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Forest regeneration affects litter fungivorous thrips fauna (Insecta: Thysanoptera) in Atlantic forest

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Abstract

Forest regeneration can affect the soil-dwelling insect fauna by promoting an increase in tree diversity and accelerating the accumulation of litter biomass in this environment. This study evaluated the effect of forest regeneration of Atlantic Forest fragments on the fungus-feeding thrips community. In each fragment, two treatments were selected: (i) intermediate successional stage (ISS) and (ii) early successional stage (ESS). Each treatment had three transects, each one with 10 sampling units, comprising 240 sampling units. We sampled 221 adult thrips, 135 individuals in the ISS, and 86 individuals in the ESS. We found 35 Thysanoptera species in 15 genera, all of them belonging to Phlaeothripidae. Abundance, richness, and Shannon's diversity were higher in the ISS than in the ESS. The low number of individuals and high species richness suggests a remarkable distribution of thrips fauna in the litter. Although some taxa were more related to ISS, species composition structure did not differ between successional stages. Our study indicates that the fungivorous thrips fauna associated with litter was affected by the different natural regeneration states, suggesting that these fungivorous insects are sensitive to different successional stages.

Keywords: Fungivory, insect diversity, leaf-litter, microenvironment, soil fauna.

A regeneração florestal afeta a fauna de tripes fungívoros (Insecta: Thysanoptera) na Mata Atlântica

Resumo

A regeneração florestal pode afetar a fauna de insetos que habitam o solo, ao promover um aumento na diversidade de árvores e acelerar o acúmulo de biomassa da serapilheira nesse ambiente. O objetivo deste estudo foi avaliar o efeito da regeneração florestal de fragmentos da Mata Atlântica na comunidade de tripes fungívoros. Em cada fragmento, foram selecionados dois tratamentos: (i) estágio sucessional intermediário e (ii) estágio sucessional inicial. Cada tratamento compreendeu três transectos, cada um com 10 unidades amostrais, totalizando 240 unidades amostrais. Foram amostrados 221 tripes adultos, 135 nas áreas de sucessão intermediária e 86 indivíduos nas áreas de sucessão inicial. Encontramos 35 espécies de Thysanoptera em 15 gêneros, todos pertencentes à família Phlaeothripidae. Abundância, riqueza e diversidade de Shannon foram maiores em locais de sucessão intermediária. Esse baixo número de indivíduos e a alta riqueza de espécies sugerem uma distribuição notável da fauna de tripes na serapilheira. Embora alguns táxons estivessem mais relacionados ao estágio intermediário de sucessão, a estrutura de composição das espécies não diferiu entre os tratamentos. Nosso estudo indica que a fauna de tripes fungívoros associada à serapilheira foi afetada pelos diferentes estados de regeneração natural, sugerindo que esses insetos são sensíveis a diferentes estágios sucessionais.

Palavras-chave: Fungivoria, diversidade de insetos, microambiente, fauna do solo, serapilheira.

Introduction

Forest vegetation loss generally means the loss of structural components and ecological processes that maintain animal diversity. This is especially true for small organisms that live on the forest floor, which comprise a guild sensitive to such environmental alterations (Silva, Feitosa & Eberhardt, 2007; Hoop, Ottermanns, Caron, Meyer & Roß-Nickoll, 2010). Forest regeneration, on the other hand, positively affects invertebrate fauna that inhabit the litter, since the advance of regeneration tends to increase the diversity of many species of this fauna (Franco, 2016), resulting in diversity and composition of the regenerated forest similar to that of the primary forest (Chazdon, 2012). This effect of forest regeneration on the litter microenvironment extends to its insect fauna (Szinwelski, Rosa, Schoereder, Mews &

Sperber, 2012; Machado, Pereira, Correia, Diniz & Menezes, 2015).

The litter environment has an important role in the maintenance and recovery of forest ecological processes, especially because of its rich and diverse fauna of fungivorous invertebrates (Pereira, 2010; Meloni & Varanda, 2015). This fauna is related to the decomposition processes, cycling of nutrients (Vendrami, 2012; Pereira, Pereira, Anjos, Amorim & Menezes, 2013); and plant diversity (Pereira, 2010). On the other hand, the litter fauna can also be influenced by plant diversity (Pereira, 2010), both positively, considering that an increase in vegetation generates a greater volume of litter and thus greater availability of resources (Barberena-Arias & Aide, 2003), as well as negatively, in case of weeds that invade mainly degraded areas (Basset, 2014). However, the relationship between forest regeneration and fungivorous insects is not yet completely understood.

Thysanoptera, also known as thrips, constitute a representative group of litter dwellers, especially in tropical forests (Mound, 1977; Pinent, Romanowski, Redaelli & Cavalleri, 2006; Wang *et al*., 2012). These insects feed on a variety of resources (Mound & Marullo, 1996), but nearly 50% of the species feed on fungal spores or hyphae while living on dead tree branches and leaves or associated with litter (Mound & Marullo, 1996; Tree, Mound & Walter, 2010). Apart from the high diversity of these insects in the soil, very little is known about their ecology and how they are affected by abiotic and biotic factors present in the litter. There is some evidence that their occurrence depends on the presence of old trees in various stages of decay (Kucharczyk, Kucharczyk & Wyrozumski, 2015), and it is also known that some bark-dwelling thrips species are more adapted to younger forests (Dubovský, Fedor, Kucharczyk, Masarovič & Balkovič, 2010). Intriguingly, the few available studies on litter thrips suggest that this fauna has high richness, aggregate distribution, and very low abundance (Mound, 1977; Pinent *et al*., 2006; Wang & Tong, 2012).

The present study aimed to investigate the effect of the forest natural regeneration state on the abundance, composition, richness, and diversity of litter thrips. We tested the following hypotheses: 1) fungivorous Thysanoptera diversity should be higher in more advanced successional stage forest areas, as in such places the higher vegetation density should translate into higher inputs and standing stocks of litter; 2) the Thysanoptera composition should differ between the different natural regeneration stages, assuming that forest vegetation structure and regeneration time affect the litter thrips fauna.

Material and Methods

Study area

The study was carried in four ombrophilous forest fragments in the Atlantic Forest region of Boa Nova National Park (PARNA of Boa Nova), located in the municipality of Boa Nova, southwestern Bahia State, Brazil (ICMBIO, 2020) (Figure 1). This park is located in an area that is characterised by the transition from a semiarid to a wet climate, and lies on a subcoastal plateau, with rather rugged terrain. The altitude varies between 440 m and 1111 m, with an average annual rainfall of 1300 mm and an average annual temperature of 23°C (MMA, 2020).

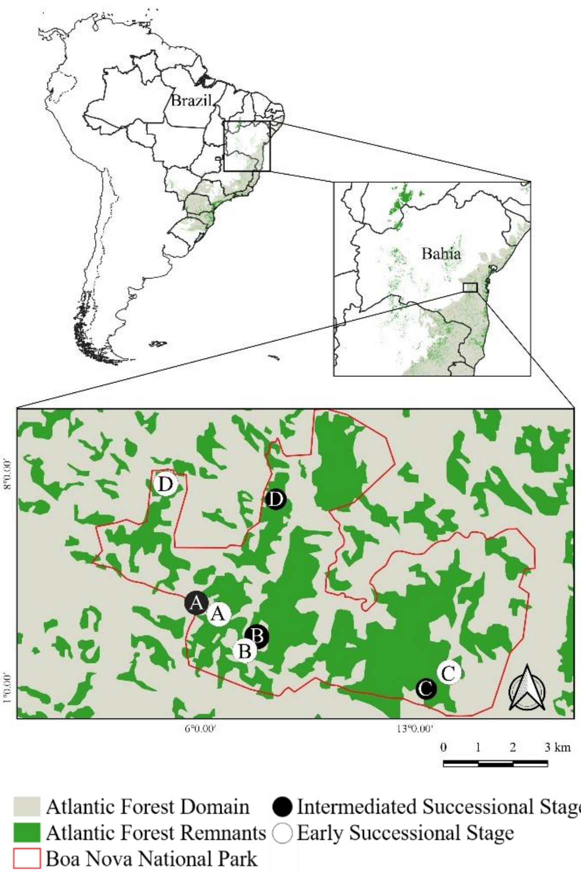

Figure 1. Map of the study region, indicating the location of the study sites in Boa Nova National Park (red outline). Gray areas indicate Atlantic Forest and green areas indicate Atlantic Forest remnants, whereas circles indicate the successional stage (black: intermediate successional stage; white: early successional stage) and the letters indicate fragments with sampling sites (A-D).

Thrips sampling and identification

Samplings were taken between January and April 2015, when the thrips density in the litter is highest, increasing the probability of collecting adults (Pinent *et al*., 2006; Anu, Sabu & Vineesh, 2009; Wang & Tong, 2012). The interval between two sampling events was not regular, ranging from 2 to 20 days, depending on the climatic conditions. We selected secondary forest fragments with of least 3 km^2 where there were no current deforestation activities and where we could demarcate two areas with different vegetation structures (treatments) per fragment. In each fragment, the treatments were spaced at least 500 m apart, allowing independence between areas and increasing the chances of obtaining an appropriate sample size. Each fragment was represented by a mosaic of patches with higher or lower vegetation loss, resulting from historical anthropisation. This history was represented mainly by coffee and cocoa plantations and by wood extraction and did not vary considerably in structure from one fragment to the other.

Some of the forest fragments have been isolated from human activities for about 45 years, while others have been abandoned for less than 30 years. Thus, fragments were divided into two treatments according to their vegetation structure, i.e. the regeneration state of the remaining vegetation. One treatment was denominated the intermediate successional stage (ISS) and whereas the other one was denominated the early successional stage (ESS). Thrips sampling was designed according to the regeneration conditions identified in the region. Therefore, the most regenerated treatment represents the highest level of regeneration. Considering that the region does not present areas of primary vegetation, it was not possible to establish a control group. Each forest fragment had two treatments and the characteristics of vegetation and their parameterisations are described in Table 1.

Table 1. Characterization of the ISS (intermediate successional stage) and ESS (early successional stage) treatments.

Trait	ISS	ESS
Regeneration time	> 45 years	< 30 years
Vegetation structure	Predominance of trees and/or shrubs	Predominance of shrubs and herbs; epiphytes almost absent
Forest cover	Closed canopy, high vegetation density	Semi-closed canopy with gaps
Occurrence of grasses, ferns and invasive plants	Absent or present with low frequency	Present in the interior of the forest

In each treatment, we defined three transects of 100 m long and 200 m apart, parallel to the border of the forest and 100–300 m away from it. In each transect, we placed ten sampling units 10 m apart, comprising 24 transects and 240 sampling units. Each sampling unit consisted of an area of 25 cm^2, where the superior layer of litter was harvested and immediately deposited into paper bags. The collected litter was composed of leaves, roots, branches and other plant structure fragments. Field sampling was carried out during the mornings, and on the same day, the harvested litter was placed into modified Berlese-Tullgren funnels for thrips extraction. This method is based on a light gradient, for which we used incandescent lamps with a power of 25 W. The fallen, extracted material was preserved in 45% alcohol. Funnels were run for 72 h, after which the extracted material was taken for sorting and mounting in the laboratory. Thrips were mounted on permanent microscopy slides following the protocol of Mound & Marullo (1996) and identified with the help of taxonomical keys provided by Mound & Marullo (1996) and Mound (1977).

Data analyses

To compare the abundance, richness, and Shannon diversity between treatments, we used a generalised mixed-effects model analysis (GLMM) based on the eight replicates to take into account the non-independence of the treatment pairing and the Wald chi-square test for testing treatment significance. Two models were adjusted; in model 1, the treatment factors of succession stage and fragment were considered as random factors, while in model 2, the treatment was considered as a fixed factor and the fragment as a random factor. The AIC (Akaike information criterion) criterion and amount of variance present in the residue were used as criteria to select the best model. This procedure was adopted after finding the probability distribution that best fits the data. For normal probability adjustments, we used a generalised linear mixed model (GLMM). Total abundance was based on counts of adult and immature individuals, richness was based on adults only, and diversity was measured using Shannon's diversity index. Differences in the thrips community composition between treatments were assessed by an analysis of similarity (ANOSIM) test, using the Bray-Curtis distance as a measure of dissimilarity. To examine the compositional distance between areas (as assessed by ANOSIM), we used non-metric multidimensional scaling (NMDS).

Considering that richness is influenced by the number of individuals sampled, we obtained rarefaction and extrapolation of the richness of the two treatments from an asymptotic estimator for the Hill series numbers (Chao *et al*., 2014). The rarefied richness was obtained from the incorporation of the number of individuals sampled and the distribution of the abundances of the assemblages in the two treatments. Additionally, the richness of each treatment was estimated considering the number of rare species from the non-parametric jackknife method.

To test for the effect of treatments on abundance, diversity, richness, and composition, we used R 3.4, supported by the "vegan", "lme4", "MASS", "car", "nmle", and "diversity" packages (R Development Core Team, 2017).

Results and Discussion

Richness, abundance and composition

We sampled 313 thrips, of which 221 were adults. They all belonged to the family Phlaeothripidae, with over 90% of the species being fungivorous and members of the tribe Glyptothripini. We collected more individuals and thrips species in ISS than on in ESS fragments (Table 2). The most abundant species in the ISS were *Orthothrips* sp. 1 (22,96%) and *Orthothrips* sp. 2 (15,55%), whereas *Orthothrips* sp. 1 (25,58%) and *Eurythrips* sp. 8 (16,27%) were the most frequent in the ESS, with the latter species occurring only in these areas.

These fungivorous thrips occurred in very low numbers, which seems to be a pattern of the thrips fauna associated with the litter. The data presented here confirm that Thysanoptera is a remarkable group in the forest litter, not abundant but interestingly exhibiting high species richness.

Table 2. Thrips species, total number of individuals (N)**,** relative frequency (F), total number of individuals per fragment (A, B, C, D) and per treatment (January - April 2015).

Thrip specie	N	F (%)	Fragment				Treatment	
			A	B	C	D	ISS	ESS
Orthothrips sp.1	53	23.98	13	10	19	11	31	22
Orthothrips sp.2	25	11.31	1	17	3	4	21	4
Eschatothrips sp.1	14	6.335	2	2	6	4	6	8
Eurythrips sp.2	14	6.33	1	11	1	1	3	11
Eurythrips sp.8	14	6.33	-	14	-	-	-	14
Chthonothrips nigrocinctus	12	5.43	10	1	1	-	10	2
Chthonothrips sp.1	12	5.43	6	1	5	-	9	3
Eurythrips sp.1	10	4.52	1	3	6	-	9	1
Eschatothrips sp.2	8	3.62	-	4	2	2	5	3
Eurythrips sp.5	8	3.62	4	2	-	2	6	2
Tylothrips sp.2	6	2.71	-	-	4	2	4	2
Glyptothrips sp.1	4	1.81	2	2	-	-	1	3
Orthothrips sp.3	4	1.81	-	1	-	3	4	-
Eschatothrips sp.3	3	1.36	1	1	1	-	2	1
Hoplandrothrips sp.	3	1.36	-	2	-	1	2	1
Orthothrips sp.4	3	1.36	-	3	-	-	1	2
Tylothrips sp.1	3	1.36	-	3	-	-	3	-
Adraneothrips sp.	2	0.90	-	-	2	-	1	1
Chorithrips heptatoma	2	0.90	-	2	-	-	2	-
Eurythrips sp.6	2	0.90	-	1	-	1	2	-
Glyptothrips sp.3	2	0.90	-	2	-	-	2	-
Preeriella sp.	2	0.90	-	2	-	-	2	-
Tylothrips sp.3	2	0.90	-	2	-	-	2	-
Tylothrips sp.5	2	0.90	-	-	1	1	1	1
Chamaeothrips sp.	1	0.45	1	-	-	-	-	1
Chthonothrips sp.2	1	0.45	-	-	1	-	1	-
Eurythrips sp.3	1	0.45	-	1	-	-	-	1
Eurythrips sp.4	1	0.45	-	-	1	-	1	-
Eurythrips sp.7	1	0.45	1	-	-	-	1	-
Glyptothrips sp.2	1	0.45	-	-	-	1	1	-
Karnyothrips sp.	1	0.45	1	-	-	-	-	1
Psalidothrips sp.	1	0.45	-	-	1	-	1	-
Symphyothrips sp.	1	0.45	-	-	1	-	-	1
Tylothrips sp.4	1	0.45	-	-	1	-	1	-
Zeugmatothrips gracilis	1	0.45	-	-	1	-	-	1
Total abundance	221	100,00	44	87	57	33	135	86
Cumulative observed richness	35	-	13	22	18	12	29	22

ISS: intermediate successional stage; ESS: early successional stage) in Boa Nova National Park, Bahia, Brazil.

This situation is well-illustrated by the 30 thrips species described by D.J. Hood from the litter of a small forest area of only 50 km^2 in southern Brazil, almost all based on very few specimens (Mound, 1977).

There was a predominance of rare species in the fauna of both treatments. The ISS showed a higher estimated richness of thrips, which is a reflection of a larger quantity of rare species (Figure 2A). However, when we consider the richness obtained by the number of individuals, no differences were observed between treatments (Figure 2B).

Pinent *et al*. (2006) examined the litter thrips fauna from southern Brazil using a similar collecting approach and found 158 individuals in 33 species, almost all fungivorous Phlaeothripidae. Although this small number of individuals affects the ecological analysis, the species richness of this fauna is remarkable, and revealing the factors behind this low abundance is an interesting issue for further studies on litter Thysanoptera.

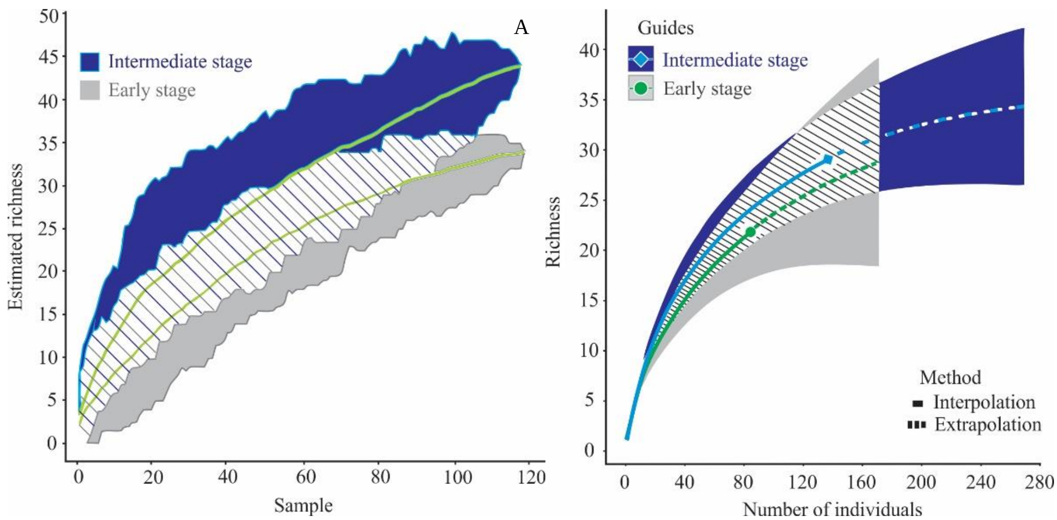

Figure 2. Thrips species accumulation curve for estimated richness (A - first-order jackknife method) and according to rarefaction by the number of individuals sampled in the initial and intermediate stage treatments (B) in Boa Nova National Park, Bahia, Brazil (January, April 2015).

Forest regeneration effects on thrips fauna

Considering species composition, the regeneration treatments did not present a composition more similar to each other (ANOSIM: r = -0.141; p = 0.881; Figure 3), although ISS had more than twice the number of exclusive species (13) found in ESS (6) (Table 1). In contrast to other groups, such as ants and beetles, an effect of regeneration on the composition is expected, because, the composition of species is a component of diversity that generally takes longer to recover (Dunn, 2004; Silva *et al*., 2007; Hopp *et al*., 2010). One hypothesis is that the macrostructure (abiotic factors) of the analysed environments did not affect these populations. In addition, these thrips might be generalist fungivores, and the differences in food resources between treatments should not have a major impact on the thrips fauna. Nevertheless, there was an association with the occurrence of some species, as *Eurythrips* sp. 8, *Orthothrips* sp. 3, and *Tylothrips* sp. 1, showing that although a generalisation does not exist from the point of view of the community structure, there is an association with some thrips taxa (Table 1).

Barberena-Arias & Aide (2003), examining litter insect groups in tropical forest fragments undergoing regeneration, found similar results regarding the species composition. These authors observed that forest fragments with 30 years and 60 years of regeneration showed no difference in species composition, revealing that, after around 30 years of forest regeneration, the species composition of some insect taxa were re-established. These results were related to a higher volume of litter in the two sets of older areas, and the occurrence of unique species that strongly affected the analysis of species composition. Our results of the composition analysis were also influenced by the large numbers of doubletons and singletons as well as low overall abundance.

The models that best explain the variation in thrips abundance, richness, and diversity between areas, as well as those that presented the lowest AIC, were those in which treatments are fixed factors and fragments random factors when compared to the model in which both factors are considered randomly. In all cases, the fragment was an important source of variation (Table 3). We found a treatment effect on richness (X^2 = 9.090, p = 0.003), abundance (X^2 = 5.679, p = 0.017), and diversity (X^2 = 9.065, p = 0.003), all of these being significantly lower in the ESS (Figures 4a-4c).

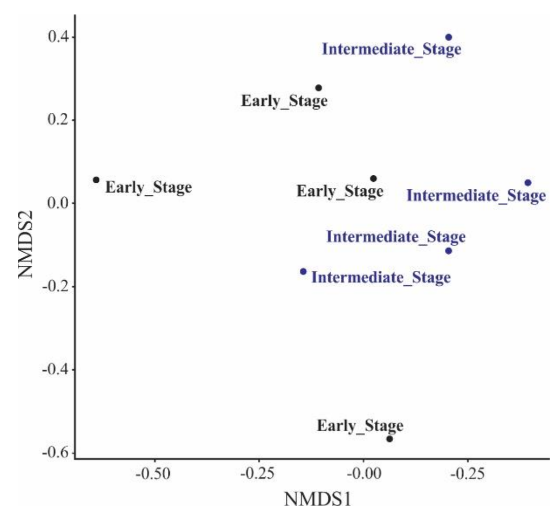

Figure 3. Non-metric multidimensional scaling (NMDS) of the thrips species composition based on species abundance in relation to early and intermediate stage treatments in Boa Nova National Park, Bahia, Brazil (January-April, 2015).

Table 3. Linear mixed model – Random (Model 1) and Fixed (Model 2) effects – fit by maximum likelihood for richness, abundance and Shannon diversity of thrips in Boa Nova National Park, Bahia, Brazil (January – April, 2015).

Variable	Model 1	Model 2		
	Richness			
Groups	Variance	Variance	Estimate	t value
Intercept			8.50 ± 1.37	6.220
Fragment*	4.55 ± 2.13	4.38 ± 2.09		
Treatments*	3.17 ± 1.78			
Residual	4.37 ± 2.09	3.09 ± 1.76	3.75 ± 1.24	3.015
AIC	49.0	45.1		
Variable	Abundance			
Groups	Variance	Variance	Estimate	t value
Intercept			21.50 ± 5.7	3.794
Fragment*	73.47 ± 8.57	75.62 ± 8.7		
Treatments*	28.87 ± 5.37			
Residual	76.17 ± 8.73	52.84 ± 7.3	12.25 ± 5.14	2.383
AIC	71.0	67.8		
Variable	Shannon Diversity			
Groups	Variance	Variance	Estimate	t value
Intercept			1.73 ± 0.10	16.784
Fragment*	0.012 ± 0.11	0.01 ± 0.12		
Treatments*	0.025 ± 0.16		0.36 ± 0.12	3.011
Residual	0.042 ± 0.20	0.03 ± 0.17		
AIC	9.3	5.0		

Variance ± Standard Deviation; Variance ± Standard Error. Model 1: Variable ~ 1 + (1 | Frag) + (1 | Treatments) and Model 2: Variable ~ Treatments + (1 | Frag). *Intercept.

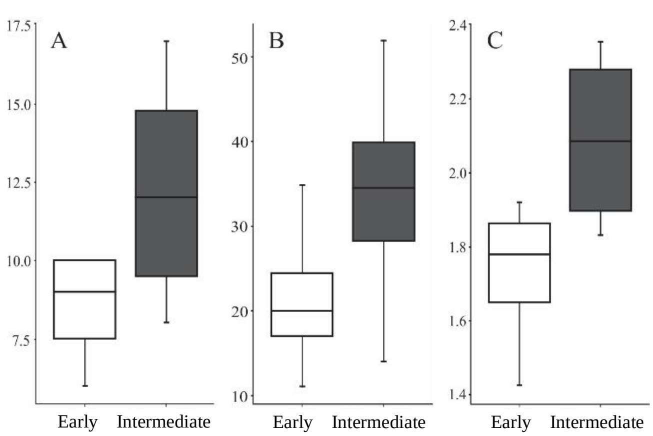

Figure 4. Richness (A), Abundance (B) and Shannon diversity index (C) of the thrips assemblages in the litter of early and intermediate stages of succession in Boa Nova National Park, Bahia, Brazil, January – April 2015.

Although the fragments were apparently homogeneous, they represented large variations in the structure of the thrips community (Table 3). This may be a reflection of the history of the type of land use of each area (i.e. burned, cut, and cultivated). Past land use can directly affect the plant species composition of secondary forests (Brown & Lugo, 1990), which can also influence its associated invertebrate fauna. For instance, litter ant communities from secondary forests previously occupied by pastures were restored more slowly than in areas where the soil was less drastically altered when the succession started (Bihn, Verhaaghb, Brañdlea & Brañdl, 2008).

Forest degradation affects the diversity of many litter insect groups, but forest regeneration tends to minimise this effect (Dunn, 2004; Silva *et al*., 2007; Bihn *et al*., 2008; Hoop *et al*., 2010; Ottermanns *et al*., 2011). Therefore, the lower diversity of thrips observed in ESS (Figure 4c) might be a result of the long-lasting effect of past degradation in such places, caused by deforestation through human activities (Bihn *et al*., 2008). Studies with other groups of fungivorous insects indicate that conservation status and the complexity of the forest vegetation might have a direct effect on these litter-living insects (Barberena-Arias & Aide, 2003; Bihn *et al*., 2008; Oliveira, Gomes, Pires, Marinho & Della Lucia, 2014). These organisms seem to be frequent in forest litter, under different structural conditions and different states of forest regeneration. Considering species richness, they are more frequent in more regenerated forests (Figure 4a). However, even in these, the richness is lower, and the composition is differentiated relative to mature forests (Barberena-Arias & Aide, 2003; Bihn *et al*., 2008).

Conclusion

The litter seems to encompass a community of invertebrates sensitive to environmental changes, such as loss of vegetation. Furthermore, data from studies in tropical forests show that changes in vegetation composition affect the structure and composition of the litter, significantly influencing its microclimatic conditions. Our results indicate a positive effect of natural forest regeneration on the diversity and richness of fungivorous thrips associated with litter. Indeed, the Thysanoptera fauna presented different ecological patterns between areas with approximately 45 years of regeneration and those with less than 30 years of regeneration. However, our study did not detect differences in the species composition between these two regeneration states.

The number of thrips species in the litter was also considerably higher when compared to other microhabitats such as trees and grasses, but the abundance of these insects tends to be relatively low. Litter fungivorous insects are important indicators of the effect of environmental variations in forests, as they are involved in important ecological processes that maintain such forests and are affected by disturbances experienced by the litter. The results provided here will support further studies on the effect of forest regeneration on litter microfauna.

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