Insect herbivores species associated to pioneer tree species: contrasting within forest and ecotone canopy habitats

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Abstract. The present article investigates the patterns of distribution of insect herbivores species in forest canopies dominated by *Byrsonima sericea* and *Mabea fistulifera*, pioneer tree species, in disturbed and preserved ecotones and within-forest habitats of a seasonal semideciduous tropical forest. The study was developed in the State Park of Rio Doce, South-Eastern Brazil. Both studied species are frequent in the same type of low and open forests. Moreover, *M. fistulifera* occurs in the disturbed borders (successional ecotones), while *B. sericea* in the ecotones with natural lakes, very common in this environment. We sampled insects living on 15 *B. sericea* and 23 *M. fistulifera* in the dry and wet seasons of 2001 and 2002. A total of 670 insect individuals, distributed in 114 morphospecies were found on *B. sericea* (60 spp.) and *M. fistulifera* (66 spp.), but only 12 (10.5 %) co-occurred. Insect species richness did not vary significantly between host species or habitats, but overall mean value was higher on *B. sericea* than *M. fistulifera*. Species richness seems to increase with time, regardless of seasonality. Concerning insect species composition, *M. fistulifera* and *B. sericea* had very distinct insect herbivore fauna, and *B. sericea* had distinct fauna between the lake ecotone and inside the forest. In one hand, recent climatic shifts may have caused severe ecological changes, which could have resulted in a relatively poor insect herbivore community. In the other hand, long-term evolutionary exposition of those plant genera to herbivores should have resulted in a greatly specialized insect herbivore community.

Key words: Insect herbivore, host plant specialization, habitat fidelity, species distribution in forest canopies.

Resumo: Espécies de insetos herbívoros associados a árvores pioneiras: contrastando habitats de dossel dentro de matas e em ecotones. Este artigo investiga padrões da distribuição de espécies de insetos herbívoros em dosséis de florestas dominados por *Byrsonima sericea* e *Mabea fistulifera*, espécies pioneiras, em habitats de ecotones perturbados e naturais, e em interior de mata, em uma floresta tropical semidecidual estacional. O estudo foi desenvolvido no Parque Estadual do Rio Doce, sudeste do Brasil. Ambas as espécies estudadas são freqüentes no mesmo tipo de habitat florestal. Além disso, *M. fistulifera* ocorre em bordas perturbadas (ecotone successional), enquanto *B. sericea* ocorre em ecotones naturais com lagos, comuns na bacia do médio Rio Doce. Nós amostramos os insetos de 15 indivíduos de *B. sericea* e 23 de *M. fistulifera*, nas estações secas e chuvosas de 2001 e de 2002. Um total de 670 indivíduos de insetos, distribuídos em 114 morfoespécies foi encontrado em *B. sericea* (60 spp.) e *M. fistulifera*. (66 spp.), mas somente 12 (10.5 %) ocorreram nas duas espécies. A riqueza de espécies de insetos não variou significativamente entre as plantas hospedeiras ou os habitats, mas a média total foi mais elevada para *B. sericea* que para *M. fistulifera*. Independentemente de sazonalidade, a riqueza de espécies parece aumentar com o tempo. Com relação à composição da espécies de insetos, a *M. fistulifera* e *B. sericea* tiveram uma fauna muito distinta. Além do mais, B. sericea apresentou uma fauna distinta entre o ecotóne do lago e o interior da mata. Por um lado, mudanças climáticas recentes causaram alterações ecológicas importantes que deve ter resultado em uma comunidade relativamente pobre de insetos herbívoros. Por outro, a longa exposição evolutiva destes herbívoros aos gêneros de planta estudados deva ter resultado em uma comunidade extremamente especializada.

Palavras-chave: Insetos herbívoros, especialização em planta hospedeira, fidelidade de habitat, distribuição de espécies em dosséis florestais.

Introduction

Tropical forest canopies were considered for a while as one of the most important reservoir of species diversity in the planet, especially of insect species (Erwin, 1989, 1991; Basset, 2001). Recent research has pointed towards a more realistic contribution of canopy habitats to insect diversity (Basset *et al.*, 2003). Nevertheless, the canopy physical structure, eco-physiology, biomass, and resources may affect a reasonable amount of insect population distribution (Ribeiro & Basset, 2007). Regardless the expansive growth of quantitative research on tropical canopies, each forest has its own natural history and evolution, as well as ecological features which may shape differently the relative importance of each forest compartments. A few general patterns were already explored, but further research on less studied forest or tree life histories are urgently needed.

Amongst insect herbivores, the groups Curculionidae, Lepidoptera, Chrysomelidae, Thysanoptera and Homoptera are the most speciose in the various tropical rainforest canopies studies (Basset, 2001; Novotny *et al.*, 2003), which, in fact, does not make them any different from any other plant vegetation (Ribeiro, 2003). In broad terms, Coleoptera are the richest group in the canopy as in any other vegetation type, but family frequencies and their relative importance vary between continents and ecosystems (Basset, 1997; Kitching *et al.*, 1997; Ribeiro, 2003).

Canopies are the location with highest photosynthetic activity in a forest, and so are quite suitable for insect population maintenance (Novotny *et al.*, 2003). The variation in young versus mature leaves is influential for insect distribution (Basset, 1991), as well as levels of leaf sclerophylly, which seems to favour gall-forming species in the upper canopy and free-feeding chewers in the understorey (Ribeiro & Basset, 2007). In addition, habitat conditions ought to be also important (Bernays & Funk, 1999; Ribeiro *et al.*, 2005). For instance, nutrient and chemical composition of foliage, free enemy spaces (Lawton & Price, 1979; Lawton, 1986; Bernays & Minkenberg, 1997; Ribeiro & Basset, 2007) or tree architectural traits (Riba, 1998; Ribeiro *et al.*, 2003)

are habitat components which may affect insect species distribution. However, the difference between habitat fidelity and host feeding specialization is poorly understood. Recent articles have shown that tropical canopies may hold a greater number of generalist insect herbivores than ever expected (Basset, 1992; Novotny *et al.*, 2002).

The interaction between upper canopy and the atmosphere is a very important aspect to be considered while studying microclimate gradients across foliage layers (Basset *et al.*, 2003). One particularly approach to this subject could be the canopy at real ecotones between forests and other vegetation types. Mature forest borders adjacent to artificial or natural herbaceous vegetation tend to be covered with live foliage from the upper crowns towards the branches closer to the ground. This branch pattern tend to create a canopy-type of foliage edge. Natural, as well as anthropical ecotones may affect insect movement, population dynamics and community structuring (Campos et al. 2006a).

Research on this specific habitat-ecotone subject is extremely rare (see Foggo *et al.*, 2001; Ribeiro, 2003). We acknowledge only one study about the insect herbivore species distribution in canopy of gallery forests in natural ecotones with cerrado vegetation, in the Brazilian savanna (Ribeiro *et al.*, 1998), besides a companion work to the present article, on ant assemblies (Campos *et al.*, 2006b). Most forest edges, even natural ones, are dominated by pioneer tree species. The size of these trees tends to be low, creating a gradual decreasing in the canopy height from inside forest towards the borders. Most importantly, these species invest more in growth than defence, and thus may cause increasing diversity of herbivore species, and eventually define a distinct specialist/generalist rates. (Coley, 1983; Coley *et al.*, 1985). Notwithstanding, forest ecotones are usually dominated by fewer tree species. According to current theory, trees with pioneer life history may favour generalist insects, but high abundance of a few tree species can affect the insect species on the opposite direction, favouring the population of specialists. Another neglected aspect is whether evolutionarily old plant communities would accumulate

a greater rate of specialist herbivore species than a more dynamic wet tropical forest (Ribeiro, 2003; Ribeiro & Basset, 2007).

Semideciduous tropical rainforests of South-Eastern Brazil (in the domain of the Atlantic Rainforest) survive in a highly fragmented landscape, with nearly 95 % of its original area lost. Therefore, remaining forest canopies are a mixed of persistent and successional tree species. A species of Euphorbiaceae, *Mabea fistulifera* Mart., dominates many forest borders in this ecosystem, hereafter called successional ecotones. This is also a species frequent in natural low forests, normally related to sandy and well drained soils.

Besides artificial border, some river basins and drainages are complex and eventually rich in lakes and other natural forest-water edges. One particularly well studied system is the Mid-Doce River basin, Minas Gerais State, which composes one of the largest lake systems of South America. Hence, the natural ecotones between the forest and lakes provide ideal comparative borders to study effect of canopy dynamics near transitional areas. In some lakes, the dominant tree species is a Malphigiaceae species, *Byrsonima sericea* DC., frequent in low forest with wet soils. This species is also common in gallery forests of savanna vegetation.

This present article aims to compare the effects of habitat structure (ecotone versus forest canopy) on the insect herbivore species richness and abundance distribution between *B. sericea* and *M. fistulifera*, in different seasons and years. The following hypotheses and predictions are addressed:

1. There are differences in the insect herbivore species richness and abundance per tree crowns compared between host species and habitats. It is predicted that A) ecotone habitats will have less insect species richness per crown than forest interior, due to a simpler canopy structure, defined by a small number of tree species. Conversely, if B) specialist insect species prevail in this community, the number of insect species between host species is not expected to change significantly, although densities per crown may change accordingly to population dynamics of dominant insects.

2. There are differences in insect species composition between host species, habitats, and along

time. It is expected a greater variation on insect species composition along time in the ecotones compared to interior forest, due to ecological unpredictability or inconstancy in the former habitat. Moreover, specialist species will predominate in the ecotones in response to the great host plant abundance.

Materials and Methods

Study area

The study was developed within the State Park of Rio Doce, in the middle basin of Doce river, South Eastern Brazil (19° 48′ 18″ – 19° 29′ 24″ S; 42° 38′30″ – 42° 28′ 18″ W (Fig. 1). This is the largest preserved remain of rainforest in the State of Minas Gerais (36.000 ha). This Park has an altitude of between 230m a 515m above sea level (SOCT, 1981), and is under the influence of a mesothermic wet tropical climate (Antunes, 1986) with clear wet (October – March) and dry seasons (April – September) well defined (Gilhuis, 1986). The Park is covered with a very heterogeneous semidecidual seasonal rainforest (Lopes, 1998; Veloso *et al.*, 1991).

Chosen sampling sites are the "Trilha do Gambá" – TG – low forest (average 10 m tall trees) with a mix of persistent and pioneer tree species, but well preserved and well structure canopy (with both studied species inside the forest); the "Orla da Lagoa do Bispo D. Helvécio" - OLH – a sudden natural ecotone between low forest with herbaceous vegetation in the Dom Helvécio lake ashore, adjacent
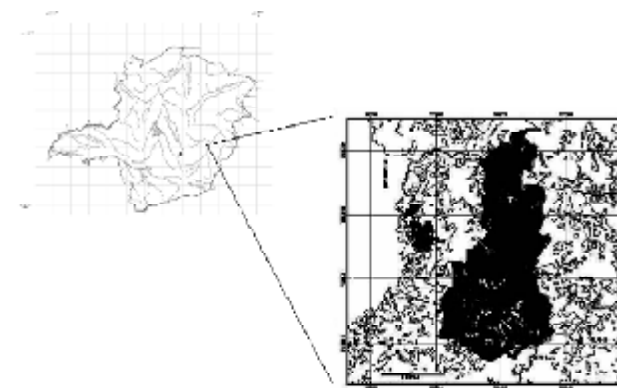

Figure 1. State PArk of Rio Doce, and sampling sites: SD – Salão Dourado, OLH – Orla da Lagoa do Bispo D. Helvécio e TG – Trilha do Gambá.

to TG (dominated by *B. sericea* and without *M. fistulifera*); the "Salão Dourado" – SD – successional ecotone between secondary fire-disturbed forest and an agro-ecosystem dominated by pastures in floodable soil, in a separate area in the park (dominated by *M. fistulifera* and without *B. sericea*).

Host plants

Studied plants are ecologically important, pioneer species in the region. *Byrsonima sericea* ("murici") reaches 10 to 20m and is a heliophyla species, capable to survive in mature forests in dense stands. It has a large geographic distribution, occurring from forests and gallery forests in the South-Eastern to semi-arid white forest in North-Eastern Brazil (Lorenzi, 1992). In the study area, *B. sericea* is commonly found in the lakes ashore (up to 5-8 m tall trees) and in lowland grounds, near temporary water creeks and channels (up to 20 m trees).

Mabea fistulifera is a semi-decidual early pioneer species, heliophyla species, which can reach up to 20 m tall (Lorenzi, 1992). It is found in open low forest or in disturbed forests (10-20m tall) or in the artificial ecotones between forests and pastures and other cultivations (4-8m tall). It is a fast growing species, with remarkable regenerative capability, and very simple crown architecture. This species can easily grow back a whole crown from a lateral meristem (S.P. Ribeiro, pers. Comm.).

Insect Sampling Design

Insect herbivores were sampled on the crowns of *B. sericea* and *M. fistulifera*, using a beating devise, modified such as Ribeiro *et al.* (2005). A random branch (amongst those physically accessible in the crown – see below) received 10 beats with a hard stick above the collecting device. Insects collected were pushed into a central orifice and kept in a plastic bag attached to this orifice. After, they were identified into family and sub-family level in the laboratory, and then the most abundant and frequent morphospecies were sent for identification by experts. In the present paper, we focused on Coleoptera high taxonomic resolution, and analysed feeding guilds in general, based on morphospecies. To access the tree crowns

a 4 m tall ladder was used in the ecotone. In the forest, where the canopy was higher, single rope climbing techniques and safe free-climbing techniques were used to access tree crowns.

Beating samples were taken in the wet seasons of 2001 and 2002 (February), and in the dry seasons of 2001 and 2002 (September). However, for logistical problems, in the dry season of 2001 only the ecotone trees were sampled, and thus this sampling period was used only to investigate species composition variation, and not for statistical comparisons. The trees in the ecotones were sampled in low and high branches to explore stratification patterns (averaged for present analysis).

A total of 15 *B. sericea* in the ecotone and eight in the forest were sampled in the whole project, and 23 *M. fistulifera* in the border and eight in the forest, summing up 54 trees and 278 beating samples, as in three sampling periods. The number of populations studied and trees marked in each population scaled up along the sampling periods. Ten trees of each species in their respective ecotone habitats and six of each within the forest are the initial numbers sampled from the beginning of the project. Hence, this sub-set of 32 trees was used to study patterns of species richness and abundance in repeated measure ANOVA models (see below). The whole beating sample was used to study insect species composition, patterns of species distributions and fauna similarity among the populations and habitats, using multivariate analyses (see below). The sample size difference between ecotones and forest reflects the actual tree species densities in these habitats.

Statistical analysis

The effect of habitat (ecotone vs. forest) and host plant (*B. sericea* vs. *M. fistulifera)* on the insect species distribution were tested across distinct sampling period (wet season of 2001, wet and dry season of 2002). This model was evaluated thought a Multivariate Analysis of Variance (MANOVA), where tree species and habitat were tested as fixed factors, and sample periods were evaluated as multiple dependent variables for the number of insect richness or abundance - in different models – for the same

32 marked trees. MANOVA is adequate for analysing time repeated data because it does not require the dependent variables to be equally correlated as repeated-measures. Such unstructured variance-covariance matrix is then the best choice to investigate response of insect richness and abundance variation to habitat and host plant, over time of sampling, nevertheless also allowing the study of seasonality effect (VON ENDE, 2001).

In parallel, ANOVA with repeated measures were produced to test levels of significance related to interactions between host plant, habitat, and sampling period. Univariate repeated analysis concomitantly with a MANOVA approach, were the best choice in exploring more than two repeated measures, as MANOVA looses power proportionally to the number of dependent variable analysed (VON ENDE, 2001). Hence, for these analyses 96 beating samples were processed. To create a balanced design which could allow the investigation of interaction between host plant and habitats, the ecotone habitats were joined together in comparison to the forest habitat. ANOVA with Repeated Measures were performed as far as the data matrix did not depart significantly from sphericity, in which case an epsilon adjustment was applied (VON ENDE, 2001), using procedure in GLM Repeated Measures procedure of SPSS 11.5 software. ANOVA models were used with Sum of Squares Type III of this software, which deals better with unbalanced replicates. It is important to stress that comparison among mean number of species and individuals per crown, and between crowns and populations, are aimed in this analyses (tested of hypothesis 1). Therefore, ecological implications on the number of species and individuals sustained on an individual crown, in a certain plant community, are explored instead of estimations of Gamma Diversity.

Discriminant analysis was used to investigate insect species distribution between host species and habitats. SPSS for windows 11.5 was used to perform all parametric models cited above. Variation in species composition among seasons and sampling periods was described with a UPGMA cluster analysis, developed with the Community Analysis Package 2.1

(Pisces Conservation ltd, 2002). For multivariate analysis on insect community, a less balanced sampling effort was used, in order to explore total sampling size developed in this project. Hence, data collected in the wet and dry seasons of 2001 and 2002, from 22 trees of *B. sericea* and 31 of *M. fistulifera*, were analysed.

RESULTS

Species richness and abundance distribution

A total of 670 insects sorted in 114 herbivore morphospecies was found on *B. sericea* (60 spp.) and *M. fistulifera* (66 spp.) crowns, being that only 12 morphospecies (10.5 %) co-occurred in both species. From a total of 31 insect herbivore families, Curculionidae (24 spp.), Chrysomelidae (19 spp.), Anobiidae (2 spp.), Cicadellidade (5 spp.), Buprestidae (3 spp.) and Membracidae (2 spp.) were the most abundant. Nevertheless, only few species reached high abundance numbers. Among the most abundant Coleoptera genera (Fig. 2) we found *Mycrozurus* sp (Curculionidae), one species of *Syphraea* sp (Chrysomelidae), *Parasypharea* sp (Chrysomelidae), *Colaspis* sp (Chrysomelidae), and *Tricorynus* sp (Anobiidae). The greatest abundance of *Mycrozurus* sp was found only on *B. sericea* crowns, and mainly in the ecotone.

The subset data of 32 marked trees, studied along three sampling seasons for species richness and
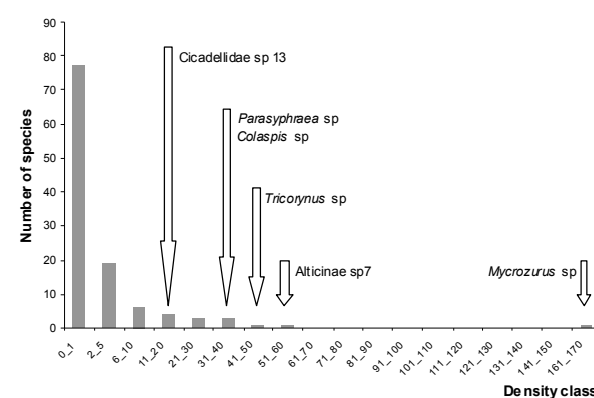
Figure 2. Distribution frequencies of herbivore morphospecies from beating samples in 53 trees of *M. fistulifera* and *B. sericea*. Most abundant genera of Coleoptera and morphospecie of sap-sucker indicated.

abundance per crown, summed 264 insects of 74 morfoespécies. The analysis of mean species number per tree sample showed a small number of herbivore species in a sampled branch (overall mean varied from 1.6 ± 0.14 in 2001-wet season to 2.0 ± 0.15 in 2001-dry season). Herbivore species richness did not varied significantly between host species and habitats, within any sampling period (MANOVA, Tab.1, Fig. 3). On the other hand, the average number of insect species across sampling period, showed a higher number of species on *B. sericea* than *M. fistulifera* (2.05 ± 0.17 vs 1.56 ± 0.17, between-subjects effects, repeated measures ANOVA, $F_{1,28}$ = 4.05, $P < 0.05$). Moreover within-subjects linear contrasts (deviation contrasts, generated by GLM in SPSS) showed a trend towards species richness increasing with time, regardless of seasonality ($F_{1,28}$ = 4.46, $P < 0.045$).

The insect abundance responded significantly to the interaction term between host plant and habitat, but only in the wet season of 2001 (Tab.2). This finding was influenced by higher insect abundance (3.3 ± 0.45) found in *B. sericea* in the forest (MANOVA, interaction term, $F_{1,28}$ = 5.9, $P < 0.02$, Fig. 4). Regardless the lack of a statistical significance for other seasons, values as high as 4.2 (± 0.9) mean insect individuals was observed on some *B. sericea* trees in the lake ashore, which was

Table 1. Tests of Between-Subjects Effects of MANOVA model for **insect herbivores species richness in** *B. sericea* and *M. fistulifera* found in a low forest and its ecotone habitats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	P
Corrected Model	Feb/2001	5.175(a)	3	0.514	0.631	0.462
	Feb/2002	14.167(b)	3	4.722	1.214	0.323
	Sep/2002	2.136	3	0.104	0.634	0.603
Plant	Feb/2001	0.633	1	0.633	1.19	0.212
	Feb/2002	11.408	1	11.408	2.658	0.068
	Sep/2002	0.075	1	0.075	0.16	0.713
Habitat	Feb/2001	0.208	1	0.208	0.257	0.385
	Feb/2002	1.833	1	1.833	0.282	0.475
	Sep/2002	0.133	1	0.133	0.200	0.653
Plant * Habitat	Feb/2001	0.833	1	0.833	1.129	0.342
	Feb/2002	0.033	1	0.033	0.011	0.518
	Sep/2002	1.500	1	1.500	1.500	0.100
error	Feb/2001	18.833	28	0.858		
	Feb/2002	87.333	28	3.18		
	Sep/2002	3.607	28	0.607		

a R Squared = 0.086 (Adjusted R Squared = -0.012)
b R Squared = 0.140 (Adjusted R Squared = 0.047)
c R Squared = 0.067 (Adjusted R Squared = -0.033)

Table 2. Tests of Between-Subjects Effects of MANOVA model for insect herbivores species abundance in *B. sericea* and *M. fistulifera* found in a low forest and its ecotone habitats.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	P
Corrected Model	Feb/2001	14.542(a)	3	4.847	4.072	0.016
	Feb/2002	45.208(b)	3	15.069	1.862	0.159
	Sep/2002	12.669(c)	3	4.223	0.757	0.528
Plant	Feb/2001	5.633	1	5.633	4.732	0.038
	Feb/2002	27.075	1	27.075	3.345	0.078
	Sep/2002	0.469	1	0.469	0.084	0.774
Habitat	Feb/2001	4.408	1	4.408	3.703	0.065
	Feb/2002	3.008	1	3.008	0.372	0.547
	Sep/2002	0.919	1	0.919	0.165	0.688
Plant * Habitat	Feb/2001	7.008	1	7.008	5.887	0.022
	Feb/2002	6.075	1	6.075	0.750	0.394
	Sep/2002	11.719	1	11.719	2.099	0.158
Error	Feb/2001	33.333	28	1.190		
	Feb/2002	226.667	28	8.095		
	Sep/2002	156.300	28	5.582		

a R Squared = 0.304 (Adjusted R Squared = 0.229)
b R Squared = 0.166 (Adjusted R Squared = 0.077)
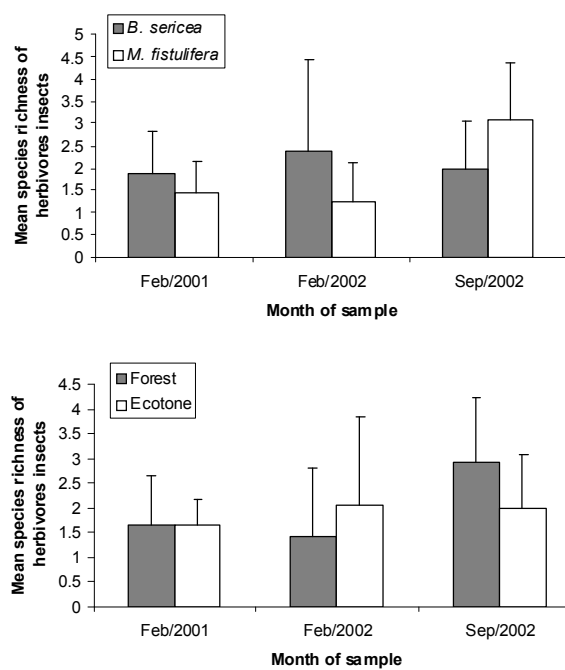c R Squared = 0.075 (Adjusted R Squared = -0.024)

Figure 3. Insect herbivores mean species numbers per (a) host species and (b) habitat for three different sampling periods.

mostly caused by a patchy distribution of the specialist *Mycrozurus* sp. concentrated on few tree crowns, in any dry or wet season.

Species composition distribution

Insect species composition and relative densities in the two host plants and habitats suggest distinct
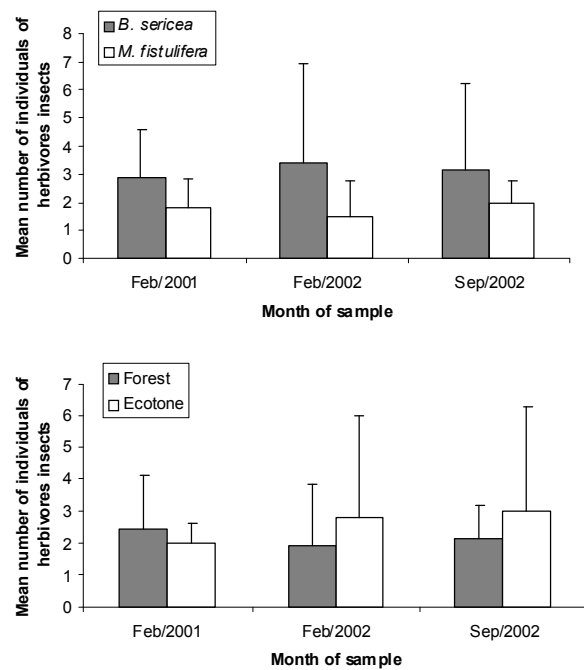
Figure 4. Insect herbivores mean individual numbers per (a) host species and (b) habitat for three different sampling periods.

insect herbivore species compositions. A noticeable separation between the fauna on *B. sericea* and on *M. fistulifera* was observed, but further separation was found also within *B. sericea* located in different habitats. In a Discriminant analysis using a combination of plant species and habitats as centroids, the Function 1 (Eigenvalue = 2.46) explained 50.3% of data variation (χ^2_{264} = 338.6; $P <$ 0.001, Tab.3). Although Function 2 (Eigenvalue = 1.82) did not distinguish significantly the centroids (χ^2_{174} = 185.9; $P >$ 0.255), it explained 37.5% of data variation (Tab.3). The insect herbivore fauna composition founded on *B. sericea* population in the lake ecotone was distinct from any other host population, and showed a strong positive correlation with Function 1. The presence of high numbers of *Mycrozurus* sp, *Parasyphraea* sp and *Colaspis* sp defined the main canonical coefficients behind Function 1 (Tab.3, Fig. 5), besides *Naupactus* sp (Curculionidae) and *Chlamisus* sp (Chrysomelidae), which were also relatively more abundant and frequent in the lake ecotone. Similarly, *B. sericea* fauna in the forest was also positively correlated to

Function 1 as well as Function 2. As a consequence, it was further separated from *B. sericea* trees in the ecotone. However, it is worthwhile noticing that a unique high frequency of *Parasyphraea* spp. was the important pattern characterizing this host population. Therefore, the habitats composed by *B. sericea* crowns in the forest or in the ecotone supported nearly the same herbivore species, although with completely distinct species relative densities.

Table 3. Canonical discriminant functions, tests of significance, insect species with highest canonical coefficients for Function 1, and correlation between centroid groups and discriminant functions.

Discriminant Functions	1	2	3
Wilks' Lambda	0.064	0.227	0.633
χ^2	338.6	185.9	68.3
df	264	174	86
P	0.001	0.246	0.925
Eigenvalue	2.46	1.82	1.06
% of Variance	50.3	37.3	12.4
Discriminant Variables	1	2	3
Parasyphraea sp (Chrysomelidae)	0.860	0.497	0.604
Systena sp (Chrysomelidae)	-0.287	0.512	0.003
Curculionidae	-0.343	-0.133	0.341
Colaspis sp (Chrysomelidae)	0.330	0.035	0.340
Mycrozurus sp (Curculionidae)	0.408	0.180	0.624
Naupactus sp (Curculionidae)	0.335	-0.385	0.068
Chlamisus sp (Chrysomelidae)	-0.340	-0.337	-0.33
Group Centroids	1	2	3
B. sericea Water - ecotone	-1.429	-0.134	0.483
B. sericea Water - forest	-1.103	0.002	-1.930
B. sericea no water	1.353	-0.53	0.062
M. sericea no water	1.351	0.167	0.179

Mabea fistulifera insect fauna showed strong negative correlation with Function 1 for both forest and ecotone populations, but did not distinguish amongst themselves. The clear separation of *B. sericea* and *M. fistulifera* was due to the absence of common species, along with remarkable particularities, such as the relatively high abundance and frequency of one species of *Syphraea* sp and an unidentified species of Cicadellidae, both exclusive in the latter host species (Tab.3, Fig.5).

The present sampling design was not able to detect any clear trend in species shifting along time or seasons, for none of host tree species. In general, wet season samples showed dissimilarity index lower than 20% between hosts and habitats, while dry season samples differ more than 35 % from the remaining samples, except for ecotone population of *M. fistulifera* in 2001, and within-forest population of *B. sericea* in 2002, both very much similar to all wet season samples.

DISCUSSION

Other studies developed in this forest showed similar results to ours, i.e., a remarkably small average number of species and individuals per sample, clearly lower than usually found in other tropical forest canopy. Neves (2006) and Soares (2006) found in an canopy sample of 73 tree species in the Rio Doce
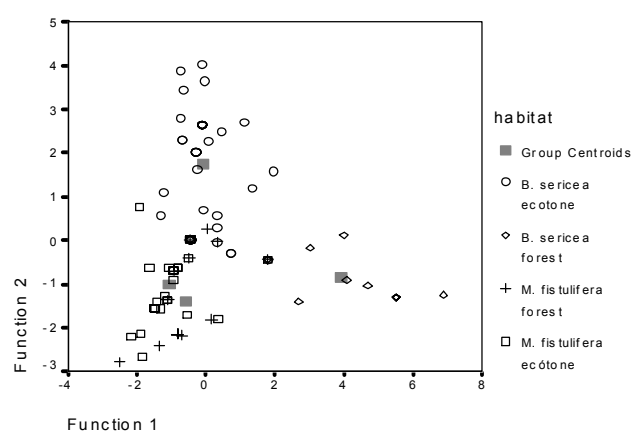

Figure 5. Discriminant analysis on insect herbivore species composition and densities distribution among the following centroids: 1- *M. fistulifera*/ecotone, 2- *M. fistulifera*/within forest, 3- *B. sericea*/within forest and 4- *B. sericea*/ecotone.

Park equivalent figures to ours, as well as in a study on an emergent tree species, the *Anadenanthera macrocarpa*, authors also encountered few insect species and individuals (Campos *et al.*, 2006b). Therefore, any result obtained in this forest contrast with other biomes sampled by the very same method in the tropics (Basset *et al.*, 2001; Ødegaard, 2000). Soares (2006) has proposed that Rio Doce forest may support a particularly insect species-poor community due to its ecological young age. Geological studies suggest the whole region was broadly covered by xeric ecosystems and more opened vegetation no later than 4,000 years ago.

Nevertheless, the composition and relative importance of insect herbivore families were very much as found in most tropical ecosystems. The dominant herbivorous families were Curculionidae, Chrysomelidae and Anobiidae, independently of habitat or host plant. For instance, Basset *et al.* (2001) found in Gabon (using beating and other sampling methods) that tree canopies were dominated by Chrysomelidae and Curculionidade. Many other works in tropical canopies all over the world (e.g. Basset & Samuelson, 1996; Hammond *et al.*, 1996), with several sampling methods, agree that Chrysomelidae and Curculionidae are the most abundant and speciose families. Ribeiro (2003) emphasises that insect family relative densities and diversity in tropical rainforest or savanna canopies do not differ dramatically from those found in any other environment. Such review suggests a strong evolutionary and phylogenetic constraint behind insect community composition, to which the present data corroborate.

Species richness did not vary between host species or habitats within each sampling period. However, overall results suggest a greater mean insect species number per crowns of *B. sericea* than *M. fistulifera*. The same trend was not observed in the cumulative number of herbivore species on each host species, which were similar among the hosts. In part, this pattern resulted from the low average number of species per host tree individual.

The mean insect species numbers found on *M. fistulifera* or *B. sericea* was greater than that found

on Brazilian cerrado tree species, which is an expected result. The seasonal semidecidous forest of Minas Gerais State has many common tree species with the cerrado, and thus an entangled ecologic and evolutionary history with that biome, though poorly understood. Still, the higher humidity or better soil conditions could result in a greater alpha diversity of insect herbivores per tree individuals when compared to cerrado host trees. A similar pattern was found in comparing the total cumulative number of insect herbivore species per tree, which varied between 185 to 320 in tropical rainforest habitats and 16 to 137 in cerrado tree species (Ribeiro 2003), and 114 in the present study.

The number of insect herbivore species associated to a host plant depends on its geographic distribution and local abundance (NEUVONEN & NIEMELÄ, 1981; LAWTON, 1982; LEATHER, 1986; MARQUIS, 1991), as well as chemical and nutritional leaf contents (CONNOR *et al.*, 1980; STRONG *et al.*, 1984). *Mabea fistulifera* is a latex species, which is a well known appetite inhibitor, mainly for chewers (FARRELL *et al.*, 1991). On the other hand, *Byrsonima* is a cerrado genus, and when found in the Atlantic rainforest domain, as in the present study, the species occur in low canopy forests, normally in sandy and less nutrient rich soils. Therefore, *Byrsonima* species tend to have sclerophyllous leaves, which are clearly less palatable to free-feeding herbivores (DINIZ & MORAIS, 1997).

Latex in *M. fistulifera* and sclerophylly in *B. sericea* may prevent colonization and survivorship of herbivores, particularly generalists. A noticeable contrast with recent findings in insect herbivore communities in tropical forest, is the fact that this tree species are supporting an apparently specialist herbivore guild. At least the dominant species found on these plants are exclusive species, and typically associated to the same plant species all year long, over the last four years (S.P. Ribeiro, pers. comm.). NOVOTNY *et al.* (2002) found more than 40 % of generalist insect herbivore on many tree species in Papua New Guinean tropical forest. We only had 10.5 % of insect species overlap, even though these tree species were co-occurring in the same forest. *Mycrozurus* sp. was clearly one of these specialist

and dominant species found only on *B. sericea*, being a strong determinant of the canopy community structure, namely in the lake ashore.

Each tree species crown traits may create distinct microhabitat conditions that could influence insect species fidelity, based on ecological aspects, such as microclimatic constancy, predator and parasitoid free spaces zones (BASSET, 1992; BARNAYS & MINKENBERG, 1997; RIBEIRO *et al.*, 2005). On the contrary of *B. sericea* fauna, that seems to be specialist but also partially exclusive to one or another habitat (such as the *Mycrozurus* sp.), the insect fauna found in *M. fistulifera* follows the host species whatever habitat occupied. In the present study a majority of the species were found in this plant across the distance of 13 Km between the studied populations. Therefore, habitat differences between ecotones and within forest canopies may result in the different insect herbivore species composition found between *B. sericea* populations, while *M. fistulifera* herbivore species seems to have closer identity to that host tree species.

CONCLUDING REMARKS

Our results corroborates other recent publications on canopy habitats and herbivore species distribution (RIBEIRO *et al.*, 2005; RIBEIRO & BASSET, 2007), which have challenged the classical concept of pioneer host species been predominantly occupied by generalist insect herbivores (COLEY *et al.*, 1985).

The present work corroborates the perception that surrounding habitats is an important aspect to be taken in consideration in studies of insect-plant interaction. In addition, our findings also reassure previous conclusions as pointed by RIBEIRO (2003) and RIBEIRO & BASSET (2007). Evolutionarily old plant community, specially if adapted to extreme conditions, as those found in xeric or sclerophyllous ecosystems of Brazil (as antique as the Tertiary ages), may accumulate a greater proportion of specialist insect species than found in equatorial, nutrient rich wet forests.

As pointed by DRAKE (1990), historical information may clarify patterns unlikely to be described by contemporary ecological processes. Our work suggest that recent climatic shifts may have resulted

in a relatively poor insect herbivore community, although long-term evolutionary exposition of those plant genera to herbivores should have resulted in a greatly specialized insect herbivore community.

Acknowledgments

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