## ECOLOGY, BEHAVIOR AND BIONOMY

# Distribution Pattern of Herbivorous Insects in a Remnant of Brazilian Atlantic Forest

Veralucia S. Barbosa[1], Inara R. Leal[1], Luciana Iannuzzi[2] and Jarcilene Almeida-Cortez[1]

*[1]Depto. Botânica; [2]Depto. Zoologia. Universidade Federal de Pernambuco, Av. Prof. Moraes Rêgo s/nº*
*Cidade Universitária, 50670-901, Recife, PE*
*veraluciab@yahoo.com.br, irleal@ufpe.br, iannuzzi@ufpe.br, jacortez@ufpe.br*

*Neotropical Entomology 34(5):701-711 (2005)*

Padrões de Distribuição de Insetos Herbívoros em um Remanescente de Floresta Atlântica Brasileira

RESUMO - Neste estudo foram selecionados três habitats que correspondem a um gradiente de proporção de plantas pioneiras – bordas, trilhas no interior de floresta e áreas nucleares de floresta – e descreveu-se a assembléia de insetos herbívoros neles presente. Foram testadas cinco hipóteses sobre a composição da assembléia: (1) as ordens de insetos herbívoros apresentam diferentes distribuições de abundância e de riqueza entre os habitats, (2) a similaridade de espécies é menor entre habitats do que dentro dos habitats, (3) a abundância é maior em borda, seguida de trilha e interior, (4) a riqueza é maior no interior, seguido de trilha e borda e (5) existe diferença na abundância e riqueza de insetos herbívoros entre as estações. Os insetos foram amostrados durante novembro de 2000 e maio de 2001 através da inspeção das plantas ao longo de 10 transectos de 1000 m$^3$ por habitat, cinco em cada estação. Foram amostrados 1.424 indivíduos de 367 espécies de seis ordens. Orthoptera e Coleoptera foram os herbívoros mais abundantes em borda e interior da floresta, respectivamente. Coleoptera apresentou a maior riqueza em borda de floresta enquanto Lepidoptera no interior. A fauna amostrada foi mais similar dentro de um mesmo habitat que entre os habitats. A abundância, riqueza e diversidade foram maiores na borda que em trilha e interior em ambas estações. Sugere-se que a baixa riqueza no interior da floresta se deva à perda de herbívoros especializados em plantas de floresta madura, as quais estariam também localmente extintas na área estudada.

PALAVRAS-CHAVE: Assembléia de herbívoros, defesa das plantas, diversidade de insetos, fragmentação, herbivoria, interação planta-inseto

ABSTRACT - In this study we selected three habitats that correspond to a light gradient, and consequently a proportion of pioneer plant species gradient – edges, trails and forest core – and described their herbivorous insect assemblage. We tested five hypothesis about the herbivorous assemblage: (1) there is a different distribution of abundance and richness of order between habitats, (2) species similarity between habitats is smaller than within habitat, (3) in forest edge the herbivores are more abundant than in trails and interior of the forest, (4) in nuclear areas herbivore richness and diversity are higher than in the trails and edge, and (5) the abundance and richness of herbivores are different between seasons. Herbivorous were sampled during November 2000 - May 2001 by scanning the plants in ten 1,000-m$^3$ transects per habitat, five per season. We sampled 1,424 adult individuals from 367 species of six orders. Orthoptera and Coleoptera were the most abundant herbivores in the edge and interior, respectively. Coleoptera showed the highest species diversity in the forest edge, while Lepidoptera was in the interior. The similarity of the fauna between habitats was smaller than within habitats. The values of abundance, richness and diversity in the edge were higher than those of trails and interior for both seasons. We suggest that the low richness of herbivores in the interior of the forest is due to a reduction of specialist groups associated to plant species characteristic of mature forest, which are locally extinct in the study area.

KEY WORDS: Fragmentation, herbivorous insect assemblage, herbivory, insect diversity, plant defense, plant-insect interaction

Insects are widely distributed in all habitats of the world and constitute the most diverse group of organisms (CSIRO 1991). The number of insect species known by the science is about 751,000 (Wilson 1999), but most authorities agree that there are much more species that have not yet been described. Conservative estimates suggest that this figure is 2 million (CSIRO 1991), however investigations about beetles in the canopy of tropical rain forest extend this number to 30 million (Erwin 1983). Whether we estimate 2-30 million species or an order of magnitude less, insects constitute around half of global species diversity (Gullan & Craston 1994). This marked numeric dominance means that insects are fundamentally important in processes that regulate terrestrial ecosystems, especially in the tropics (see revision in Loreau *et al*. 2002).

Insects present various feeding habits including carnivorous, saprophagous, parasitic, and most commonly herbivorous (CSIRO 1991). The increasingly high diversity and biomass of herbivorous insects, in spite of their small sizes, make them the most impacted organisms to the vegetation (Brown 1985). High rates of plant tissue consumption by insects, as well as by other herbivores, may alter plant growth, reproduction, and survivorship (Crawley 1989). Indirectly, herbivores also reduce competition for other plant species (Coley *et al.* 1985, Huisman *et al.* 1999), alter nutrient cycling (Huntly 1991), and disturb soils or other substrates (Ritchie & Olff 1999). Through these direct and indirect effects, herbivores modify population demography, succession and plant species diversity, and consequently, impact community dynamics and structure (Coley 1983, Huntly 1991).

In recent decades, much attention has been focused on the mechanisms by which the environment may alter the production of chemical defenses by plants, thereby altering their susceptibility to herbivores (i.e., 'resource availability theory' *sensu* Coley *et al*. 1985, but see also Brown 1985, Edwards-Jones & Brown 1993, Coley & Barone 1996, Barone & Coley 2001). Theoretical considerations and evidence from fieldworks suggest that early successional plant species should direct only a few resources to defense against herbivores, and should then provide better food sources for generalized herbivores than later successional and climax plants (Brown 1985, Coley *et al*. 1985, Barone & Coley 2001). Following this premise, we could speculate that the abundance of the herbivorous insects, mainly generalist species, would be higher in environments where pioneer species are dominant as in forest edges. However, as the forest core has higher plant species richness than edges (Brown 1985, Humphrey *et al*. 1999), and plant species richness is a measure of resource heterogeneity for herbivores (Marquis & Braker 1994), it is also reasonable to suppose that the interior of the forest supports higher herbivorous insect richness than edges. Although it is an interesting subject of study, few studies focus on composition of herbivorous assemblage in different stages of ecological succession (but see Brown 1985, Edwards-Jones & Brown 1993).

The aim of the present work was to describe the assemblage of herbivorous insects in a remnant of the Atlantic Forest in the northeastern Brazil. We selected three habitats that represent a light gradient, and consequently a proportion of pioneer plant species gradient – edges, trails and forest core – and investigated the composition of herbivorous insect assemblage by dry and rainy seasons. We addressed five questions about the herbivorous assemblage: (1) is there a different distribution of abundance and richness of order between habitats? (2) Is species similarity between habitats smaller than within habitat? (3) Are the herbivores more abundant at the edge of the forest than in trails and interior region? (4) Are herbivore richness and diversity higher in nuclear areas than in the trails and at the edge? And (5) are the abundance and richness of herbivores different between seasons?

## Material and Methods

The study was carried out at the Parque Estadual de Dois Irmãos (7°55'43''-8°09'17''S; 34°52'05''-35°00'59''W), a 390-ha fragment of Atlantic Forest near Recife, Pernambuco State, northeast Brazil. The climate matches Koeppen's tropical (As'), with a minimum temperature of 18ºC and monthly average of 23ºC (Coutinho *et al*. 1998). The annual rainfall is around 2,460 mm, with the wettest period between March and August, and the driest between September and February (Coutinho *et al*. 1998). The study site is located on low altitude plateaus (10-100m a.s.l.) of Formação Barreiras, where prevailing soils are latosols (IBGE 1985). The reserve is isolated from other forest remnants by sugar cane and urban areas (Machado *et al*. 1998).

The vegetation is classified as tropical lowland forest, one of the Brazilian Atlantic Forest types that occur at 50-100 m altitude (IBGE 1985). The forest structure shows the four levels of vegetation typical of Neotropical lowland forests (Tabarelli 1998), and presents a plant community similar to other Atlantic lowland forests described in the literature with Leguminosae, Lauraceae, Euphorbiaceae, Melastomataceae, and Sapotaceae as the richest families (Guedes 1998). Detailed information on climate, geomorphology and plant and animal species in the study site is available in Machado *et al.* (1998).

Herbivorous insects were sampled by scanning (cf. Freitas *et al*. 1999) during November 2000-May 2001, using 10 transects of 50m x 1m x 2m (1000 $m^3$) in the three habitats: forest edge (hereafter edge), trails in the interior of the forest (hereafter trails), and in the core area of the forest (hereafter interior). Edge transects were established in the limit between the forest and no forested area, with the highest luminosity. Trail transects were set in 100 m far from the forest edge in pre-existing trails opened by local people. Interior transects were placed 100 m far from the forest edge and any trails or gaps. Both herbaceous and shrubby (when present) strata were carefully inspected for herbivorous insects on one side of transect. Insects were collected, maintained in 70% ethanol, and identified to family (CSIRO 1991). Lepidoptera larvae and adults of the other sampled orders were sorted to morph species. Insects are deposited at the Laboratório de Invertebrados Terrestres of the Departamento de Zoologia of the Universidade Federal de Pernambuco.

The first hypothesis, that the orders of herbivorous insects should have different distribution in the three habitats, was tested by comparing the total abundance (i.e., the number of individuals collected in 10 transects) and richness (i.e., the number of species collected in 10 transects) of each order in edge, trail and interior using chi-square (Zar 1996). For the second hypothesis, i.e., that similarity between habitats is smaller than within habitat, we firstly calculated the Morisita-Horn´s index of similarity of each transect (NTSYSpc 2.01, Rohlf 1998). Morisita-Horn is an index of similarity quantitative, which require some measure of abundance for each species in the sample (Krebs 1998). A dendrogram was made using the values of the Morisita-Horn´s index and using the linking UPGMA method (NTSYSpc 2.01, Rohlf 1998). To test if the similarity index, and consequently the clusters of transects in the habitats, could be explained by chance, we ran the Monte Carlo test 2000 times. Monte Carlo gives values of simulated similarity obtained from the matrix of the data by replacing the originals sample values (Manly 1997). Thus, if the similarity index of the original data (*i.e.*, without simulation) is significantly higher than simulated ones the similarity is significant ($\alpha = 0.05$). The permutations were done by the software Randmat ver. 1.0 for Windows (http://eco.ib.usp.br/labmar).

Besides the abundance and richness of the herbivore assemblage, we also calculated the Shannon-Wiener's diversity index for each transects (Krebs 1998). Shannon-Wiener's index is the most popular measure of diversity and combines the species richness and evenness in a unique number, which gives us additional information about the herbivorous assemblage of each transect (Krebs 1998). Moreover, since the fieldwork had been carried out across two seasons, we also evaluated the seasonality effects on the herbivorous assemblage. The five transects sampled from November to February represent the dry season and the others sampled from March to May as rainy season. Therefore, to test the three last hypotheses – i.e., abundance, richness and diversity of herbivores should be different between habitats and seasons – we used a two-way ANOVA, followed by Tukey (Zar 1996). The normality of residues was tested by Lilliefors (Zar 1996). Species richness was $\log_2$ transformed. All the statistical procedures were performed with Systat (Wilkinson l996).

## Results

A total of 1,312 adult herbivorous insects were identified, distributed among 284 species in five orders (Table 1). We decided to include lepidopteran larvae once they were sorted to morph species, increasing the number of individuals to 1,424 and the species to 367 (Table 1). These data were used for further analyses. Considering the whole herbivorous insect assemblage of Dois Irmãos reserve, Orthoptera was the most abundant order (429 specimens), followed by Homoptera (345 specimens), Coleoptera (284 specimens), and Heteroptera (244 specimens). Coleoptera was the richest order (123 species), followed by Lepidoptera (83 species), and Homoptera (73 species).

When the herbivorous insect assemblage was compared between habitats, we found a difference distribution of abundance and richness of orders corroborating our first hypothesis (Figs. 1 and 2). The abundance of insect orders was significantly different between habitats (÷ = 118.58, df = 10, P < 0.0001, Fig. 1). Orthoptera were more representative of edge (268 specimens) and trails (113), while Homoptera was more abundant (88) in the interior of the forest (Fig. 1). In terms of richness, the distribution of herbivorous species in the orders was also significantly different between habitats (÷ = 25.18, df = 10, P = 0.005, Fig. 2). Coleoptera presented more species in the edge (63) and in trails (37), while Lepidoptera in the interior regions of the forest (31, Fig. 2).

Our second hypothesis was also confirmed, since the herbivorous assemblage of transects in different habitats present smaller values of the Morisita-Horn's index than transects within the same habitat (Fig. 3). Despite this generalization, the dendrograma showed only two main significant clusters (see clusters A and B in Fig. 3). The first one is composed by seven transects of edges (from B1 to B7), while the second includes six transects of the trails (from T1 to T5, T7, and T9) and five of the interior (M2, M5, M7, M8, and M9). This result indicates that the fauna of edge is more different from those of trail and interior, which are more similar. Three small clusters included the other trail and interior transects (M10-T8, M4-T6, M1-M6-T10-M3) were significant between them, but not significantly linked with the two large clusters (Horn's Index > 0.2, P < 0.05, 2000 replicates, Fig. 3).

The abundance and richness of insects were higher in the edge (790 specimens of 165 species), followed by trails (398 specimens of 114 species) and interior of the forest (236 specimens of 88 species). Fig. 4 shows the abundance, richness and the Shannon-Wiener diversity index values for habitats and seasons. The average values of abundance were significantly different between habitats (F = 25.53, df = 24, P < 0.0001) and between habitats and seasons (F = 4.65, df = 24, P = 0.019) corroborating our third hypothesis. But, contradictorily to our predictions, these differences were not significant when compared just between the seasons (Fig. 4A). Herbivorous insects in edge transects were more abundant than trails (Q = 6.14, P < 0.001) and interior (Q = 8.77, P < 0.001), and there were no differences between these two last habitats.

The significant differences of richness and of the Shannon-Wiener' index values between habitats and seasons confirmed our fourth and fifth hypotheses. The richness was significantly different between habitats (F = 19.05, df = 24, P < 0.0001), seasons (F = 7.46, df = 24, P < 0.05) and between habitats and seasons (F = 5.46, df = 24, P < 0.05, Fig. 4B). Transects in the edge were richer than those in trails (Q = 4.22, P < 0.01), and interior (Q = 6.92, P < 0.001), and there were no differences between these two last habitats. In relation to seasons, the richness was higher in the edge during dry season, but in the trails and interior the values were higher in the rainy season (Fig. 4B). The Shannon-Wiener values were significantly different between habitats

Table 1. Abundance and richness of herbivorous insects at edge, trail and interior of the forest at Parque Estadual de Dois Irmãos, Recife, PE.

| Taxa | Abundance | | | Richness | | |
|---|---|---|---|---|---|---|
| | Edge | Trails | Interior | Edge | Trails | Interior |
| Coleoptera | | | | | | |
| Anobiidae | | | 1 | | | 1 |
| Bostrichidae | 1 | | 1 | 1 | | 1 |
| Brentidae | 1 | | | 1 | | |
| Bruchidae | 2 | 1 | 1 | 2 | 1 | 1 |
| Buprestidae | 8 | 3 | | 5 | 3 | |
| Cerambycidae | | 1 | 1 | | 1 | 1 |
| Lamiinae | | | 1 | | | 1 |
| Coccinellidae | 26 | 13 | 5 | 9 | 4 | 2 |
| Chrysomelidae | 10 | 9 | 3 | 10 | 2 | 1 |
| Cassidinae | 5 | | | 2 | | |
| Cryptocephalinae | 15 | 1 | | 5 | 1 | |
| Eumolpinae | 21 | 6 | 2 | 3 | 4 | 1 |
| Fulcidacinae | 2 | | | 1 | | |
| Hispinae | 5 | 4 | 1 | 4 | 3 | 1 |
| Megascelinae | 44 | 4 | 1 | 8 | 2 | 1 |
| Orsodacninae | 10 | | | 1 | | |
| Curculionidae | 17 | 5 | 3 | 6 | 5 | 3 |
| Elateridae | | 3 | | | 3 | |
| Lycidae | 1 | 23 | 3 | 1 | 3 | 1 |
| Mordellidae | | | 1 | | | 1 |
| Scarabaeidae | 1 | | | 1 | | |
| Aphodiinae | | 2 | | | 1 | |
| Tenebrionidae | | 3 | 2 | | 1 | 2 |
| Unidentified | 3 | 3 | 5 | 3 | 3 | 5 |
| Total | 172 | 81 | 31 | 63 | 37 | 23 |
| Heteroptera | | | | | | |
| Coreidae | 5 | | | 3 | | |
| Pentatomidae | 70 | 17 | 2 | 6 | 3 | 2 |
| Pyrrhocoridae | 24 | 4 | | 1 | 1 | |
| Tingidae | 2 | 20 | 22 | 1 | 1 | 1 |
| Unidentified | 61 | 15 | 2 | 15 | 3 | 2 |
| Total | 162 | 56 | 26 | 26 | 8 | 5 |
| Homoptera | | | | | | |
| Coccoidea | 31 | 40 | 43 | 2 | 5 | 1 |
| Cercopidae | 3 | 3 | 2 | 1 | 3 | 1 |
| Cicadelidae | 14 | 16 | 7 | 13 | 5 | 4 |
| Fulgoridae | 17 | | 3 | 1 | | 1 |
| Membracidae | 37 | 4 | 4 | 7 | 3 | 4 |
| Unidentified | 61 | 31 | 29 | 7 | 8 | 7 |
| Total | 163 | 94 | 88 | 31 | 24 | 18 |

Cont. ...

Table 1. Continuation.

| Taxa | Abundance | | | Richness | | |
|---|---|---|---|---|---|---|
| | Edge | Trails | Interior | Edge | Trails | Interior |
| Lepidoptera | | | | | | |
| Geometridae | | 5 | 3 | | 5 | 3 |
| Licenidae | 2 | | | 2 | | |
| Unidentified | 23 | 44 | 35 | 21 | 24 | 28 |
| Total | 25 | 49 | 38 | 23 | 29 | 31 |
| Orthoptera | | | | | | |
| Acrididae | 181 | 16 | 2 | 8 | 4 | 2 |
| Leptysminae | 17 | | | 2 | | |
| Grillidae | 5 | 19 | 8 | 3 | 5 | 4 |
| Pyrgomorphidae | 25 | 2 | | 3 | 1 | |
| Romaleidae | 1 | 1 | | 1 | 1 | |
| Tetiigonidae | 37 | 75 | 38 | 3 | 4 | 4 |
| Unidentified | 2 | | | 2 | | |
| Total | 268 | 113 | 48 | 22 | 15 | 10 |
| Phamatodea | | | | | | |
| Phasmidae | | 5 | 5 | | 1 | 1 |
| Total | 0 | 5 | 5 | 0 | 1 | 1 |
| General total | 790 | 398 | 236 | 165 | 114 | 88 |

($F = 6.34$, df = 24, $P < 0.01$), seasons ($F = 5.23$, df = 24, $P < 0.05$) and marginally significant when combining habitats and seasons ($F = 3.37$, df = 24, $P = 0.051$, Fig. 4C). The diversity of herbivorous insects in the edge was higher than in the interior ($Q = 4.35$, $P < 0.005$), and there was not difference between edge and trail, neither between trail and interior (Fig. 4C). When we compared the diversity seasonally, the pattern was the same as the richness, i.e., values were higher in the edge during dry season, while trails and interior showed higher diversity in the rainy season (Fig. 4C).

## Discussion

In this study we described the herbivorous insect assemblage in three habitat of an Atlantic Forest remnant – edges, trails in the interior of the forest, and forest core. The fauna is very different between habitats, and edge transects presented higher values of abundance, richness and diversity for both seasons. We suggest that the low richness of herbivores in the interior of the forest is due to a reduction of specialist groups associated to plant species characteristic of mature forest, which are locally extinct in the study area.

The distribution of herbivorous orders described here is in accordance to other studies (Marinoni & Dutra 1991, Marinho *et al.* 1997, Pinheiro *et al.* 2002) in spite of different methodologies. Coleoptera is always between the most abundant and rich insect order since it is the most representative insect taxon with 350,000 species known (Lawrence *et al.* 1999). Moreover, this group occurs in a large variety of habitats and it presents a high diversity of food habit (CSIRO 1991). Other important orders in our study such as Orthoptera, Lepidoptera, and Homoptera, are less representative in works without food habit restriction (Marinoni & Dutra 1991, Marinho *et al.* 1997, Pinheiro *et al.* 2002). Such orders are strictly herbivorous and therefore were overestimated in our study.

When comparing the herbivorous assemblage between habitats we found a different composition of orders, corroborating our first hypothesis. Polyphagous insects are expected to live preferentially in edge area while specialists are expected to have the highest richness in the interior of the forest (Rao *et al.* 2001). We observed this pattern for some orders, for example Lepidoptera, the richest order in our interior transects. Despite having a great variety of feeding strategies, most larvae feed on a restricted group of plants, sometimes related, being adapted to the host toxin (Rao *et al.* 2001). We can speculate the same explanation for the Phasmatodea, whose species were collected only in our interior transect, and are specialized in Piperaceae and Maranthaceae (Berger & Wirth 2004). In relation to generalist insects, Orthoptera, most abundant in our edge transects, are the principal polyphagous insects together with ants (Araújo *et al.* 1997). For Heteroptera the proportion of generalist species decreases with the successional gradient (Brown 1985), and our data show the same pattern of higher abundance and richness in the edge. Therefore, although we did not identify our herbivore assemblage to the species level, our data are consistent with the trends of orders: the

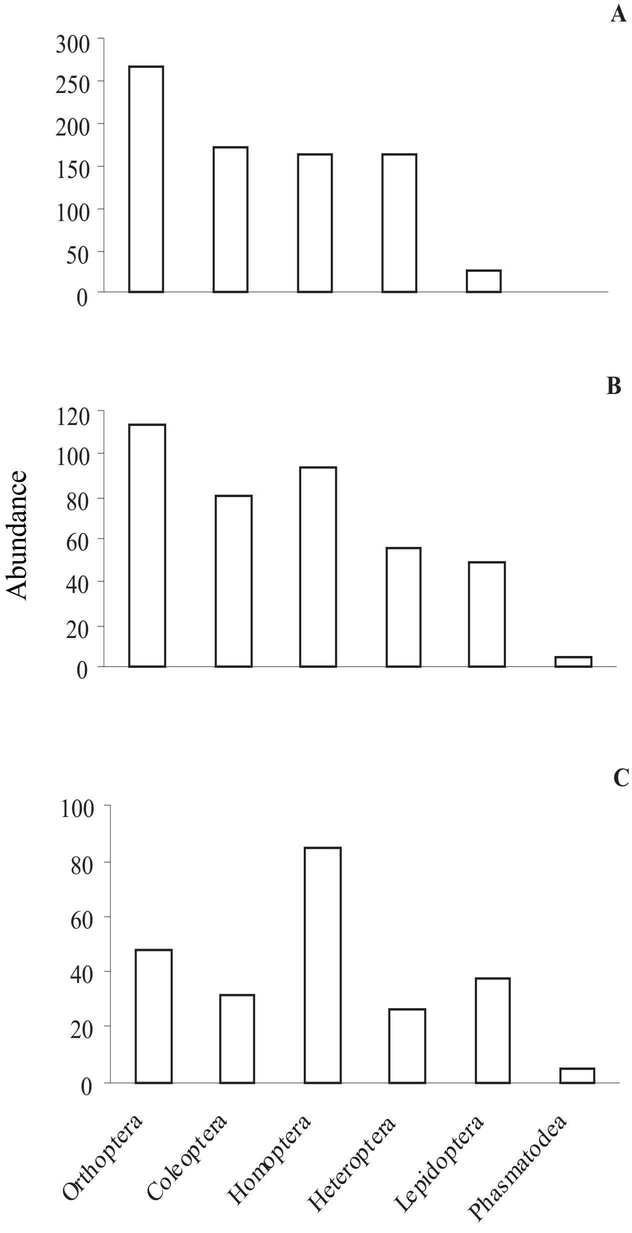

Figure 1. Abundance of herbivorous insect orders at edge (A), trail (B) and interior (C) of the forest at Parque Estadual de Dois Irmãos, Recife, PE, Brazil.

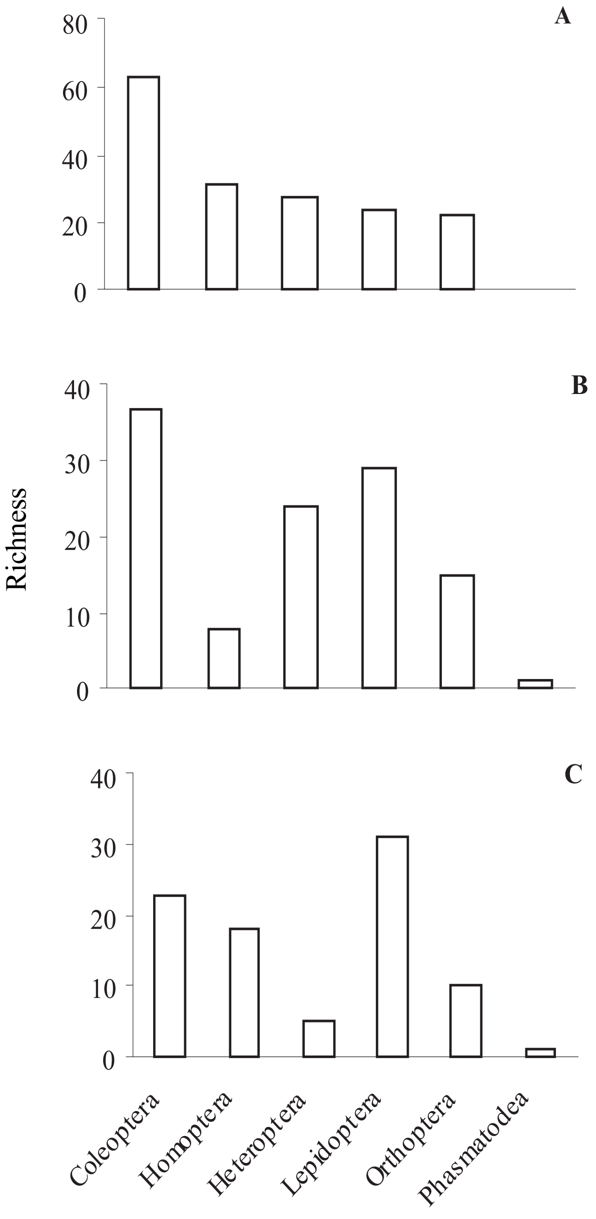

Figure 2. Richness of herbivorous insect orders at edge (A), trail (B) and interior (C) of the forest at Parque Estadual de Dois Irmãos, Recife, PE, Brazil.

more generalist groups being more common in edge areas, while orders with specialist members occur more commonly in the interior of the forest.

The herbivorous insect fauna was more similar within habitat than between habitats corroborating our second hypothesis. Despite this general pattern, some transects of trails and interior form significant clusters indicating a similar fauna for both habitats. This pattern was expected since the trails sampled were located in the interior of the forest, presenting microclimatic and floristic similarity with the interior transects. On the other hand, the edge transects were sampled in the limit between the forest and no forested area, with the highest luminosity. Therefore the microclimatic conditions, composition and structure of the vegetation are different from those of trails and interior of the forest, responding for the difference between them.

Our results also corroborate the third hypothesis that the abundance of herbivorous insects in edge areas is higher than in trails and least in interior regions of the forest. Other studies have found the same pattern of higher abundance of herbivores in early successional habitats (e.g., Brown 1985, Edwards-Jones & Brown 1993). This pattern is expected to be due to the higher frequency of pioneer species, whose higher growth rate results in a lower predicted investment in

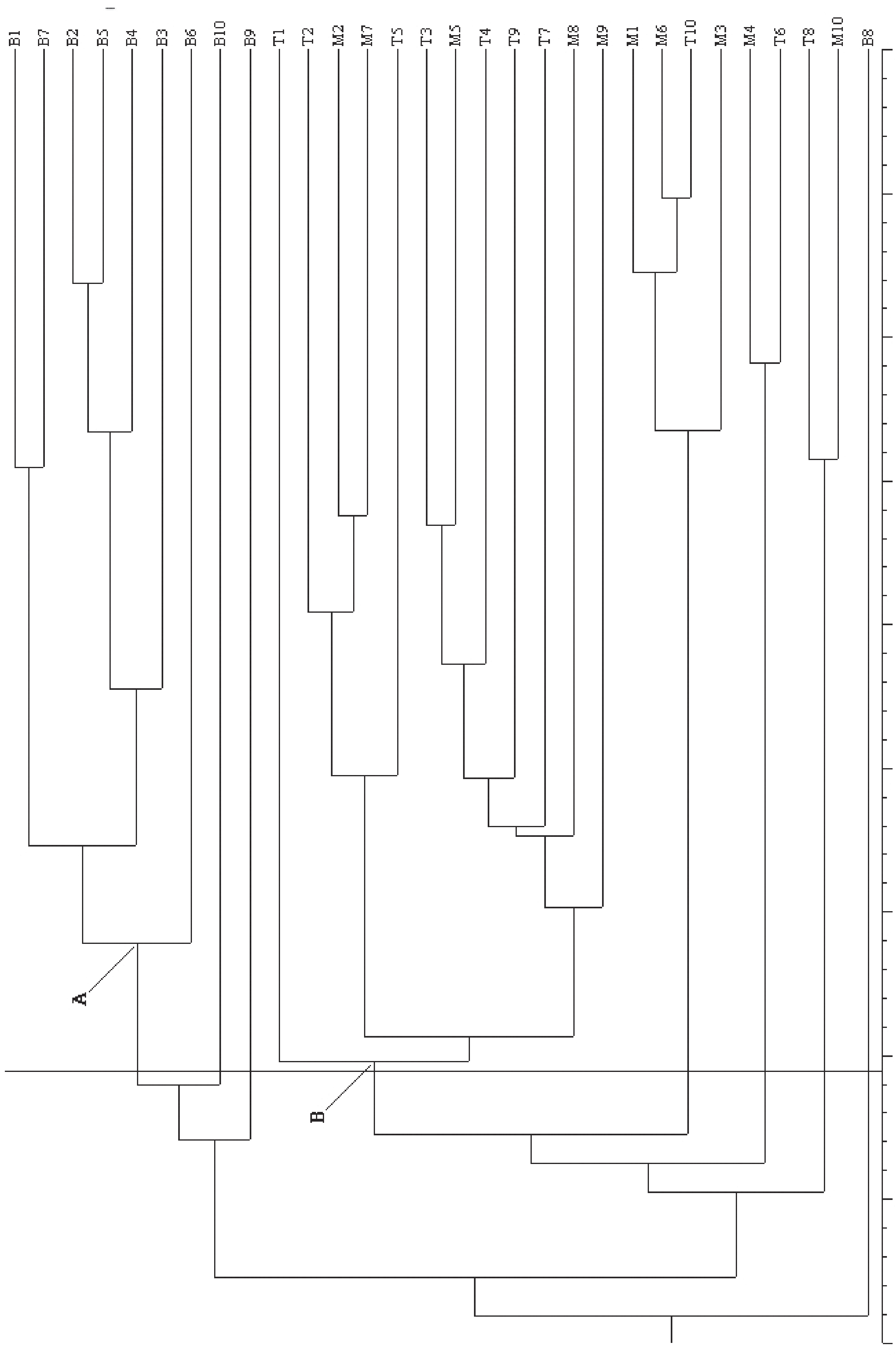

Figure. 3. Similarity dendrogram for herbivorous insect assemblage of edge (B1 to B 10), trail (T1 to T10) and interior of the forest (M1 to M10) at Parque Estadual de Dois Irmãos, Recife, PE, Brazil. To test if the similarity index, consequently, the clusters of the habitats, could be explained by chance, we ran the Monte Carlo test 2000 times. Clusters above the horizontal line are significant ($\alpha = 0.05$).

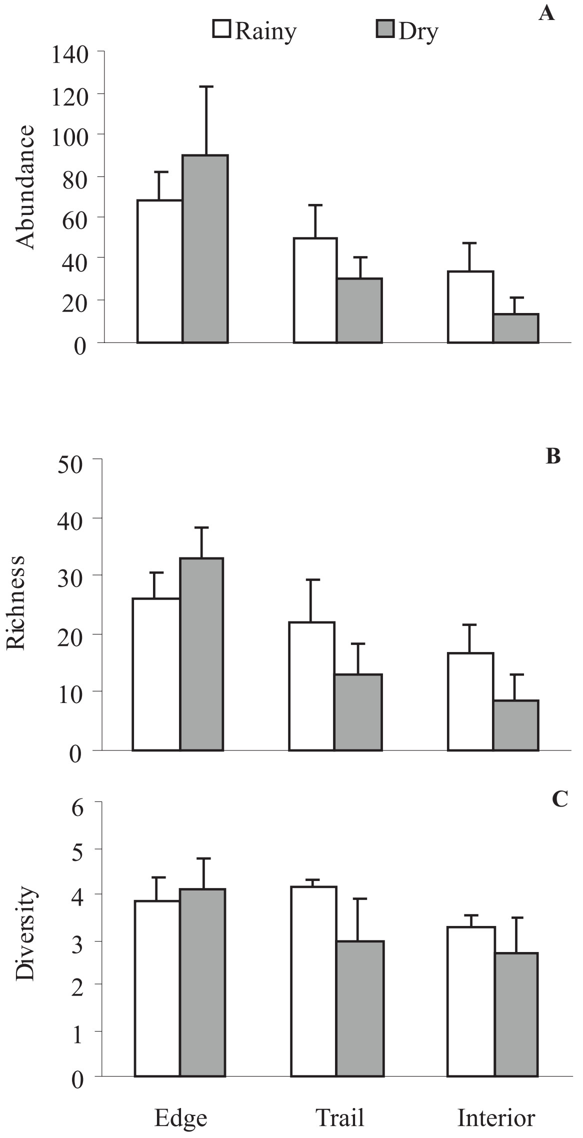

Figure 4. Average and standard deviation of abundance (A), richness (B) and Shannon-Wiener diversity index values (C) of herbivorous insect assemblage during rainy and dry season at Parque Estadual de Dois Irmãos, Recife, PE, Brazil.

defense (Coley *et al.* 1985). Herbivores tend to prefer fast-growing plants and avoid slow-growing plants (Coley 1983, Coley *et al*. 1985, Coley & Barone 1996, Barone & Coley 2001). Additionally, the richness and diversity of herbivores followed the same pattern as the abundance, contrary to our fourth prediction of higher values in the interior of the forest due to higher diversity of plant in this habitat. This pattern could be explained by three possible reasons: (1) our premise that plant richness is a measure of resource heterogeneity for the herbivorous insects is not true, (2) the vegetation stratum sampled at the edge is richer than in the interior, and (3) the degree of disturbance at the study site is relatively high and some later successional plant species are extinct at Dois Irmãos Reserve, and consequently some specialist herbivorous insects could also be locally extinct.

Our premise that plant richness is a measure of resource heterogeneity for the herbivorous insects has been suggested by Marquis & Braker (1994). The authors state that higher richness and diversity of herbivorous species could be related to the higher structural complexity, abundance and richness of the plant community of the interior of the forest. Another possibility to explain the higher richness in the edge is that the vegetation stratum sampled – i.e., the lowest stratum was composed mainly by herbaceous species - in the interior of the forest is not richer than at the edge. However, in the interior of the forest the lowest stratum also contains seedlings and juveniles of canopy and emergent trees, which may increase the total plant richness for this habitat.

The higher richness of the herbivorous insects in the interior of the forest is also attributed to the specialization of some groups to specific plant chemical substances. This specialization favors the insects that encounter fewer compounds with behavioral (deterrent) or physiological (toxic) negative effects than the polyphagous insects (Caldas & Moutinho 1993). Therefore, the higher herbivore richness at the edge of the study site should be due to reduction of specialist herbivores in the interior of the fragment. These groups of insects could be locally extinct due to the absence of later successional plants species at the study site. In fact, Tabarelli (1998) points out that Dois Irmãos Reserve shows dramatic fragmentation impacts and some species of the families Arecaceae, Fabaceae, Lauraceae, Lecythidaceae, Sapotaceae, Rutaceae and Apocynaceae are present only in small populations or are locally extinct. Didham *et al.* (1996) also proposed that more specialized taxa could be directly or indirectly more susceptible to fragmentation, once they are more closely related to the host, prey or habitat, showing less flexibility to compete under environment changes. Thus, generalist species respond more successfully to environmental changes and are able to survive in remnant forests (Didham *et al*. 1996, Gibb & Hochuli 2002). In this context, it is reasonable to suggest that the herbivorous insect fauna at Dois Irmãos Reserve is composed basically of generalist species, thereby explaining the higher richness in the edge than the interior of the forest.

We observed significant differences in herbivores richness and values of the Shannon-Wiener's index during the season, confirming our fifth prediction. In the dry season the values of richness and diversity of phytophagous were highest for the edges followed by trails and interior of the forest. However, during the wet season only the values of richness had the same pattern, but the diversity was highest for the trails followed by edge and interior of the forest. If we considered the influence of the seasons in each habitat, the parameters for edge areas were highest during the dry season, while for the trails and the interior of the forest the same parameters showed higher values during the wet season. Some insect species could develop a series of strategies and adaptations, such as dormancy, diapause and migration in a high seasonality environment, due to resource reduction (Pinheiro *et al.* 2002). Even in the study area the seasonality is not so high, the dry season is also the hottest months of the year. Therefore it is possible that several species were not collected due to the absence (migration) or others physiological strategies to be protected from high temperatures during the dry season (Janzen & Schoener 1968, Janzen 1973, Wolda 1988, Pinheiro *et al*. 2002).

Our studies found no significant difference for the abundance when we compared the seasons. Several studies have demonstrated that the insect population reduces during the dry season and gradually increases at the start of the raining season (e.g., Janzen & Schoener 1968, Janzen 1973, Wolda 1988, Pinheiro *et al*. 2002), other studies found none or little reduction of insect abundance during the dry season (Pinheiro *et al*. 2002). These differences were observed in tropical habitats especially those with sharp seasonality, for example Cerrado and Caatinga (Pinheiro *et al*. 2002, Iannuzzi *et al*. 2003, Maia *et al*. 2003). Another way to evaluate the seasonal influence on insect populations is to analyze each order separately. Therefore each taxon responds different to season, depending of the resource availability, which each one explores because some orders have species in different trophic levels that depend upon different food resources (Pinheiro *et al*. 2002).

The high values of abundance, richness and diversity of phytophagous insects for the edge during the dry season could be explained by the observations of Schowalter *et al*. (1986). According to them, rain and storms could directly influence the herbivory rates by reducing the survivorship and food resources of the insects and the host susceptibility. Those abiotic factors could affect fling time, oviposition behavior and result in death during the larval stage (Marquis & Braker 1994). Thus, as insects are more exposed at the edge, we can speculate that the abiotic factors can influence them more in this region than in the interior of the forest.

The low richness and diversity in core areas found in this study could be due to a habitat reduction and environmental disturbance decreasing specialist insects in the interior of the forest. Since this study was conducted in just one forest fragment, it would be interesting to verify the herbivorous insect richness in the core area of fragments with different sizes and disturbance levels to present these patterns.

## Acknowledgments

We are particularly grateful to Cintia Ramos for field assistance. We thank Alexandre de Barros, the manager of the Parque Estadual de Dois Irmãos, for allowing us access to the study site, to Bill Shipley for providing comments on earlier versions of the manuscript, and two anonymous referees. André M. Santos, José Roberto Botelho de Souza, and Paulo José Parreira Santos for helping with the statistics analyses. Scott V. Heald for improving the English version of the manuscript.

## Literature Cited

**Araújo, M.C., G.C. Coelho & L. Medeiros. 1997.** (eds.) Interações ecológicas e biodiversidade. Ijuí, Editora UNIJUÍ, 252p.

**Barone J.A. & P.D. Coley. 2001.** Herbivory and plant defenses, p.465-492. In M.R. Guariguata & G. Kattan (eds.), Ecología y conservación de bosques neotropicales. Costa Rica, Libro Universitario Regional, 692p.

**Berger, J.R. & R. Wirth. 2004.** Predation-mediated mortality of early life stages: A field experiment with nymphs of an herbivorous stick insect (*Metriophasma diocles*). Biotropica 36: 424-428.

**Brown, V.K. 1985.** Insect herbivores and plant succession. Oikos 44: 17-22.

**Caldas, A. & P.R.S. Moutinho. 1993.** Composição e diversidade da fauna de formigas (Hymenoptera, Formicidae) em áreas sob remoção experimental de árvores na Reserva Florestal de Linhares, ES, Brasil. Rev. Bras. Entomol. 37: 299-304.

**Coley, P.D. 1983.** Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Monogr. 53: 209-233.

**Coley, P.D. & J.A. Barone. 1996.** Herbivory and plant defenses in tropical forests. Annu. Rev. Ecol. Syst. 27: 305-335.

**Coley, P.D., J.P. Bryant & F.S. Chapin. 1985.** Resource availability and plant antiherbivore defense. Science 230: 895-899.

**Coutinho, R.Q., M.F. Lima Filho, J.B. Souza Neto & E.P. Silva. 1998.** Características climáticas, geológicas, geomorfológicas e geotécnicas da Reserva Ecológica de Dois Irmãos, p.21-49. In I.C. Machado, A.V. Lopes & K.C. Pôrto (eds.), Reserva Ecológica de Dois Irmãos: Estudos em um remanescente de mata Atlântica em área urbana (Recife – Pernambuco – Brasil). Recife, Editora Universitária da UFPE, 326p.

**Crawley, M.J. 1989.** Insect herbivores and plant population dynamics. Annu. Rev. Entomol. 34: 531-564.

**CSIRO. 1991.** The insects of Australia. A textbook for students and research workers. New York, Cornell University Press, 1135p.

**Didham, R.K., J. Ghazoul, N.E. Stork & A.J. Davis. 1996.** Insects in fragmented forests: A functional approach. TREE 11: 255-260.

**Edwards-Jones, G. & V.K. Brown. 1993.** Successional trends in insect herbivore population densities: A field test of a hypothesis. Oikos 66: 463-471.

**Erwin, T. L. 1983.** Tropical forest canopies: The last biotic frontier. Bull. Entomol. Soc. Am. 29: 14-19.

**Freitas, A.V.L., I.R. Leal & S.O. Ferreira. 1999.** Selection of oviposition sites by a lepidopteran community of a tropical forest in Southeastern Brazil. Biotropica 31: 372-375.

**Gibb, H. & D.F. Hochuli. 2002.** Habitat fragmentation in an urban environment: Large and small fragments support different arthropod assemblages. Biol. Conserv. 106: 91-100.

**Guedes, M.L.S. 1998.** A vegetação fanerogâmica da Reserva Ecológica de Dois Irmãos, p.157-172. In I.C. Machado, A.V. Lopes & K.C. Pôrto (eds.), Reserva Ecológica de Dois Irmãos: Estudos em um remanescente de mata Atlântica em área urbana (Recife – Pernambuco – Brasil). Recife, Editora Universitária da UFPE, 326p.

**Gullan, P.G. & P.S. Craston. 1994.** Insects: An outline of entomology. London, Chapman & Hall, 491p.

**Huisman, J., J.P. Grover, R. Van Der Wal & J. Van Andel. 1999.** Competition for light, plant-species replacement and herbivore abundance along productivity gradients, p.239-269. In H. Olff, V.K. Brown & R.H. Drent (eds.), Herbivores: Between plants and predators. Oxford, Blackwell Science, 639p.

**Humphrey, J.W., C. Hawes, A.J Peace, R. Ferris-Kaan & M.R. Jukes. 1999.** Relationships between insect diversity and habitat characteristics in plantation forests. Forest Ecol. Manag. 113:11-21.

**Huntly, N.J. 1991.** Herbivores and the dynamics of communities and ecosystems. Annu. Rev. Ecol. Syst. 22: 477-503.

**Iannuzzi, L., A.C.D. Maia, C.E.B. Nobre, D.K. Suzuki & F.J. de A. Muniz. 2003.** Padrões locais de diversidade de Coleoptera (Insecta) em vegetação de caatinga, p.367-389. In I.R. Leal, M. Tabarelli & J.M.C. da Silva (eds), Ecologia e conservação da caatinga. Recife, Editora Universitária da UFPE, 804p.

**IBGE 1985.** Atlas Nacional do Brasil: Região Nordeste, Rio de Janeiro, IBGE.

**Janzen, D.H. 1973.** Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevations, time of day, and insularity. Ecology 54: 687-702.

**Janzen D.H. & T.W. Schoener. 1968.** Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49: 96-110.

**Krebs, C.J. 1998.** Ecological methodology. New York, Benjamin/Cummings Publishers, 620p.

**Lawrence, F.A., A.M. Hasting, M.J. Dallwitz, T.A. Paine & E.J. Zurcher. 1999.** Beetles of the world. A key and information system for families and subfamilies. Version 1.0 for MS-Windows. Melbourne, CSIRO Publishing, 1 CD-ROM.

**Loreau, M., S. Naeem & P. Inchausti. 2002.** Biodiversity and ecosystem functioning: Synthesis and perspectives. Oxford, Oxford University Press, 294p.

**Machado, I.C., A.V. Lopes & K.C. Porto. 1998.** (eds.) Reserva Ecológica de Dois Irmãos: Estudos em um remanescente de mata Atlântica em área urbana (Recife – Pernambuco – Brasil). Recife, Editora Universitária da UFPE, 326p.

**Maia, A.C.D., L. Iannuzzi, C.E.B. Nobre & C.M.R. De Albuquerque. 2003.** Padrões locais de diversidade de Cerambycidae (Insecta, Coleoptera) em vegetação de caatinga, p.391-433. In I.R. Leal, M. Tabarelli & J.M.C. da Silva (eds), Ecologia e conservação da caatinga. Recife, Editora Universitária da UFPE, 804p.

**Manly, B.F.J. 1997.** Randomization, Bootstrap and Monte Carlo methods in biology. London, Chapman & Hall, 399p.

**Marinho, C.G.S., S.M. Soares & T.M.C. Della Lucia. 1997.** Diversidade de invertebrados edáficos em áreas de eucalipto e mata secundária. Acta Biol. Leopoldensia 19:157-164.

**Marinoni, R.C. & R.R.C. Dutra. 1991.** Levantamento da fauna entomológica no estado do Paraná. I. Introdução. Situações climáticas e florísticas de oito pontos de coleta. Dados faunísticos de agosto de 1986 a julho de 1987. Rev. Bras. Zool. 8: 31-73.

**Marquis, R.J. & H.E. Braker. 1994.** Plant-herbivore interactions: Diversity, specificity, and impact, p.261-281. In L.A. McDade, K.S.Bawa, H.A. Hespenheide & G.S. Hartshorn (eds.), La Selva, ecology and natural history of a neotropical rain forest. Chicago, The University of Chicago Press, 486p.

**Pinheiro, F., I.R.Diniz, D.Coelho & M.P.S. Bandeira. 2002.** Seasonal pattern of insect abundance in the Brazilian cerrado. Austral Ecol. 27: 132-136.

**Randmat ver. 1.0 for Windows. 2001.** http://eco.ib.usp.br/labmar.

**Rao, M., J. Terborgh & P. Nuñez. 2001.** Increased herbivory in forest isolates: Implications for plant community structure and composition. Conserv. Biol. 15: 624-633.

**Ritchie, M.E. & H. Olff. 1999.** Herbivore diversity and plant dynamics: Compensatory and additive effects, p.175-204. In H. Olff, V.K. Brown & R.H. Drent (eds.), Herbivores: Between plants and predators. Oxford, Blackwell Science, 639p.

**Rohlf, F.J. 1998.** NTSYSpc, numerical taxonomy and multivariate data analysis system, ver. 2.01. Exeter Software: Setauket, New York.

**Schowalter, T.D., W.W. Hargrove & D.A. Crossley Jr. 1986.** Herbivory in forested ecosystems. Annu. Rev. Entomol. 31: 177-196.

**Tabarelli, M. 1998.** Dois Irmãos: O desafio da conservação biológica em um fragmento de floresta tropical, p.311-323. In I.C. Machado, A.V. Lopes & K.C. Pôrto (eds.), Reserva Ecológica de Dois Irmãos: Eestudos em um remanescente de mata Atlântica em área urbana (Recife – Pernambuco – Brasil). Recife, Editora Universitária da UFPE, 326p.

**Wilkinson, L. 1996.** Systat, version 6.0. Illinois, SPSS, Chicago.

**Wilson, E.O. 1999.** Biodiversity. Washington, National Academic Press, 521p.

**Wolda, H. 1988.** Insect seasonality: Why? Annu. Rev. Ecol. Syst. 19: 1-18.

**Zar, J.H. 1996.** Biostatistical analysis. New Jersey, Prentice Hall Inc., 662p.

*Received 26/III/04. Accepted 27/V/05.*