burning on the abundance of litter dwelling invertebrates in coastal blackbutt forests of southeastern Australia. *Journal of Insect Conservation*, 3 (3): 191-199.

Recebido em 21 de julho de 2015.