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"Artrópodes como indicadores biológicos de perturbação antrópica"

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ABSTRACT

In this study, the responses of terrestrial arthropods to different types of anthropogenic disturbance were examined, aiming to select and test ecological indicators. Ten groups of terrestrial arthropods were selected and sampled in an Atlantic Forest reserve with two sites with contrasting histories of disturbance, one with history of selective logging (preserved) and another with history of slash-and-burn (disturbed). The abundance of exotic species was higher in the disturbed area, and this pattern seems to be an adequate indicator of anthropogenic disturbance. Species richness was not significantly correlated between any pair of taxa. In contrast, species composition was significantly correlated among most groups, and clearly discriminates the disturbed from the undisturbed site. The composition of fruit-feeding butterflies and epigaeic Coleoptera were the best indicators in this study, discriminating between the disturbed and the undisturbed sites even in higher taxonomic categories, and acting as surrogates of the remaining arthropod groups. To validate the above findings, two additional Atlantic Forest reserves with different kinds of anthropogenic disturbance were sampled, aiming to find consistent responses to the three sources of disturbance. Fruit-feeding butterflies were used as focal group due to its usefulness as ecological indicators in the first study. Shifts in the species composition, abundance and proportion of three subfamilies (Brassolinae, Charaxinae and Satyrinae) were found to be consistent in our three study areas with different disturbance types and degrees. Results indicate that fruit-feeding butterflies may be promptly employed as disturbance indicators in the Atlantic Forest. On the other hand, disturbance effects on the fauna of the Brazilian Cerrado are still poorly understood. In the third study, the abundance of epigaeic arthropod orders and trophic guilds was assessed in cerrado sites subjected to three burning frequencies: frequent (HighFi), intermediary (MidFi) and infrequent (LowFi). None of the orders or trophic guilds analyzed had higher abundance in the LowFi, being either more abundant in the HighFi or MidFi, or did not differ among the burning frequencies. Results indicate that some arthropod groups may not only be resilient to fire effect, but actually benefit from fire effect in cerrado. Based on the results, springtails (Collembola) and ants (Hymenoptera, Formicidae) seem to be particularly appropriate focal groups for further exploratory studies at species level aiming to verify their indicator properties, since they are abundant in samples and, in the case of ants, relatively well known in the Cerrado. To sum up, the present study supports the potential of using arthropods as ecological indicators in different biomes, showing new directions to future research.

RESUMO

No presente estudo, foram examinadas respostas de artrópodes a diferentes tipos de perturbação antrópica, com o intuito de selecionar e testar indicadores ecológicos. Para tal, dez grupos de artrópodes terrestres foram selecionados e amostrados em uma reserva de Floresta Atlântica com duas áreas com histórico contrastante de perturbação: uma com corte seletivo ('conservada') e outra com corte raso e queimada ('perturbada'). A abundância de espécies exóticas foi maior na área perturbada, padrão que aparentemente é um bom indicador de perturbação antrópica. Não houve correlação significativa da riqueza de espécies entre nenhum dos taxa selecionados. Por outro lado, a composição de espécies discriminou claramente a área perturbada da conservada, e foi significativamente correlacionada entre maior parte dos grupos. A composição de espécies de borboletas frugívoras e besouros epigéicos foram os melhores indicadores de perturbação, discriminando ambas as áreas mesmo com baixa resolução taxonômica e atuando como representantes de outros grupos de artrópodes. Para poder validar os resultados encontrados na primeira etapa, foram amostradas outras duas reservas de Floresta Atlântica com diferentes tipos de perturbação antrópica, com o objetivo de se verificar se existem respostas consistentes para três diferentes fontes de perturbação. Uma vez que se mostraram boas indicadoras de perturbação, borboletas frugívoras foram escolhidas como grupo focal. Mudanças na composição de espécies, abundância total e representatividade de três subfamílias (Brassolinae, Charaxinae e Satyrinae) foram consistentes nas áreas de estudo com diferentes tipos e graus de contraste de perturbação. Os resultados indicam que borboletas frugívoras podem ser prontamente aplicadas como indicadoras de perturbação antrópica em Floresta Atlântica. Por outro lado, os efeitos de perturbações na fauna do Cerrado ainda são pouco conhecidos. No terceiro estudo, a abundância de ordens e guildas tróficas de artrópodes epigéicos foi comparada entre áreas de uma reserva de

Cerrado com diferentes frequências de queima: frequente (HighFi), intermediária (MidFi) e infrequente (LowFi). Nenhuma das ordens ou guildas tróficas analisadas apresentou maior abundância na LowFi, sendo mais abundantes na HighFi ou MidFi, ou não apresentando diferença entre as frequencias de queima. Os resultados indicam que alguns grupos de artrópodes podem não apenas ser resilientes aos efeitos do fogo, mas de fato se beneficiar dele. Os resultados encontrados devem ser considerados uma primeira abordagem a partir da qual estudos mais detalhados devem ser feitos. De acordo com os resultados, Collembola e formigas são grupos focais promissores para estudos exploratórios adicionais com o intuito de verificar suas propriedades indicadoras na escala de espécie, uma vez que são abundantes nas amostras e, no caso das formigas, relativamente bem conhecidas no Cerrado. Os resultados do presente trabalho reafirmam o potencial de artrópodes como indicadores ecológicos em diferentes biomas, e apontam as direções a ser tomadas em futuros estudos nesta área.

INTRODUÇÃO GERAL

Diagnosticar e monitorar a diversidade biológica são atividades essenciais para a avaliação da conservação ou da restauração da biodiversidade. Dada a dificuldade de se tomar medidas diretas de todo o ambiente, por razões práticas ligadas a tempo, custo ou ausência de conhecimento taxonômico (Bockstaller & Girardin, 2003; Duelli & Obrist, 2003; Sauberer et al., 2004; Oertly et al., 2005), o desenvolvimento de atalhos que satisfaçam essa necessidade de avaliação e monitoramento é fundamental (McGeoch, 1998; Niemi & McDonald, 2004). Neste contexto foi criada e desenvolvida a área de investigação de indicadores biológicos, que são organismos cujas características (como presença, abundância e atributos individuais) refletem condições ambientais ou fenômenos biológicos difíceis, inconvenientes ou caros para serem medidos diretamente (Landres et al., 1988; McGeoch, 1998; Rølstad *et al.*, 2002).

A maioria dos indicadores biológicos é identificada através da confiabilidade da sua resposta à alguma característica do ambiente (Kitching *et al.*, 2000; Dale & Beyeler, 2001; para definições veja McGeoch, 1998). No entanto, para serem usados com confiança os indicadores biológicos devem ser testados de forma independente daquela usada na sua identificação inicial (uma premissa poucas vezes testada de forma efetiva). Uma vez que o caráter de indicador biológico tenha sido estabelecido, sua robustez deve ser testada, por exemplo, re-amostrando o mesmo tipo de ambiente sob circunstâncias temporais ou espaciais diferentes (Weaver, 1995; Majer & Nichols, 1998).

Embora a criação de protocolos de monitoramento seja uma das prioridades atuais para a conservação de ambientes tropicais (Toit *et al.*, 2004) e muitos indicadores biológicos tenham sido propostos para ecossistemas terrestres ao longo dos últimos anos, poucos foram efetivamente testados no campo (McGeoch, 1998; Simberloff, 1998). Adicionalmente, poucos estudos investigaram os efeitos de perturbação antrópica em mais de um grupo simultaneamente, diminuindo o potencial de generalização das informações obtidas de um grupo para outro e consequentemente limitando a abrangência dos resultados (McGeoch, 1998; Simberloff, 1998; veja Gardner et al., 2009 para excessões).

No Brasil, alguns exemplos do potencial de aplicação de indicadores biológicos na avaliação de sistemas naturais são: a) Zoneamento de áreas para implementação de Unidades de Conservação; b) Implementação de planos de manejo em unidades de conservação já estabelecidas (Avaliação Ecológica Rápida – AER – veja também Meffe & Carrol, 1997); c) Estudo Prévio de Impacto Ambiental e respectivo Relatório de Impacto Ambiental (EIA/RIMA); d) Diagnóstico ambiental para fins de certificação, licenciamento ou compensação ambiental. A falta de testes de indicadores biológicos e a inexistência de protocolos de bioindicação em ambientes terrestres impossibilitam que uma avaliação rápida, objetiva e precisa seja efetuada em habitats que porventura necessitem de informação sobre sua condição de conservação. A vontade política para estabelecer programas de monitoramento provavelmente aumentaria se cientistas puderem desenvolver meios para diagnóstico da biodiversidade que fossem confiáveis e com bom custo-benefício (Sauberer et al., 2004).

De acordo com New (1995), a indicação dos níveis de perturbação ou mudança de um sistema é a principal contribuição dos invertebrados no diagnóstico da conservação biológica. Assim, os objetivos gerais do presente estudo foram: 1) avaliar os efeitos de perturbação antrópica em diferentes grupos de artrópodes terrestres, 2) identificar grupos e/ou resoluções taxonômicas mais adequados para uso em bioindicação e 3) testar a efetividade desses indicadores em diferentes tipos de perturbação.

Este estudo divide-se em três partes. No primeiro capítulo, os efeitos da perturbação antrópica foram verificados em dez grupos de artrópodes terrestres, dentre os quais foram discutidos os mais adequados como indicadores ecológicos em Floresta Atlântica (objetivos 1 e 2);

No segundo capítulo, a aplicabilidade de um dos grupos de indicadores ecológicos, borboletas frugívoras, foi testada amostrando-se outras áreas de Floresta Atlântica com diferentes históricos de perturbação antrópica (objetivos 2 e 3);

Por fim, no terceiro capítulo a abundância de ordens e guildas tróficas de artrópodes epigéicos foi usada em uma reserva de Cerrado sujeita a diferentes frequencias de queima, para se verificar se uma abordagem com baixa resolução taxonômica seria útil para indicação biológica nesse sistema (objetivo 1).

Com esses três capítulos, o estudo pretende preencher ao menos parcialmente uma lacuna existente no Brasil, com a proposição e teste de indicadores biológicos, gerando dados básicos sobre efeitos da perturbação antrópica sobre artrópodes em Mata Atlântica e Cerrado, e fornecendo também subsídios para a execução de diagnóstico e/ou monitoramento em áreas que necessitem desse tipo de informação.

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CAPÍTULO 1 - Selecting terrestrial arthropods as indicators of small-scale disturbance: a first approach in the Brazilian Atlantic Forest

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Selecting terrestrial arthropods as indicators of rainforest disturbance.

Abstract

The growing pressure placed by human development on natural resources creates a need for quick and precise answers about the state of conservation of different areas. Thus, identifying and making use of ecological indicators becomes an essential task in the conservation of tropical systems. Here we assess the effects of small-scale disturbance on terrestrial arthropods and select groups that could be used as ecological indicators in the Brazilian Atlantic Forest. Arthropods were sampled within a continuous forest in the Serra do Mar State Park, southeastern Brazil, both in disturbed and undisturbed areas of the reserve. The abundance of exotic species was higher in the disturbed site, and this pattern seems to be an adequate indicator of anthropogenic disturbance. Species richness of Araneae, Carabidae, Scarabaeidae, Staphylinidae, and epigaeic Coleoptera (pooled) was higher in the undisturbed site, while that of fruit-feeding butterflies was higher in the disturbed site. Species richness was not significantly correlated between any pair of taxa. In contrast, species composition was significantly correlated among most groups, and clearly discriminates the disturbed from the undisturbed site. Moreover, fruit-feeding butterflies and epigaeic Coleoptera composition discriminated disturbed and undisturbed sites even when species were grouped into higher taxonomic levels, which may be a way of overcoming the difficulty of identifying arthropod species from poorly studied, species-rich ecosystems. Potential applications for these indicators include the choice and evaluation of sites for the establishment of natural reserves, elaboration of management plans, and the assessment of ecological impacts due to human activities, either for the purposes of licensing or legal compensation.

***Keywords*: anthropogenic disturbance, ecological indicator, multi-taxa, surrogacy, species composition**

1. Introduction

Practical approaches concerning the assessment of the ecological integrity of natural systems require the selection of organisms or groups of organisms that work as ‘shortcuts’, i.e., surrogates of the other elements of the system and of the ecological processes in which they are involved (Kremen et al., 1993; McGeoch, 1998; Feinsinger, 2001; Niemi and McDonald, 2004). These organisms may act as indices of environmental conditions or biological phenomena that are difficult, inconvenient or expensive to be directly measured (Landres et al., 1988), comprising an attempt to synthesize information and recognize key aspects that at length should guide reliable conservation decisions (Niemeijer, 2002; Niemi and McDonald, 2004).

Biological indication may take place in several ways, such as changes in species richness and abundance, shifts in biological attributes (such as body size or symmetry) or, in a more general way, by some change in species composition from an undisturbed state (New, 1995; Hodkinson and Jackson, 2005). Besides the universal need for developing ways to assess status and trends in environmental state (Niemi and McDonald, 2004), selecting organisms as indicators of anthropogenic disturbance to help conservation decisions is still a challenge in most biodiverse countries, where taxonomic and natural history knowledge is greatly deficient (Kim and Byrne, 2006). This task is especially urgent in the megadiverse countries, since their natural systems are being continually destroyed by human activities (e.g., Bawa et al., 2004; Hong and Lee, 2006; Miles et al., 2006).

The Brazilian Atlantic Forest is considered a ‘hotspot’ (sensu Myers et al., 2000) due to its high species diversity associated with high rates of endemism and elevated level of disturbance, attaining highest conservation priority (MMA, 2000; Myers et al., 2000). Having once covered 1.5 million km^2 of the Brazilian territory, the Atlantic Forest is now reduced to ca.

12% of its original condition, with its remnants occurring mostly in small fragments (Ribeiro et al., 2009). Besides habitat loss, Atlantic Forest suffers from wood harvesting, plant collecting, hunting, invasion by exotic species, among other anthropogenic pressures (see Tabarelli et al., 2005). Due to its shattered state, the development and testing of indicators to assess and monitor the state of Atlantic Forest remnants should be a priority (Tabarelli et al., 2005).

Terrestrial arthropods share a number of qualities that make them highly adequate as biological indicators. These include their sensitivity to habitat change, rapid responses to disturbance, and easy and cost-effective sampling (e.g., Brown, 1996; McGeoch, 1998; Basset et al., 2004; Hodkinson and Jackson, 2005; Lawes et al., 2005; Lewinsohn et al., 2005; Pearce and Venier, 2006; Bouyer et al., 2007; Gardner et al., 2008; Basset et al., 2008). However, their usefulness has been systematically neglected in conservation planning in Brazil, which focuses their attention on more “charismatic”, but sometimes less informative groups (Landres et al., 1988; Lewinsohn et al., 2005). Even when arthropods were used in the assessment of anthropogenic disturbances in Brazil (see Lewinsohn et al., 2005), multi-taxonomic approaches have rarely been applied for this purpose (for exceptions see Barlow et al., 2007; Fonseca et al., 2009; Pardini et al., 2009), making it difficult to extrapolate the results from one taxon to another.

The main goal of this study was to select a set of arthropod taxa as small-scale ecological indicators (sensu McGeoch, 1998) of disturbance in the Brazilian Atlantic Forest. The specific objective was to answer the following questions: a) How does forest disturbance affect arthropod groups in their abundance, species richness, and diversity? b) Does disturbance change species composition of different arthropod groups? c) Does a higher taxon approach affect the discriminatory ability of the arthropod groups? d) Can some arthropod groups be established as efficient surrogates for others? Based on the responses of each group, we then propose which arthropod groups should be employed and/or deserve to be further investigated as indicators of small-scale rainforest disturbance.

2. Methods

2.1. Study area

The study was carried out in the Santa Virgínia nucleus of Serra do Mar State Park (23°17' - 23°24' S, 45°03' - 45°11' W), located on the Paraitinga-Paraibuna plateau, in the eastern region of the state of São Paulo, southeastern Brazil (Fig. 1a). The region is located on mountainous relief, with altitudes ranging from 870 to 1100 m (Ururahy et al., 1987). The regional climate is humid, without a dry season, with mean annual rainfall of 2180 mm, and no monthly rainfall below 65 mm (DNMet, 1992). The region was originally covered with Atlantic Forest vegetation, classified as montane rainforest (Ururahy et al., 1987).

The Santa Virgínia nucleus has an area of ca. 18 000 ha (J.P. Villani, pers. comm.) and is located inside a well-preserved vegetation continuum of 1 109 546 ha along the Serra do Mar (Ribeiro et al., 2009), a large mountain range near the Atlantic Ocean in southeastern Brazil (Fig. 1b). The Brazilian Ministry of the Environment considers the region where Serra do Mar State Park is located as an “area of extreme biological importance”, of highest priority toward conservation of the Atlantic Forest (MMA, 2000).

In the 1960s, part of the forest that currently belongs to the Santa Virgínia nucleus suffered slash-and-burn management, and was subsequently replaced by pasture. Nowadays, this part of the reserve is a forest mosaic composed of old growth forest, abandoned pastures occupied by woody vegetation, abandoned *Eucalyptus* plantations, and secondary forest at different regeneration stages (see Tabarelli and Mantovani, 1999 and references therein). Another section of the reserve (~8 km distant from the former) was severely logged for hardwood before the establishment of the Serra do Mar State Park in 1977 (J.P. Villani, pers. comm.), and now is a fairly well-preserved old-growth forest, with some nearby remnants of primary forest. Hereafter, these sites with different disturbance degrees will be referred to as “disturbed” and “undisturbed”, respectively. It is worth emphasizing that both sites are embedded within a continuous, well-preserved forest context in the Serra do Mar region (see Ribeiro et al., 2009).

By comparing sites within a vegetation continuum, we seek to minimize noise due to fragmentation effects. We also hypothesize that if responses by arthropods are found in such apparently low-contrast sites, meaningful responses should also be achieved under higher-contrast conditions.

2.2. Sampling design and procedures

Twelve replicated sampling stations were set in the Santa Virgínia nucleus, six in the disturbed site and six in the undisturbed site, so that disturbance degree was homogeneous within sites (Fig. 1c). Replicates were set within structurally similar vegetation in both sites, but within spots with different history of disturbance. A pitfall trap sampling unit plus a bait trap sampling unit (each composed of five traps) set in the same location comprised a sampling station. Sampling stations were at least 100 m apart from each other (median: disturbed = 136.6 m; undisturbed = 141.1 m).

The bait traps were cylinders of netting, with an internal funnel, baited with a mixture of mashed banana and sugar cane juice, fermented for at least 48 h. Bait traps were disposed along pre-existing trails in the understory of each site, suspended at a height of 1.5–2.0 m above the ground with a distance of at least 23 m between adjacent traps. The average distance between traps did not differ among sampling stations (ANOVA F = 0.213, P = 0.996). The traps were checked every 48 h, and the baits replaced at each visit (see Uehara-Prado et al., 2007 for details on the sampling scheme).

The pitfall traps consisted in 500 ml clear plastic cups, 85 mm wide at the opening and 120 mm in depth, flush with ground level, with a polystyrene cover suspended above the cup by wooden sticks. Each trap contained ca. 50 ml of a mixture of 69.9% water, 30.0% propylene glycol, 0.1% formaldehyde, and a few drops of detergent. Pitfall traps were placed in lines parallel to the bait traps lines, inside the forest understory, at 2 m intervals, and at least 20 m from the trails.

Pitfall and bait traps were kept simultaneously in the field for six and eight days/month, respectively. Sampling was done monthly from November 2004 to May 2005, including the most favorable season for the capture of arthropods in southeastern Brazil (butterflies: Brown, 1972; Scarabaeidae: Hernández and Vaz-de-Mello, in press; Opiliones: Almeida-Neto et al., 2006). Sampling effort was 60 840 trap-hours for pitfall traps; the effective effort for butterflies was 33 600 trap-hours (considering 10 hours of sampling/day).

Most fruit-feeding butterfly species captured in the bait traps could be identified in the field and were released after marking. The few specimens that could not be recognized even with a field guide (Uehara-Prado et al., 2004) were collected for later identification. The remaining arthropods collected in bait and pitfall traps were stored in 70% ethanol. In order to maximize the consistency of sorting, all pitfall samples were sorted by the first author or by laboratory assistants under his supervision. The first author also conducted the pitfall and bait trap sampling in the field.

2.3. Focal group selection

Except for the fruit-feeding butterflies, included in this study due to previous experience (Uehara-Prado et al., 2007), taxonomic groups were selected based on two simple criteria: 1) ease of sorting and 'adequate' abundance in the samples, i.e. neither too abundant (unfeasible to handle with) nor too scarce (low sample size) and 2) possibility of reliable identification, which demanded taxonomists to correctly identify the taxa, or at least to separate specimens into unidentified taxonomic species. The scarcity of structured regional terrestrial arthropod samplings in the Atlantic Forest of the state of São Paulo prevents the application of more sophisticated criteria (e.g., Bouyer et al., 2007). Additionally, some groups selected in this study (see below) have already been suggested as potential ecological indicators or have at least been shown to be sensitive to human-caused disturbance (e.g., Rainio and Niemelä, 2003; Pearce and Venier, 2006; Barlow et al., 2007; Bragagnolo et al., 2007; Nichols et al., 2007). The taxa not selected at this stage were sorted into several levels of detail, from family (e.g., Formicidae) to "other" (several arthropod orders pooled), and stored for future studies.

Nine taxa in the sample met the criteria adopted for their inclusion in at least part of the analyses: landhoppers (Amphipoda, Tallitridae), woodlice (Isopoda, Oniscidea), ground-dwelling spiders (Araneae), harvestmen (Opiliones), ground beetles (Carabidae), rove beetles (Staphylinidae), scarab beetles (Scarabaeidae), false-blister beetles (Oedemeridae), and all epigaeic beetles pooled (Coleoptera). False-blister beetles captured in bait traps were initially considered by-catches, but their abundance justified their inclusion in the analysis.

Taxonomic accuracy varied among arthropod groups (Table 1S). All individuals could be identified to species level in Amphipoda (a single exotic species, *Talitroides topitotum*), Oedemeridae (two species in the genus *Matusinhosa*), and fruit-feeding butterflies (52 species).

Due to a high proportion of undescribed species and/or a lack of taxonomic knowledge on the different groups (i.e., a ‘taxonomic bottleneck’, see Kim and Byrne, 2006), the remaining taxa were separated either into unnamed taxonomic species or, whenever possible, into species. The proportion of taxonomic entities identified to species level (i.e., Latin binomials) in these groups ranged from 1.3% for rove beetles to 66.7% for harvestmen (median = 15.6%) (Table 1S). Other families of epigaeic Coleoptera were sorted to species or unnamed species, but due to their low occurrence in the samples, they were included only when data for epigaeic Coleoptera were pooled. Juvenile specimens of spiders were discarded from analyses. Although harvestmen females of the genus *Mischonyx* (= *Ilhaia*) could not be identified to species, the level of analysis used in this group (abundance of the order) allowed their inclusion in the dataset (see results).

2.4. Statistical analyses

The null hypothesis of no difference in abundance within arthropod groups between disturbed and undisturbed sites was assessed by the *t*-test on $\log_{10}(x+1)$ transformed abundance data. Fisher’s logarithmic series parameter (α) was compared between sites by the bootstrapping procedure (see Magurran, 2004) using the PAST software (Hammer et al., 2001). Overall similarity between sites was calculated by the Sørensen index. Species richness of arthropod groups with 12 or more species (see Table 1) was compared between sites by individual-based rarefaction analysis. The statistical significance (at $P < 0.05$) of differences in species richness was evaluated by comparing 95% confidence limits in the point of the rarefaction curves with same abundance (see Magurran, 2004). Rarefaction analyses were performed using the Analytic Rarefaction 1.3 software (available from http://www.uga.edu/strata/software/anRareReadme.html).

To evaluate if disturbance affected the species composition of the selected groups, we performed a non-metric multidimensional scaling (NMDS) on the resemblance matrix of Bray-Curtis distances for arthropod groups with $S \geq 12$ (see Table 1), with 1000 random restarts. This ordination method has been frequently used in ecological studies (e.g., Minchin, 1987, Clarke and Ainsworth, 1993; Brehm and Fiedler, 2004), and presents several advantages, such as minimizing the arch effect, releasing linearity constraints, and not requiring multivariate normality of data (Minchin, 1987). Moreover, as in other indirect gradient analyses, NMDS depicts the environment in the organism's point of view, or in Clarke and Ainsworth's (1993) words, allow the biota to "tell their own story". To test the null hypothesis of equal species composition between disturbed and undisturbed forest sites, we applied an analysis of similarities (ANOSIM – Clarke, 1993) on the matrix of Bray-Curtis similarities, with 999 permutations. Before running these multivariate techniques, a dispersion weighting was applied to the original dataset in order to downweight species of highly variable abundance, clumped into replicates (Clarke et al., 2006). These analyses were done using the PRIMER software (Clarke and Gorley, 2006).

To evaluate if grouping species into higher taxonomical categories would result in loss of multivariate information, we performed a NMDS on the matrix of families or subfamilies of the same dataset. We first performed a visual inspection of both ordinations and then compared their stress values. An increase in stress value in higher taxonomic category was interpreted as loss of multivariate information (Caruso and Migliorini, 2006; Clarke and Gorley, 2006).

We tested species richness surrogacy by two approaches (following Sauberer et al., 2004): 1) pairwise correlations of species richness among taxa; and 2) correlation of species richness of one taxon with the pooled richness of the remaining taxa. Correlations were done with Pearson's coefficient on $\log_{10}(x+1)$ transformed data. A procedure to control for false discovery rate (FDR) was applied, due to the large number of correlations tested (Benjamini and Hochberg, 1995). To test surrogacy on species composition, RELATE tests (PRIMER software - Clarke and Gorley, 2006) with Spearman's correlation coefficient were used to correlate Bray-Curtis similarity matrices based on species composition. This function calculates the Spearman rank correlations between two similarity matrices and calculates the significance of this correlation by a permutation test. When comparisons were done between hierarchically related taxa (e.g., family vs. order), the lower taxon was removed from the higher taxon dataset.

3. Results

3.1. Abundance, species richness, and diversity

The proportion of individuals in both sites varied widely from group to group (Fig. 2). The most abundant taxon in the sample was Amphipoda, with 3593 individuals, 97.7% of which were found in the disturbed site (Fig. 2). Harvestmen were more abundant in the disturbed site as well (75.4%, Fig. 2), mainly due to individuals of the genus *Mischonyx* (see Table 1S). In contrast, 77.9% of the false-blister beetles were sampled in the undisturbed site (Fig. 2). Although woodlice abundance did not differ significantly between the sites (Table 1), 80 of the 82 individuals of the exotic species *Styloniscus spinosus* were found in the disturbed site (Table 1S).

The most speciose group within the selected taxa was the epigaeic Coleoptera, followed by Staphylinidae, Araneae, fruit-feeding butterflies, Carabidae, and Scarabaeidae (Table 1). Araneae and Staphylinidae showed a decrease in both species richness and abundance in disturbed sites, while the converse occurred for fruit-feeding butterflies (Table 1; Fig. 2). The species richness of Carabidae, Scarabaeidae, and epigaeic Coleoptera pooled was higher in the undisturbed site, while their abundance did not differ between disturbed and undisturbed sites (Table 1; Fig. 2). Differences in species richness of the remaining taxa between disturbed and undisturbed sites were not analyzed due to their low species richness. Fisher's α comparisons between sites followed the same pattern of species richness, with the only exception of Carabidae, whose diversity did not differ between sites (Table 1). Sørensen's similarity between disturbed and undisturbed sites ranged from 0.42 in Scarabaeidae and Staphylinidae to 0.57 in Carabidae (Table 1).

3.2. Species composition

Non-metric multidimensional scaling results for Araneae, fruit-feeding butterflies, Carabidae, Staphylinidae, and epigaeic Coleoptera clearly showed different species composition between disturbed and undisturbed sites (Fig. 3). These results were confirmed by ANOSIM (Table 2). Scarabaeidae was the only group that showed no difference between sites (Fig. 3). When species data were aggregated into subfamilies (fruit-feeding butterflies, Carabidae, Scarabaeidae and Staphylinidae) or families (Araneae and all epigaeic Coleoptera pooled), only fruit-feeding butterflies and epigaeic Coleoptera maintained the same pattern of aggregation in NMDS (Table 2), also confirmed by ANOSIM results (fruit-feeding butterflies: $R = 0.613$, $P = 0.002$; epigaeic Coleoptera: $R = 0.480$, $P = 0.002$).

3.3. Surrogacy

No significant results were observed in pairwise correlations of species richness (Table 3), and only fruit-feeding butterfly species richness showed a significant negative correlation with the pooled species richness of the remaining taxa. This group also showed a negative correlation with all other taxa in both approaches (Table 3), indicating that their species richness declined as the richness of the remaining taxa increased.

Comparison of species composition among arthropod groups revealed that five out of six analyzed groups had significant correlations, excluding Scarabaeidae (Table 3). Among the groups with significant correlations, fruit-feeding butterflies, Carabidae, and epigaeic Coleoptera correlated significantly with all the remaining groups, while Araneae and Staphylinidae correlated significantly with the remaining groups, but not with each other (Table 3).

4. Discussion

4.1. Abundance

Considering only the differences in abundance between study sites (Table 1), the fact that exotic species of Amphipoda and Isopoda were more abundant at the site where anthropogenic intervention was more intense in the past seems particularly promising. A similar result was obtained in the same area in a study with earthworms, which also presented more individuals of exotic species at the disturbed site (91.4%, n = 58, Fernandes et al., in press). Invasion by exotic species aided by different human activities has long been reported (Elton, 1958), and disturbed habitats are more likely to be invaded – indeed, many exotic species seem to be restricted to habitats created by human disturbance (Fox and Fox, 1986).

Our results are similar to that of previous works, which found that the abundance of a native South African terrestrial amphipod (*Talitriator africana*) was significantly higher in ecotones or disturbed habitats (Kotze and Lawes, 2008). In fact, Lawes et al. (2005) considered this amphipod an appropriate single-species ecological indicator for poor forest condition in South Africa. Although the outcomes of biological invasions remain widely unknown for

Brazilian epigaeic arthropods, it seems appealing to use presence and abundance of exotic species within Atlantic Forest remnants as an indication of anthropogenic disturbance.

When looking exclusively at the abundance of different arthropod groups in our samples, some widespread, abundant species have the potential to be good indicators of anthropogenic disturbance in the Atlantic Forest. For example, harvestmen in the genus *Mischonyx*, the ground beetle *Galeritula carbonaria*, and the fruit-feeding butterfly *Morpho epistrophus* were at least three times more abundant in disturbed than in undisturbed sites (Table 1S). In comparison to other species within their groups, the above species are larger, easily identifiable, and better known as concerns their natural history. Thus, they could be appropriate focal species for further studies with anthropogenic disturbance effects on arthropods. The great majority (77.9%) of individuals in the genus *Matusinhosa* (Oedemeridae) was sampled at the undisturbed site and should be considered for future studies as well. However, in contrast with the above examples, basic aspects of the biology of Brazilian Oedemeridae are still unknown.

We are aware that indicator-related interpretations that can be made from the results of particular taxon might be limited and that a set of species provides a more effective representation of ecological change (Lawton et al., 1998; McGeoch, 1998; Lawes et al., 2005). The applicability of these single taxa as disturbance indicators will depend critically on the generality of the results found in this study. Therefore, our results should be validated by additional studies in other areas of the Atlantic Forest domain.

4.2. Species diversity, composition, and surrogacy

The decrease in species richness with disturbance observed for five epigaeic arthropod taxa finds consistent correspondence in the literature only for tropical Scarabaeidae (Nichols et al., 2007).

This result was found despite the use of unbaited traps in this study, a less efficient method for dung beetles. Patterns of response of the other groups (Araneae, Carabidae, Staphylinidae, epigaeic Coleoptera pooled) to disturbance are either unknown or poorly studied in tropical forests (e.g., Rainio and Niemelä, 2003; Pearson, 2006). Fruit-feeding butterflies was the only arthropod group whose species richness was higher in the disturbed site, the opposite result found for other studies at a similar scale (Hill and Hamer, 2004; Barlow et al., 2007). Anthropogenic disturbance may affect species richness and diversity in several ways, and responses may vary within studies among taxonomic or functional groups or among studies within the same group (Kimberling et al., 2001; Kotze and Samways, 2001; Perfecto et al., 2003; Rainio and Niemelä, 2003; Hill and Hamer, 2004; Schulze et al., 2004; Barlow et al., 2007; Basset et al., 2008; Fonseca et al., 2009; Pardini et al., 2009). This variation may be attributed to several factors, such as the sensitivity of species richness to sampling effort, the spatial and temporal scale of the study, and disturbance intensity, frequency and type (e.g. Brown, 1996; Kimberling et al., 2001; Hill and Hamer, 2004; Barlow et al., 2007; Basset et al., 2008).

As reported in several previous studies, no surrogacy was found in correlations of species richness (e.g., Lawton et al., 1998; Perfecto et al., 2003; Schulze et al., 2004; Barlow et al., 2007). The lack of congruency in species richness correlations has been attributed to the high variability in ecological requirements inherent to the sampling of a number of different taxa (Lawton et al., 1998), among other causes (Weaver, 1995; Schulze et al., 2004; Oertli et al., 2005; Barlow et al., 2007). In this study, perhaps the sampling method was not as specific as would be desirable for some arthropod groups in order to catch such variability (e.g., Isopoda, Opiliones, and Scarabaeidae), which may have contributed to the lack of congruency found for species richness correlations. However, as the methods and sampling effort were the same in disturbed and undisturbed sites, we expect that comparability would be maintained. Additionally, our sampling protocol was designed in such a way that it could be conducted by one or two people in the field, minimizing operational costs and increasing the chance of replication in future studies (see Paoletti, 1999; Gardner et al., 2008). Adding several specific methods would certainly reduce the cost-effectiveness of our sampling. We expect that responses to anthropogenic disturbances found with non-specific sampling methods are applicable per se, and should be improved in later studies with specific methods.

The characterization of general diversity patterns of response to disturbance at the continental scale may be a very difficult task, due to functional and structural differences among biomes, and idiosyncrasies (e.g., history of disturbance) of different regional communities. However, general patterns may emerge from studies focused on specific biomes within regions (Kim and Byrne, 2006), validating the use of ecological indicators within specific geographical limits (in our case, the Serra do Mar biogeographical sub-region – see Ribeiro et al., 2009). Therefore, future studies about diversity patterns of potential ecological indicators in the Atlantic Forest should focus on increase the geographical sampling coverage of this biome, in search of well-defined patterns of response to disturbance.

As found in studies with more comprehensive taxonomic coverage (Barlow et al., 2007; Basset et al., 2008), responses to anthropogenic disturbance based on species composition were more informative than those based on species richness or diversity. In the present study, significant correlations among the species compositions of most selected arthropod groups also indicate that they represent each other and can effectively be used as surrogates of anthropogenic disturbance. This could be promising for the future application of ecological indicators in the

Atlantic Forest, as one could sort just one of the selected groups, reducing sampling and sorting-related time and costs in situations with financial constraints.

However, the problem of identifying arthropods to species level persists. Fortunately, among the selected groups, fruit-feeding butterflies and epigaeic Coleoptera maintained the quality of discrimination between disturbed and undisturbed sites, even when species were grouped into higher taxonomic categories. Discovering disturbance-related response patterns at higher taxonomic levels may be important in a practical sense, since it is a manner of overcoming the difficulty of identifying arthropod species, particularly from poorly studied, species rich systems. Sometimes, the time lag from sampling to identifying a taxon may be decisive for its inclusion in assessment and monitoring studies with financial and time constraints (Pawar, 2003; Gardner et al., 2008). Though it may not be simple to sort Neotropical Coleoptera into families without previous taxonomic training, it is obviously much easier than sorting them into species. Sorting fruit-feeding butterflies into subfamilies, in turn, is an easy task and, despite potential drawbacks of working at this taxonomic scale (see Basset et al., 2008), it would prevent species level misidentifications, which are frequent in this group, notably among the small brown Satyrinae (A.V.L. Freitas, pers. obs.).

4.3. Practical constraints and advantages

The lack of taxonomists available to sort specimens into species hindered the selection and inclusion in our analyses of several taxa in the sample. Even in the majority of the selected taxa, most specimens had unnamed taxonomic species due to a lack of taxonomic studies on the sampled groups. Therefore, there is an urgent need for support for taxonomy and natural history research in the Atlantic Forest as well as other tropical ecosystems (e.g., Kim and Byrne, 2006;

Gardner et al., 2008). Despite the clear advantage of using species composition showed by our results, the other approaches used in this study aiming for ecological indication (abundance and species richness) have their merits and drawbacks (see Basset et al., 2008). Choosing among them in practical situations may ultimately depend upon the availability of financial support and taxonomic expertise in the selected group(s).

Some benefits must be emphasized in this apparently discouraging scenario for the implementation of multi-taxonomic bioindication studies. Multiple taxa sampling in this ecosystem almost invariably adds new data on several aspects of the biology of both well and poorly studied arthropods, and possibly reveals undescribed species (e.g., Basset et al., 2004), as found in this study for Araneae, Coleoptera, Isopoda, and Opiliones. A wide taxonomic range also provides an opportunity to overcome "taxonomic chauvinism" (Pawar, 2003), as several groups not included in more specific sampling protocols may be seen in more detail and motivate further studies. Moreover, multi-taxonomic surveys can be undertaken with very little additional cost in the field, when compared to single taxon sampling (Gardner et al., 2008). Finally, as shown by our results, higher taxonomic level identification (a straightforward approach when sampling several taxa) may be enough for some groups to discriminate different disturbance levels.

5. Conclusion

In this study, we sampled, sorted, and selected arthropods that showed potential as local ecological indicators of forest disturbance in a reserve included in a large continuum of Atlantic Forest, a condition not often found in this highly fragmented ecosystem (e.g., MMA, 2000; Tabarelli et al., 2005; Ribeiro et al., 2009). Finding responses in this apparently low-contrast situation may be a good hint about the sensitivity of the selected indicators. Additional local-scale studies with different anthropogenic disturbances should enhance the generalization power of our results.

Basset et al. (2008) advocate the use of metrics based on species identity in biological assessment (as opposed to richness alone), as they “reflect a high sensitivity of arthropod assemblage to disturbance”. Our results indicate that this statement could be valid in the studied site, since the species composition of most groups differentiated the disturbed from the undisturbed site. Moreover, surrogacy in species composition showed that different arthropod groups represent each other in the response to disturbance, while this was not observed for species richness. We recommend therefore that future studies on ecological indication in Atlantic Forest (and other ecosystems) do not limit their analyses to richness-related patterns. The composition of fruit-feeding butterflies and epigaeic Coleoptera pooled were the best indicators in this study, discriminating the disturbed and the undisturbed site even in higher taxonomic categories, and acting as surrogates of the remaining arthropod groups.

Some of the potential applications of terrestrial arthropods as ecological indicators in Brazil (and elsewhere) are the evaluation of sites for the establishment of reserves, the implementation of management plans in already established reserves, and the evaluation of ecological impacts due to human activities, either for licensing or legal compensation purposes. The absence of robust, tested ecological indicators for terrestrial ecosystems makes it unfeasible to conduct a quick, objective, and precise evaluation about the conservation status of target sites (see McGeoch, 1998; Niemi and McDonald, 2004). The overwhelming pressure imposed by human activities on natural systems puts at risk not only species and their interactions, but also limits conservation and management options, reducing the number of ways in which human populations can interact with natural remnants (Brown, 1996; Kim & Byrne, 2006). Identifying the effects that such disturbances have on the biota of a locality or region is only the first step in a long journey toward the conservation of the vanishing Atlantic Forest.

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Captions

Fig. 1. Study location in Brazil. (a) Serra do Mar coastal forest ecoregion (grey); (b) the Santa Virgínia nucleus of Serra do Mar State Park (hashed), surrounded by ombrophilous montane forests (grey); (c) Sampling scheme showing sampling stations (white bars) composed by five portable bait traps (triangles) and five pitfall traps (circles) in disturbed (grey rectangle) and undisturbed (black rectangle) sites.

Fig. 2. Proportion of total arthropod individuals collected in disturbed (gray bars) and undisturbed (black bars) sites. From left to right: Oedemeridae, Staphylinidae, Araneae, Scarabaeidae, epigaeic Coleoptera pooled, Carabidae, Isopoda, fruit-feeding butterflies (Nymphalidae), Opiliones, and Amphipoda. See Table 1 for common names and abundance of each group.

Fig. 3. NMDS ordination of disturbed (open circles) and undisturbed (solid circles) sites, based on different arthropod groups. See stress values in Table 2. Drawings inside the graphs indicate the arthropod groups according to Fig. 2.

Table 1. Mean abundance, species richness, similarity and diversity of arthropods in disturbed (D) and undisturbed (U) sites in the Santa Virgínia nucleus, Serra do Mar State Park, São Paulo, Brazil. See methods for details on the disturbance history of each site.

Common name	Taxon	Mean abundance (±sd) [1]		Species richness [2]				Fisher's α [3]	
		D	U	D	U	Total	Sørensen's S	D	U
Landhoppers	Amphipoda, Talitridae	585.0 (650.9)**	13.8 (20.8)	1	1	1	-	-	-
Woodlice	Isopoda, Oniscidea	22.7 (29.8)	12.2 (9.2)^{ns}	3	4	4	-	-	-
Ground spiders	Araneae	28.3 (7.9)	50.8 (7.7)**	27	56*	63	0.48	9.04	20.13**
Harvestmen	Opiliones	16.2 (10.8)*	5.3 (4.4)	6	8	9	-	-	-
Fruit-feeding butterflies	Lepidoptera, Nymphalidae	87.8 (47.4)**	30.3 (10.7)	48*	22	52	0.51	12.84**	5.55
False-blister beetles	Coleoptera, Oedemeridae	7.8 (6.8)	27.7 (18.8)*	2	2	2	-	-	-
Ground beetles	Coleoptera, Carabidae	42.0 (36.4)	21.7 (10.2)^{ns}	14	14*	20	0.57	3.20	3.98^{ns}
Rove beetles	Coleoptera, Staphylinidae	14.3 (8.2)	28.5 (5.8)*	31	68*	78	0.42	17.39	41.77**
Scarab beetles	Coleoptera, Scarabaeidae	7.67 (6.3)	11.7 (8.8)^{ns}	6	18*	19	0.42	1.84	7.84**
Epigaeic beetles	Coleoptera [4]	83.8 (42.7)	104.2 (32.4)^{ns}	91	152*	190	0.44	32.47	63.94**

* $P < 0.05$, ** $P < 0.01$, ^{ns} $P > 0.05$

[1] Differences in abundance evaluated by *t*-test on $\log_{10}(x+1)$ transformed abundance data.

[2] Differences in species richness evaluated by visual comparison of rarefaction curves and their 95% confidence intervals.

[3] Differences in Fisher's α evaluated by the bootstrapping procedure on each site's pooled data.

[4] 27 families. See Table 1S.

Table 2. NMDS and ANOSIM results for arthropod groups sampled in disturbed and undisturbed sites in the Santa Virgínia nucleus, Serra do Mar State Park, São Paulo, Brazil.

	ANOSIM R	NMDS Stress		Ordination quality at higher taxon level[2]
		Species	Higher taxonomic level[1]	
Araneae	0.526*	0.13	0.14	Worse
Fruit-feeding butterflies	0.606*	0.05	0.05	Same
Carabidae	0.581*	0.10	0.10	Worse
Scarabaeidae	-0.043^{ns}	0.03	0.05	Worse
Staphylinidae	0.563*	0.17	0.12	Worse
Epigaeic Coleoptera	0.641*	0.12	0.13	Same

* $P < 0.01$

[1] Araneae and epigaeic Coleoptera grouped into families; Fruit-feeding butterflies, Carabidae, Scarabaeidae, and Staphylinidae grouped into subfamilies.

[2] Visual inspection of ordination diagrams.

Table 3. Correlations among groups in species richness (above diagonal) and species composition (below diagonal). Correlations of each Coleoptera family with epigaeic Coleoptera pooled exclude that family from epigaeic Coleoptera. Alpha values adjusted for false discovery rate (Benjamini and Hochberg, 1995).

	Fruit-feeding butterflies	Araneae	Carabidae	Scarabaeidae	Staphylinidae	Epigaeic Coleoptera	Remaining taxa pooled
Fruit-feeding butterflies		-0.631	-0.290	-0.369	-0.477	-0.726	-0.754[a]
Araneae	0.641**		0.156	0.046	0.687	0.599	0.329
Carabidae	0.577*	0.573**		0.306	-0.006	0.246	0.120
Scarabaeidae	-0.235	-0.037	-0.035		0.242	0.409	0.163
Staphylinidae	0.303*	0.153	0.264*	-0.047		0.4133	0.529
Epigaeic Coleoptera	0.406**	0.372**	0.344*	0.089	0.375**		-0.247

[a] Corrected $\alpha = 0.008$

* $P < 0.05$; ** $P < 0.01$

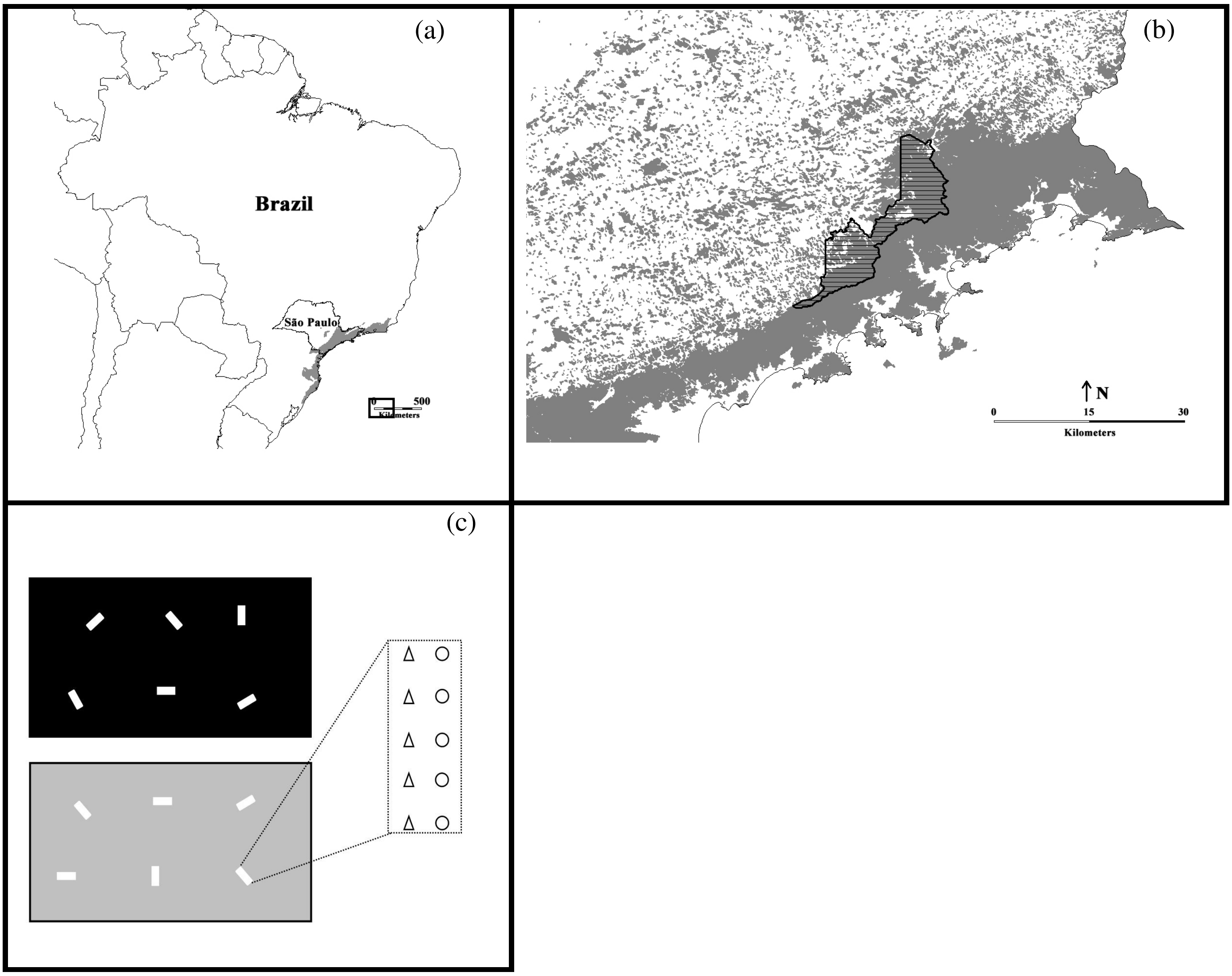

Figure 1.

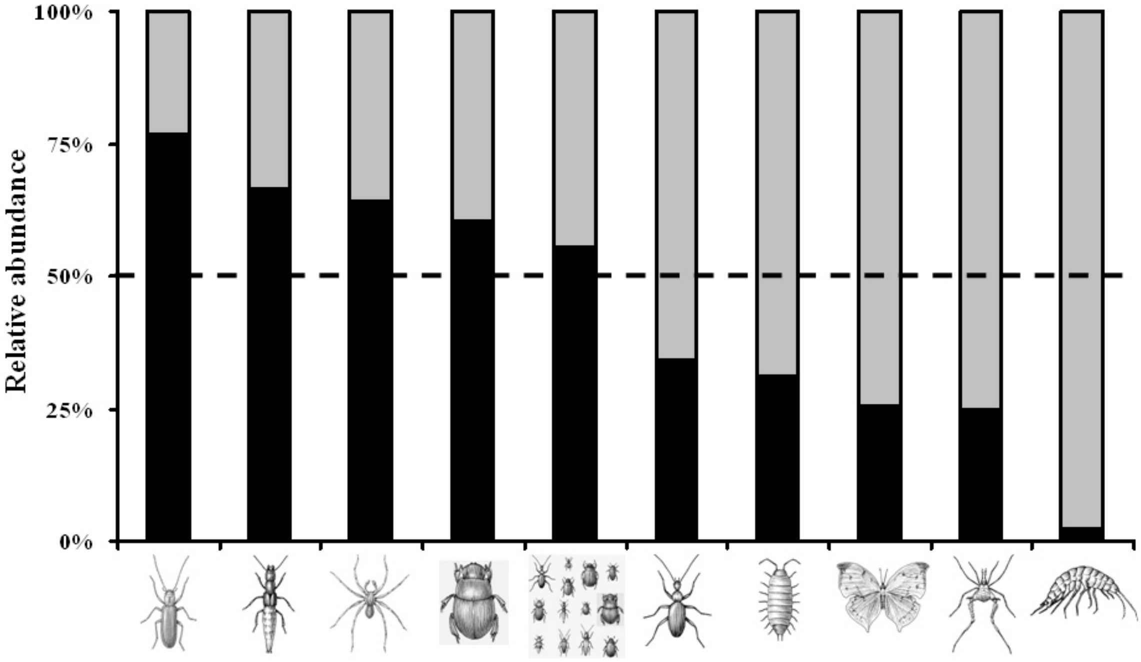

Figure 2.

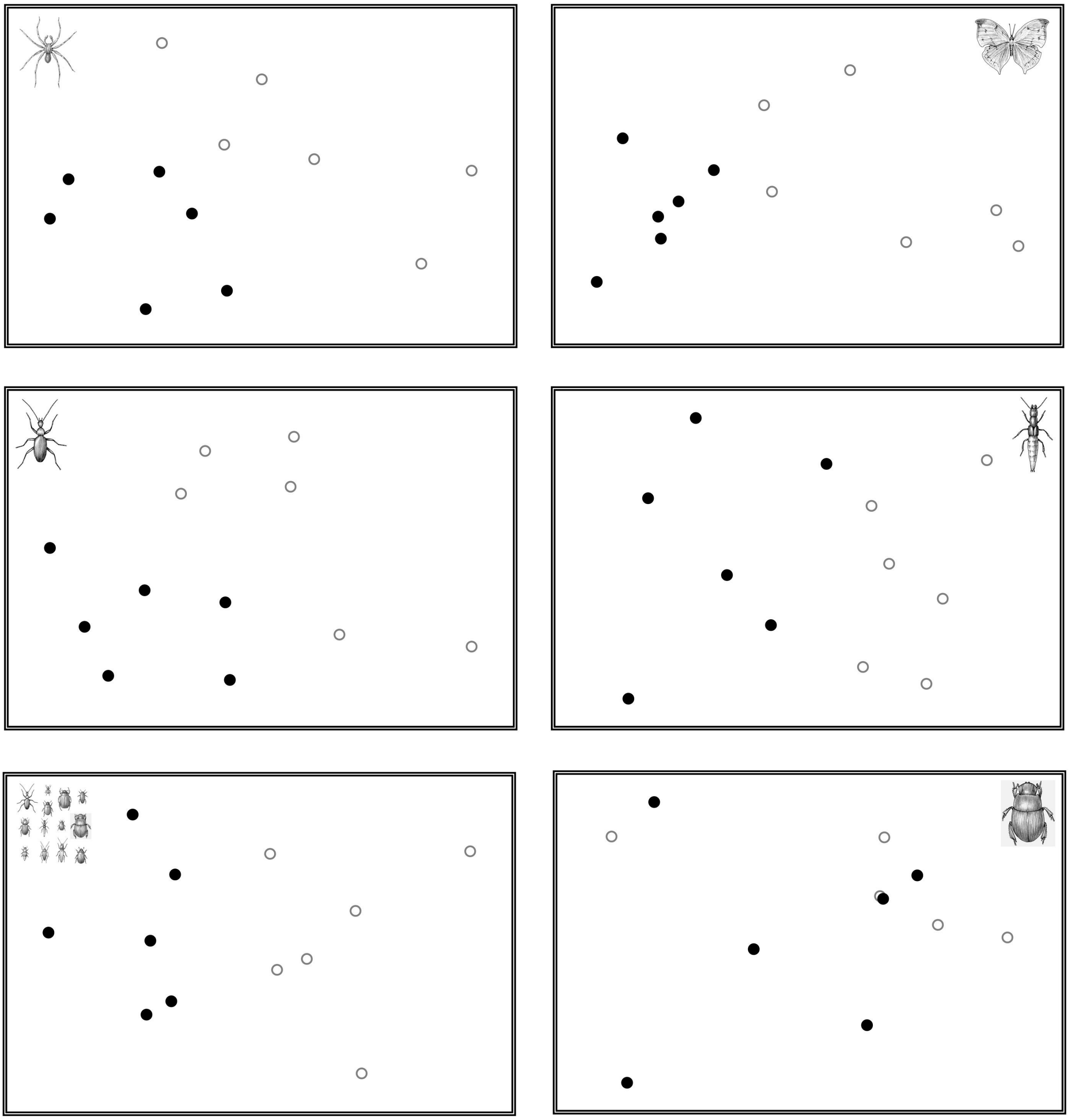

Figure 3.

Table 1S. Terrestrial arthropod species sampled in Santa Virgínia nucleus, Serra do Mar State Park, São Paulo, Brazil.

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Arachnida	Araneae	Actinopodidae	*Actinopus* sp.	0	8	8
Arachnida	Araneae	Anapidae	*Pseudanapis* sp.1	1	0	1
Arachnida	Araneae	Corinnidae	*Corinna* sp.1	0	2	2
Arachnida	Araneae	Corinnidae	*Creugas* sp.1	6	8	14
Arachnida	Araneae	Corinnidae	*Creugas* sp.2	1	1	2
Arachnida	Araneae	Corinnidae	*Creugas* sp.3	2	3	5
Arachnida	Araneae	Corinnidae	*Ianduba* sp.	2	0	2
Arachnida	Araneae	Corinnidae	*Ianduba varia*	7	9	16
Arachnida	Araneae	Corinnidae	*Meriola* sp.	7	0	7
Arachnida	Araneae	Corinnidae	*Paradiestus* sp.	1	0	1
Arachnida	Araneae	Corinnidae	*Tupirinna* sp.	3	1	4
Arachnida	Araneae	Ctenidae	*Asthenoctenus* sp.	2	0	2
Arachnida	Araneae	Ctenidae	Ctenidae sp. 2	31	36	67
Arachnida	Araneae	Ctenidae	Ctenidae sp. *3*	1	0	1
Arachnida	Araneae	Ctenidae	*Isoctenus* sp.1	1	0	1
Arachnida	Araneae	Ctenidae	*Itatiaya modesta*	19	2	21
Arachnida	Araneae	Dipluridae	*Linothele* sp.	1	0	1
Arachnida	Araneae	Gnaphosidae	Gnaphosidae sp.1	1	0	1
Arachnida	Araneae	Gnaphosidae	Gnaphosidae sp.13	3	0	3
Arachnida	Araneae	Hahniidae	Hahniidae sp.1	0	4	4
Arachnida	Araneae	Hahniidae	Hahniidae sp.2	1	0	1
Arachnida	Araneae	Idiopidae	*Idiops camelus*	8	0	8
Arachnida	Araneae	Idiopidae	*Idiops* sp.	2	0	2
Arachnida	Araneae	Linyphiidae	Linyphiidae sp.4	11	0	11
Arachnida	Araneae	Linyphiidae	Linyphiidae sp.7	1	4	5
Arachnida	Araneae	Linyphiidae	Linyphiidae sp.8	2	0	2
Arachnida	Araneae	Linyphiidae	*Meioneta sp.*	27	30	57
Arachnida	Araneae	Linyphiidae	*Scolecura parilis*	3	6	9

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Arachnida	Araneae	Linyphiidae	*Smermisia sp.*	4	0	4
Arachnida	Araneae	Linyphiidae	*Sphecozone labiata*	0	1	1
Arachnida	Araneae	Linyphiidae	*Sphecozone* sp.1	5	0	5
Arachnida	Araneae	Linyphiidae	*Sphecozone* sp.2	1	0	1
Arachnida	Araneae	Linyphiidae	*Vesicapalpus simplex*	36	16	52
Arachnida	Araneae	Lycosidae	Lycosidae sp.1	3	19	22
Arachnida	Araneae	Lycosidae	Lycosidae sp.2	0	2	2
Arachnida	Araneae	Lycosidae	Lycosidae sp.3	0	2	2
Arachnida	Araneae	Miturgidae	*Miturgidae* sp.1	1	0	1
Arachnida	Araneae	Mysmenidae	*Itapua sp.*	14	0	14
Arachnida	Araneae	Mysmenidae	*Maymena sp.*	1	0	1
Arachnida	Araneae	Mysmenidae	Mysmenidae sp.2	2	0	2
Arachnida	Araneae	Mysmenidae	Mysmenidae sp.3	1	0	1
Arachnida	Araneae	Mysmenidae	*Trogloneta sp.*	6	1	7
Arachnida	Araneae	Nemesiidae	Nemesiidae sp.15	4	0	4
Arachnida	Araneae	Nemesiidae	Nemesiidae sp.3	6	0	6
Arachnida	Araneae	Nemesiidae	*Prorachias bristowei*	1	0	1
Arachnida	Araneae	Nemesiidae	*Rachias* sp.1	1	0	1
Arachnida	Araneae	Nemesiidae	*Stenoterommata* sp.1	2	0	2
Arachnida	Araneae	Ochyroceratidae	*Ochyroceratidae* sp.1	2	0	2
Arachnida	Araneae	Oonopidae	*Dysderina sp.*	6	1	7
Arachnida	Araneae	Oonopidae	*Orchestina sp.*	2	0	2
Arachnida	Araneae	Pholcidae	*Mesabolivar sp.*	5	6	11
Arachnida	Araneae	Pholcidae	*Tupigea sp.*	7	0	7
Arachnida	Araneae	Salticidae	*Corythalia sp.*	4	1	5
Arachnida	Araneae	Salticidae	Salticidae sp.3	1	0	1
Arachnida	Araneae	Salticidae	Salticidae sp.4	1	0	1
Arachnida	Araneae	Salticidae	Salticidae sp.5	0	1	1
Arachnida	Araneae	Salticidae	Salticidae sp.7	0	1	1
Arachnida	Araneae	Theraphosidae	*Homeomma montanum*	20	2	22

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Arachnida	Araneae	Theridiidae	*Chrosiothes niteroi*	1	0	1
Arachnida	Araneae	Theridiidae	*Steatoda diamantina*	0	1	1
Arachnida	Araneae	Theridiidae	*Stemmops* sp.1	1	0	1
Arachnida	Araneae	Theridiidae	*Theridion sp.*	1	0	1
Arachnida	Araneae	Zodariidae	*Tenedos sp.*	4	2	6
Arachnida	Araneae	Zoridae	Zoridae sp.1	18	0	18
Arachnida	Opiliones	Gonyleptidae	*Gonyleptes saprophilus*	10	3	13
Arachnida	Opiliones	Gonyleptidae	*Hypophyllonomus maculipalpi*	5	1	6
Arachnida	Opiliones	Gonyleptidae	*Longiperna* sp.	1	0	1
Arachnida	Opiliones	Gonyleptidae	*Mischonyx* aff. *cuspidatus*	1	23	24
Arachnida	Opiliones	Gonyleptidae	*Mischonyx cuspidatus*	8	12	20
Arachnida	Opiliones	Gonyleptidae	*Mischonyx* sp. (non identifiable females)	4	53	57
Arachnida	Opiliones	Gonyleptidae	*Neosadocus* sp.	1	0	1
Arachnida	Opiliones	Gonyleptidae	*Pseudotroglus mirim*	1	3	4
Arachnida	Opiliones	Gonyleptidae	*Triglochinura curvispina*	1	0	1
Arachnida	Opiliones	Scleromatidae	*Jussara flamengo*	0	2	2
Crustacea	Amphipoda	Talitridae	*Talitroides topitotum*	83	3510	3593
Crustacea	Isopoda	"Philosciidae"	*Atlantoscia* sp.	31	42	73
Crustacea	Isopoda	"Philosciidae"	*Benthana werneri*	27	14	41
Crustacea	Isopoda	Plathyarthridae	*Trichorhina* sp.	1	0	1
Crustacea	Isopoda	Styloniscidae	*Styloniscus spinosus*	2	80	82
Insecta	Coleoptera	Anobiidae	*Lasioderma serricornis*	1	0	1
Insecta	Coleoptera	Artematopidae	*Artematopus* sp.1	0	1	1
Insecta	Coleoptera	Artematopidae	*Artematopus* sp.2	0	1	1
Insecta	Coleoptera	Artematopidae	*Artematopus* sp.3	1	0	1
Insecta	Coleoptera	Biphyllidae	*Biphyllidae* sp.1	1	0	1
Insecta	Coleoptera	Carabidae	*Aspidoglossa* sp.1	3	1	4
Insecta	Coleoptera	Carabidae	Bembidiini sp.1	0	1	1
Insecta	Coleoptera	Carabidae	*Dercylus* (*Asporina*) sp.1	0	20	20
Insecta	Coleoptera	Carabidae	*Euchroa* sp.1	21	1	22

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Coleoptera	Carabidae	*Euchroa* sp.2	3	0	3
Insecta	Coleoptera	Carabidae	*Feroniola* sp.1	3	0	3
Insecta	Coleoptera	Carabidae	*Galeritula brasiliensis*	0	11	11
Insecta	Coleoptera	Carabidae	*Galeritula carbonaria*	31	132	163
Insecta	Coleoptera	Carabidae	*Haplobothynus* sp.1	13	6	19
Insecta	Coleoptera	Carabidae	Lebiini sp.1	1	0	1
Insecta	Coleoptera	Carabidae	Lebiini sp.2	1	0	1
Insecta	Coleoptera	Carabidae	*Loxandrus* sp.1	9	9	18
Insecta	Coleoptera	Carabidae	*Loxandrus* sp.2	20	4	24
Insecta	Coleoptera	Carabidae	*Pelecium* sp.1	14	2	16
Insecta	Coleoptera	Carabidae	*Pelecium* sp.2	4	0	4
Insecta	Coleoptera	Carabidae	*Pentacomia* (*Mesochila*) sp.1	0	2	2
Insecta	Coleoptera	Carabidae	*Scarites* (*Scallophorites*) sp.1	6	61	67
Insecta	Coleoptera	Carabidae	*Stenolophus* sp.1	1	0	1
Insecta	Coleoptera	Carabidae	*Stenolophus* sp.2	0	1	1
Insecta	Coleoptera	Carabidae	*Trichopselaphus* sp.1	0	1	1
Insecta	Coleoptera	Chrysomelidae	Alticini sp.1	1	0	1
Insecta	Coleoptera	Chrysomelidae	Alticini sp.2	0	1	1
Insecta	Coleoptera	Chrysomelidae	Alticini sp.3	1	0	1
Insecta	Coleoptera	Chrysomelidae	Alticini sp.4	1	0	1
Insecta	Coleoptera	Chrysomelidae	*Homotyphus* sp.1	0	1	1
Insecta	Coleoptera	Chrysomelidae	*Longitarsus* sp.1	1	0	1
Insecta	Coleoptera	Ciidae	Ciidae sp.1	1	0	1
Insecta	Coleoptera	Coccinelidae	Coccinelidae sp.1	0	1	1
Insecta	Coleoptera	Corylophidae	Corylophidae sp.1	1	0	1
Insecta	Coleoptera	Curculionidae	Baridinae sp.1	0	1	1
Insecta	Coleoptera	Curculionidae	*Conotrachelus* sp.1	10	1	11
Insecta	Coleoptera	Curculionidae	Cryptorhynchini sp.1	1	0	1
Insecta	Coleoptera	Curculionidae	Cryptorhynchini sp.2	0	1	1
Insecta	Coleoptera	Curculionidae	Erirhininae sp.1	3	3	6

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Coleoptera	Curculionidae	Erirhininae sp.2	2	0	2
Insecta	Coleoptera	Curculionidae	*Mesocordylus cylindraeus*	1	0	1
Insecta	Coleoptera	Curculionidae	Petalochilini sp.1	1	0	1
Insecta	Coleoptera	Curculionidae	Scolytinae sp.1	1	0	1
Insecta	Coleoptera	Curculionidae	Sitophilini sp.1	1	0	1
Insecta	Coleoptera	Curculionidae	*Tylodema* sp.1	0	1	1
Insecta	Coleoptera	Dryopidae	Dryopinae sp.1	2	0	2
Insecta	Coleoptera	Dryopidae	*Dryops* sp.1	2	0	2
Insecta	Coleoptera	Dytiscidae	*Copelatus* sp.1	1	1	2
Insecta	Coleoptera	Dytiscidae	*Copelatus* sp.2	12	2	14
Insecta	Coleoptera	Elateridae	*Aeolus* sp.1	1	0	1
Insecta	Coleoptera	Elateridae	*Pomachilius* sp.1	0	1	1
Insecta	Coleoptera	Geotrupidae	*Athyreus cyanescens*	8	7	15
Insecta	Coleoptera	Geotrupidae	*Bolbapium* sp.1 aff. *lucidulum*	2	10	12
Insecta	Coleoptera	Geotrupidae	*Neoathyreus* sp.1 aff. *bidentatus*	0	1	1
Insecta	Coleoptera	Hybosoridae	*Chaetodus* (*Chaetodus*) *exaratus*	8	0	8
Insecta	Coleoptera	Hybosoridae	*Chaetodus* (*Chaetodus*) sp.1	1	1	2
Insecta	Coleoptera	Hybosoridae	*Cloeotus* sp.1	0	3	3
Insecta	Coleoptera	Hybosoridae	*Coilodes* sp.1	0	1	1
Insecta	Coleoptera	Hybosoridae	*Germarostes* (*Germarostes*) sp.1	0	3	3
Insecta	Coleoptera	Hybosoridae	*Germarostes* (*Haroldostes*) sp.1	0	1	1
Insecta	Coleoptera	Hydrophilidae	*Dactylosternum* sp.1	1	0	1
Insecta	Coleoptera	Hydrophilidae	*Enochrus* sp.1	4	1	5
Insecta	Coleoptera	Hydrophilidae	*Helochares* sp.1	0	1	1
Insecta	Coleoptera	Hydrophilidae	*Pelosoma* sp.1	28	8	36
Insecta	Coleoptera	Hydrophilidae	*Pelosoma* sp.2	6	1	7
Insecta	Coleoptera	Hydrophilidae	*Phaenonotum* sp.1	2	0	2
Insecta	Coleoptera	Hydroscaphidae	Hydroscaphidae sp.1	2	0	2
Insecta	Coleoptera	Leiodidae	*Dissochaetus* sp.1	29	9	38
Insecta	Coleoptera	Leiodidae	*Dissochaetus* sp.2	1	0	1

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Coleoptera	Leiodidae	Leiodidae sp.1	4	0	4
Insecta	Coleoptera	Leiodidae	Leiodidae sp.2	6	4	10
Insecta	Coleoptera	Leiodidae	Leiodidae sp.3	0	1	1
Insecta	Coleoptera	Leiodidae	Leiodinae sp.1	5	2	7
Insecta	Coleoptera	Leiodidae	Leiodinae sp.2	2	0	2
Insecta	Coleoptera	Melolonthidae	*Astaena* sp.1	0	1	1
Insecta	Coleoptera	Melolonthidae	*Trizogeniates dispar*	0	1	1
Insecta	Coleoptera	Nitidulidae	*Carpophilus* sp.1	0	1	1
Insecta	Coleoptera	Nitidulidae	*Colopterus* sp.1	2	0	2
Insecta	Coleoptera	Nitidulidae	Nitidulinae sp.2	1	0	1
Insecta	Coleoptera	Nitidulidae	*Pocadius* sp.1	64	27	91
Insecta	Coleoptera	Oedemeridae	*Matusinhosa atripennis*	31	8	39
Insecta	Coleoptera	Oedemeridae	*Matusinhosa callosicollis*	135	39	174
Insecta	Coleoptera	Phalacridae	Phalacridae sp.1	2	1	3
Insecta	Coleoptera	Ptiliidae	*Acrotrichis* sp.1	8	10	18
Insecta	Coleoptera	Ptiliidae	Ptiliidae sp.1	1	0	1
Insecta	Coleoptera	Ptiliidae	*Ptinella* sp.1	10	0	10
Insecta	Coleoptera	Ptilodactylidae	*Ptilodactyla* sp.1	2	0	2
Insecta	Coleoptera	Scarabaeidae	*Anomiopus* sp.1	10	0	10
Insecta	Coleoptera	Scarabaeidae	*Canthidium* aff. *korschefskyi*	2	0	2
Insecta	Coleoptera	Scarabaeidae	*Canthidium depressum*	15	16	31
Insecta	Coleoptera	Scarabaeidae	*Canthidium dispar*	2	0	2
Insecta	Coleoptera	Scarabaeidae	*Canthidium gigas*	1	0	1
Insecta	Coleoptera	Scarabaeidae	*Canthidium korschefskyi*	1	0	1
Insecta	Coleoptera	Scarabaeidae	*Canthidium* sp.1	2	0	2
Insecta	Coleoptera	Scarabaeidae	*Canthon amabilis*	2	0	2
Insecta	Coleoptera	Scarabaeidae	*Canthonella lenkoi*	1	0	1
Insecta	Coleoptera	Scarabaeidae	*Coprophanaeus* (*Metallophanaeus*) *saphirinus*	1	0	1
Insecta	Coleoptera	Scarabaeidae	*Dichotomius* (*Luederwaldtinia*) *assifer*	0	1	1
Insecta	Coleoptera	Scarabaeidae	*Dichotomius* (*Selenocopris*) aff. *ascanius*	16	23	39

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Coleoptera	Scarabaeidae	*Dichotomius* (*Selenocopris*) aff. *semicircularis*	3	1	4
Insecta	Coleoptera	Scarabaeidae	*Dichotomius* (*Selenocopris*) *ascanius*	1	0	1
Insecta	Coleoptera	Scarabaeidae	*Dichotomius* (*Selenocopris*) sp.1	7	4	11
Insecta	Coleoptera	Scarabaeidae	*Dichotomius* (*Selenocopris*) sp.2	2	0	2
Insecta	Coleoptera	Scarabaeidae	*Paracanthon* aff. *trichonotulum*	2	1	3
Insecta	Coleoptera	Scarabaeidae	*Sylvicanthon foveiventri*	1	0	1
Insecta	Coleoptera	Scarabaeidae	*Trichillum* aff. *halffter*	1	0	1
Insecta	Coleoptera	Scydmaenidae	*Euconnus* sp.1	1	2	3
Insecta	Coleoptera	Scydmaenidae	*Euconnus* sp.2	1	1	2
Insecta	Coleoptera	Scydmaenidae	*Euconnus* sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	Aleocharinae sp.1	0	1	1
Insecta	Coleoptera	Staphylinidae	Aleocharini sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Anotylus* sp.1	3	0	3
Insecta	Coleoptera	Staphylinidae	*Anotylus* sp.2	4	0	4
Insecta	Coleoptera	Staphylinidae	*Anotylus* sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	*Anotylus* sp.4	5	2	7
Insecta	Coleoptera	Staphylinidae	*Arthmius* sp.1	9	0	9
Insecta	Coleoptera	Staphylinidae	*Arthmius* sp.2	1	0	1
Insecta	Coleoptera	Staphylinidae	*Arthmius* sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	*Arthmius* sp.4	2	0	2
Insecta	Coleoptera	Staphylinidae	*Atheta* sp.1	11	21	32
Insecta	Coleoptera	Staphylinidae	*Atheta* sp.2	21	2	23
Insecta	Coleoptera	Staphylinidae	*Atheta* sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	*Barrojuba* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Belonuchus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Carpelimus* sp.1	1	4	5
Insecta	Coleoptera	Staphylinidae	*Chroaptomus flagrans*	1	0	1
Insecta	Coleoptera	Staphylinidae	*Coproporus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Coproporus* sp.2	1	0	1
Insecta	Coleoptera	Staphylinidae	*Dysanellus* sp.1	1	2	3

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Coleoptera	Staphylinidae	*Edaphus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Holotruchus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Homaeotarsus* sp.1	2	4	6
Insecta	Coleoptera	Staphylinidae	Homalotini sp.1	0	1	1
Insecta	Coleoptera	Staphylinidae	Homalotini sp.2	0	1	1
Insecta	Coleoptera	Staphylinidae	Homalotini sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	Homalotini sp.4	1	0	1
Insecta	Coleoptera	Staphylinidae	*Hoplandria* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Hoplandria* sp.2	1	0	1
Insecta	Coleoptera	Staphylinidae	*Lathropinus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Lissohypnus* sp.1	0	1	1
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.1	1	6	7
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.2	1	7	8
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.4	1	0	1
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.5	0	2	2
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.6	1	0	1
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.7	1	0	1
Insecta	Coleoptera	Staphylinidae	Lomechusini sp.8	1	0	1
Insecta	Coleoptera	Staphylinidae	*Mimogonus* sp.1	0	1	1
Insecta	Coleoptera	Staphylinidae	*Ochthephilum* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Osorius* sp.1	2	3	5
Insecta	Coleoptera	Staphylinidae	*Osorius* sp.2	0	4	4
Insecta	Coleoptera	Staphylinidae	*Osorius* sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	*Paederomimus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Paederomimus* sp.2	1	1	2
Insecta	Coleoptera	Staphylinidae	Philonthina sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Philonthus* sp.1	1	2	3
Insecta	Coleoptera	Staphylinidae	*Philonthus* sp.2	0	1	1
Insecta	Coleoptera	Staphylinidae	*Philonthus* sp.3	0	1	1

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Coleoptera	Staphylinidae	*Pinophilus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Platydracus* sp.1	2	4	6
Insecta	Coleoptera	Staphylinidae	*Platydracus* sp.2	2	1	3
Insecta	Coleoptera	Staphylinidae	*Platydracus* sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	*Pselaphellus* sp.1	0	2	2
Insecta	Coleoptera	Staphylinidae	*Pselaphellus* sp.2	2	1	3
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.1	5	0	5
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.2	2	1	3
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.3	2	0	2
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.4	2	0	2
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.5	1	0	1
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.6	1	0	1
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.7	1	0	1
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.8	1	0	1
Insecta	Coleoptera	Staphylinidae	Pselaphinae sp.9	1	0	1
Insecta	Coleoptera	Staphylinidae	*Quedius* sp.1	3	2	5
Insecta	Coleoptera	Staphylinidae	*Quedius* sp.2	2	0	2
Insecta	Coleoptera	Staphylinidae	*Rugilus* sp.1	10	1	11
Insecta	Coleoptera	Staphylinidae	*Rugilus* sp.2	1	2	3
Insecta	Coleoptera	Staphylinidae	*Scopaeus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Sebaga* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Sebaga* sp.2	1	0	1
Insecta	Coleoptera	Staphylinidae	*Sebaga* sp.3	1	0	1
Insecta	Coleoptera	Staphylinidae	*Styngetus* sp.1	31	2	33
Insecta	Coleoptera	Staphylinidae	*Tetradonia* sp.1	1	1	2
Insecta	Coleoptera	Staphylinidae	*Thinocharis* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Trimicerus* sp.1	1	0	1
Insecta	Coleoptera	Staphylinidae	*Zyras* sp.1	2	2	4
Insecta	Coleoptera	Tenebrionidae	*Antimachus* sp.1	1	0	1
Insecta	Coleoptera	Tenebrionidae	Asidini sp.1	2	1	3

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Coleoptera	Tenebrionidae	*Pogonoceromorphus* sp.1	2	0	2
Insecta	Coleoptera	Tenebrionidae	*Scotinus* sp.1	0	1	1
Insecta	Coleoptera	Tenebrionidae	*Scotinus* sp.2	0	3	3
Insecta	Lepidoptera	Biblidinae	*Biblis hyperia*	0	1	1
Insecta	Lepidoptera	Biblidinae	*Catonephele acontius*	0	1	1
Insecta	Lepidoptera	Biblidinae	*Catonephele sabrina*	0	1	1
Insecta	Lepidoptera	Biblidinae	*Diaethria candrena*	0	1	1
Insecta	Lepidoptera	Biblidinae	*Ectima thecla*	0	10	10
Insecta	Lepidoptera	Biblidinae	*Epiphile orea*	0	7	7
Insecta	Lepidoptera	Biblidinae	*Hamadryas amphinome*	0	1	1
Insecta	Lepidoptera	Biblidinae	*Hamadryas epinome*	0	22	22
Insecta	Lepidoptera	Biblidinae	*Hamadryas feronia*	0	1	1
Insecta	Lepidoptera	Biblidinae	*Hamadryas fornax*	1	6	7
Insecta	Lepidoptera	Biblidinae	*Myscelia orsis*	0	11	11
Insecta	Lepidoptera	Biblidinae	*Temenis laothoe*	0	1	1
Insecta	Lepidoptera	Brassolinae	*Blepolenis batea*	0	7	7
Insecta	Lepidoptera	Brassolinae	*Caligo arisbe*	21	42	63
Insecta	Lepidoptera	Brassolinae	*Caligo beltrao*	4	3	7
Insecta	Lepidoptera	Brassolinae	*Caligo brasiliensis*	0	1	1
Insecta	Lepidoptera	Brassolinae	*Catoblepia amphirrhoe*	1	3	4
Insecta	Lepidoptera	Brassolinae	*Dasyophthalma rusina*	19	6	25
Insecta	Lepidoptera	Brassolinae	*Eryphanis reevesi*	22	6	28
Insecta	Lepidoptera	Brassolinae	*Narope cyllarus*	1	0	1
Insecta	Lepidoptera	Brassolinae	*Narope cyllene*	8	0	8
Insecta	Lepidoptera	Brassolinae	*Opoptera syme*	8	3	11
Insecta	Lepidoptera	Charaxinae	*Archaeoprepona amphimachus*	3	3	6
Insecta	Lepidoptera	Charaxinae	*Archaeoprepona chalciope*	0	1	1
Insecta	Lepidoptera	Charaxinae	*Archaeoprepona demophon*	0	7	7
Insecta	Lepidoptera	Charaxinae	*Fountainea ryphea*	0	4	4
Insecta	Lepidoptera	Charaxinae	*Memphis appias*	0	1	1

Class	Order	Family or subfamily*	Species	Undisturbed	Disturbed	Total
Insecta	Lepidoptera	Charaxinae	*Memphis arginussa*	0	6	6
Insecta	Lepidoptera	Charaxinae	*Memphis moruus*	1	1	2
Insecta	Lepidoptera	Charaxinae	*Memphis otrere*	1	11	12
Insecta	Lepidoptera	Charaxinae	*Memphis philumena*	0	1	1
Insecta	Lepidoptera	Charaxinae	*Zaretis itys*	0	2	2
Insecta	Lepidoptera	Morphinae	*Morpho epistrophus*	42	137	179
Insecta	Lepidoptera	Nymphalinae	*Colobura dirce*	0	1	1
Insecta	Lepidoptera	Satyrinae	*Eteona tisiphone*	0	21	21
Insecta	Lepidoptera	Satyrinae	*Euptychoides castrensis*	1	30	31
Insecta	Lepidoptera	Satyrinae	*Forsterinaria necys*	9	21	30
Insecta	Lepidoptera	Satyrinae	*Forsterinaria quantius*	5	22	27
Insecta	Lepidoptera	Satyrinae	*Hermeuptychia hermes*	0	23	23
Insecta	Lepidoptera	Satyrinae	*Manataria hercyna*	0	1	1
Insecta	Lepidoptera	Satyrinae	*Moneuptychia griseldis*	0	13	13
Insecta	Lepidoptera	Satyrinae	*Moneuptychia paeon*	0	1	1
Insecta	Lepidoptera	Satyrinae	*Moneuptychia soter*	0	18	18
Insecta	Lepidoptera	Satyrinae	*Paryphthimoides grimon*	0	1	1
Insecta	Lepidoptera	Satyrinae	*Paryphthimoides phronius*	0	13	13
Insecta	Lepidoptera	Satyrinae	*Paryphthimoides poltys*	1	12	13
Insecta	Lepidoptera	Satyrinae	*Praepedaliodes amussis*	1	0	1
Insecta	Lepidoptera	Satyrinae	*Praepedaliodes phanias*	0	2	2
Insecta	Lepidoptera	Satyrinae	*Splendeuptychia hygina*	1	0	1
Insecta	Lepidoptera	Satyrinae	*Taygetis acuta*	11	3	14
Insecta	Lepidoptera	Satyrinae	*Taygetis mermeria*	2	24	26
Insecta	Lepidoptera	Satyrinae	*Taygetis ypthima*	19	13	32

* All Lepidoptera are Nymphalidae

CAPÍTULO 2 - Different disturbances, equal responses: testing butterflies as ecological indicators in the Atlantic Forest

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Abstract

Developing straightforward ways for assessing and monitoring ecological conditions through indicators is essential, especially in face of current threats to highly endangered natural systems. In this study, we evaluated the responses of fruit-feeding butterflies subjected to different kinds of anthropogenic disturbance in three reserves in the Brazilian Atlantic Forest, seeking consistent and useful parameters for forest assessment and monitoring. Relative abundance of butterflies showed directional responses to disturbance within reserves in Satyrinae, Charaxinae (increases in disturbed sites) and Brassolinae (decreases in undisturbed sites). A small number of individual species were indicators of specific disturbance type, mostly for each reserve separately. Species composition was different for disturbed and undisturbed sites of all reserves, and the same pattern was observed when species were grouped into subfamilies. Those responses may be related to ecological, physiological and behavioral traits for both larval and adult stages. The consistency of the present results validates fruit-feeding butterflies as an outstanding group of biological indicators that should be promptly employed in the assessment and monitoring of anthropogenic disturbance in tropical forests.

Keywords: Nymphalidae, fruit-feeding butterflies, monitoring, biological indicators

Introduction

A major endeavor in biological conservation today is to select appropriate indicators that provide credible scientific support for decisions in practical situations (Niemi & McDonald, 2004). Developing straightforward ways for assessing and monitoring ecological condition through indicators is therefore fundamental, especially in face of current threats to natural systems (McGeoch, 1998; Dale & Beyeler, 2001; Niemi & McDonald, 2004). Once stablished, ecological indicators can be employed in the assessment of the state, identification of the causes of disturbance, and as "early warning signal of changes" in the environment they inhabit (Dale & Beyeler, 2001). Afterwards, the information gathered by means of indicators can be used by managers and policy makers towards the benefit of the place they want to protect (Palmer et al., 2005).

Tropical forests have experienced a high rate of anthropogenic conversion during the 20th century, and the rhythm of destruction did not slowed down in the beginning of 21st century the way it would be desirable (e.g. Fearnside, 2005; Ribeiro et al., 2009). The destruction of tropical habitats necessarily involves losing much of Earth's biodiversity, which ultimately may imply in the loss of many ecosystem services (see Sodhi, 2008). The Brazilian Atlantic Forest, one of the word's hottest hotspots (Laurance, 2009), is a good example of how human activities can devastate natural ecosystems (Morellato & Haddad, 2000; Tabarelli et al., 2005). This highly endangered, species-rich rainforest, originally covering 1.5 million km^2 of the Brazilian territory before the European colonization in the 1500s, is now reduced to ca. 12% of it original area, mostly in fragmented landscapes (Ribeiro et al., 2009). In addition to this huge amount of habitat lost, Atlantic Forest suffers from exotic species invasion, plant harvesting and collecting, hunting, among other human-driven disturbances (see Tabarelli et al., 2005). Therefore, the development and testing of indicators to assess and monitor the condition of Atlantic Forest remnants is imperative.

Among candidate groups within arthropods for assessing and monitoring habitat changes in terrestrial systems, fruit-feeding butterflies present several advantages. They can be sampled in a standard way with bait-traps, may be promptly identified and released, have a well known systematics (Freitas & Brown, 2004) and have been shown to be good indicators of anthropogenic disturbance in several ecosystems (e.g. Brown & Freitas, 2003; Fermon et al., 2005; Barlow et al., 2007a,b, 2008), including the Atlantic Forest (Brown & Freitas, 2000; Uehara-Prado et al., 2007). Moreover, these butterflies have been shown to be the predictors of community responses of other vertebrate and invertebrate taxa (Brown & Freitas, 2000; Barlow et al., 2007a; Uehara-Prado et al., 2009). Therefore, besides being good ecological indicators, these insects also act as surrogates, representing a range of other organisms living in the same location.

In this study, we evaluated the responses of fruit-feeding butterflies assemblages subjected to three different types of anthropogenic disturbance in the Atlantic Forest: past wood harvesting, traill management and edge effects. No study to date evaluated how these butterflies respond to diverse sources of disturbance in the same biome using the same sampling design. Our objective is to find if there are consistent and useful parameters that would make disturbance assessing and monitoring in the Atlantic forest straightforward. Based on previous studies in the same biome (Brown & Freitas, 2000; Uehara-Prado et al., 2007), we expected the following: a) Pooled abundance would be higher in disturbed habitats; b) Species richness would not differ between disturbed and undisturbed habitats; c) Species composition would differentiate disturbed from undisturbed habitats; d) The proportion of Brassoline in the assemblage would be higher in undisturbed habitats, while the proportion of Biblidinae, Charaxinae and Satyrinae would be higher in disturbed habitats.

Methods

Study area

The study was conducted in three protected forest reserves located in the crest of Serra do Mar, a large mountain range near the Atlantic Ocean in southeastern Brazil (Fig. 1). The region is located in a mountainous relief, and the original forest is classified as montane rainforest (Ururahy et al., 1987). The regional climate is humid, without a dry season. Annual rainfall range from ca. 1,860 to ca. 4,400 mm in the reserves, with no mean monthly rainfall below 48 mm (SIGRH, 2008). Sudden weather changes are frequent in all areas and fog incidence very common. The three reserves studied have different histories of occupation and land use (Table 1), and in each reserve, two areas with contrasts of disturbances were selected to be sampled (see below).

Before the creation of the Serra do Mar state park in the 1970s, part of the Santa Virgínia Nucleus (SVN) suffered a slash-and-burn management followed by pasture establishment. This part of the reserve is now a mosaic composed mostly of secondary vegetation (see Tabarelli & Mantovani, 1999 and references therein). Other sector within the SVN was selectively logged for hardwood (J.P. Villani, pers comm.), and now is a fairly well preserved, old-growth forest, with some nearby remnants of primary forest.

The Boracéia Biological Station (BBS) is located within a 16,450 ha of old growth forest area owned by the São Paulo state water company (Sabesp). Part of this area contains several small road and trails used for the maintenance of electricity lines and water pipes, and therefore are periodically managed (vegetation prune). Some trails were abandoned in the 1970s and now have been used exclusively for research and teaching, remaining mostly unmanaged.

The Paranapiacaba Biological Reserve (PBR) is limited by a paved road at W-NW and by electricity high-tension lines at S-SW. Next to the road and to the electricity lines there is an active railway constructed in the mid 1800s. In this area, vegetation removal occurred since earlier colonization and particularly in the 1970s with the ease of access due to road opening. Vegetation disturbance was increased by the implementation of an industrial complex near the PBR by the 1950s, and peaked from the 1970s to the mid 1980s with the local vegetation being seriously affected by atmospheric pollution (SMA, 1990). The reserve is nowadays occupied mostly by secondary vegetation (Kirisawa et al., 2003).

Sampling units were installed in three different conditions: secondary vegetation only (PBR), old-growth vegetation only (BBS), and both situations (SVN). All reserves are embedded in a vegetation continuum of more than 300,000 ha along the Serra do Mar, where several protected areas are found (Brito & Joly, 1999; MMA 2000), in the better preserved biogeographical sub-region of the Atlantic Forest (Ribeiro et al., 2009). The Brazilian Environmental Ministry considers this region as an “area of extreme biological importance”, presenting highest conservation priority (MMA, 2000).

Sampling design and procedures

Within each forest reserve, two areas with contrasting disturbance were selected, being one more disturbed and other less disturbed as follows (see also Table 1): SVN - history of slash and burn vs. history of selective logging; BBS - managed trails vs. unmanaged trails; PBR - edge vs. interior. Hereafter these areas will be called ‘disturbed’ and ‘undisturbed’, respectively.

Twelve sampling units were installed in each reserve, six in undisturbed sites and six in disturbed sites. Five bait traps combined defined one sampling unit. Bait traps were cylinders made of netting with an internal funnel, baited with a mixture of mashed banana with sugar cane juice, fermented for at least 48 h. Bait traps were set in line in the understory of each site, along pre-existing trails, suspended 1.5–2.0 m above the ground with a distance of at least 23 m between adjacent traps. The total length of sampling transects varied from 115m to 160m, and did not differ among disturbed and undisturbed sites within reserves (t-test, $P > 0.05$ in all cases). Traps were checked every other day (48 h), and the baits replaced at each visit. Fruit-feeding butterfly individuals that could be reliably identified in the field were released after receiving an individual mark. Recaptures were not included in the analyses.

Traps were kept open in the field for eight days/month. Sampling was done monthly from November to May, a period that includes the most favorable season for the capture of butterflies in southeastern Brazil (Brown, 1972). Sampling in each reserve was done in different years (SVN: 2004-2005; BBS: 2005-2006; PBR: 2006-2007). We are aware that annual variation may hamper comparisons among reserves, but logistical constraints did not allow to sample in all reserves simultaneously. Moreover, the focus of this study relies mostly on within-reserve comparisons.

Data analyses

Species richness was compared between disturbed and undisturbed areas within each reserve by an individual-based rarefaction analysis. The statistical significance was evaluated by comparing 95% confidence intervals in the point of the curves with same abundance (see Magurran, 2004).

This analysis was performed in Analytic Rarefaction 1.3 (available from http://www.uga.edu/strata/software/anRareReadme.html).

To evaluate if disturbance affected the species composition of the selected groups, we performed a non-metric multidimensional scaling (NMDS) on the resemblance matrix of Bray-Curtis distances, with 1000 random restarts. The hypothesis of no difference in species composition between disturbed and undisturbed sites of the same reserve was tested by an analysis of similarities (ANOSIM – Clarke, 1993) on the matrix of Bray-Curtis similarities, with 1000 permutations. Before running these multivariate techniques, abundance data was $\log_{10}(x+1)$ transformed. These analyses were performed in the software Primer (Clarke and Gorley, 2006).

Previous studies have shown that fruit-feeding Nymphalidae subfamilies react differently to disturbance (Uehara-Prado et al. 2007; Barlow et al. 2008). We tested if the relative abundance of each fruit-feeding Nymphalidae subfamily in the assemblage (i.e., its representativity) was different between disturbed and undisturbed sites within each reserve with a binomial test (Sokal & Rohlf, 1995). A procedure to control for false discovery rate (FDR) was applied due to the multiplicity of tests made (Benjamini & Hochberg, 1995).

The indicator species analysis (IndVal) (Dufrêne & Legendre, 1997) was used to assess species typical of the different kinds of disturbance occuring in each reserve. This analysis combines information about the abundance (specificity) and frequency of occurrence (fidelity) of species in groups of ecologically similar sites. Species with a significant IndVal higher than 70% were considered indicators of a habitat type. A Monte Carlo randomization procedure among sites (with 999 iterations) was used to test the statistical significance of each species' indicator values (Dufrêne & Legendre, 1997).

Results

A total of 1,886 individuals in 72 butterfly species were recorded in the three reserves (Appendix 1). Species richness was 52 in SVN, 43 in BBS and 51 in PBR, with an overlap of 2 to 11 species between two reserves, and 28 species present in all reserves (Figure 2). Observed species richness surpassed 70% of estimated species richness in all sites (Table 2). The observed species richness was higher in disturbed sites of all reserves. However, rarefied species richness was only significantly higher in the disturbed site when compared to the undisturbed site in SVN (Table 2, Fig. 3). The pooled number of individuals was always higher in the disturbed sites of all reserves (t-test, $P < 0.01$ in all cases; Table 2).

NMDS ordinations indicated that fruit-feeding butterfly species composition differed between disturbed and undisturbed sites within all reserves (Fig. 4). The patterns observed in the ordinations have not changed when species were grouped into subfamilies (Table 3). Ordination results were confirmed by Anosim in all cases (Table 3).

The relative abundance of the subfamily Brassolinae in the fruit-feeding butterfly assemblage was higher in the undisturbed sites in all reserves, while for Satyrinae it was always higher in the disturbed sites (Fig. 5; Table 4). Charaxinae also had higher representativity in disturbed sites of two out of three reserves; the exception was PBR, the only reserve where the vegetation was mostly secondary. Biblidinae had higher relative abundance only in the disturbed site of SVN (Fig. 5; Table 4).

The IndVal analysis revealed 12 indicator species (i.e., with high specificity and fidelity) for the different contrasts of disturbance within the reserves (Figure 6). Three brassoline species (*Dasyophthalma rusina, Opoptera syme*, and *Eryphanis reevesi*) were indicators of less disturbed sites, while *Myscelia orsis* (Biblidinae), *Memphis otrere* (Charaxinae), and *Morpho catenarius*

(Morphinae) were indicators of more disturbed sites. Five out of six satyrine species were indicators of more disturbed sites. Two satyrine species were indicators in two reserves: *Taygetis acuta*, indicator of selective logging (undisturbed) in SVN and managed trails (disturbed) in BBS; *Forsterinaria necys*, indicator of managed trails in BBS and edge habitats in PBR (both disturbed).

Discussion

The initial expectations of difference (or lack of difference) in pooled abundance, relative abundance of subfamilies, species richness and species composition were at least partially confirmed in this study with fruit feeding butterflies subjected to three different types of anthropogenic disturbance. The generality and application of the results for biological indication will be discussed, and recommendations for future reseach will be made.

Abundance, subfamily relative abundance and indicator species

The pooled abundance of fruit-feeding butterflies was always higher in disturbed sites of the three studied reserves, corroborating findings with a similar sampling protocol in the Atlantic Plateau (Uehara-Prado et al., 2007; D.B. Ribeiro in prep.), and in the Brazilian savannah (Cerrado) (M. Uehara-Prado, forthcoming). Considering subfamilies separately, the higher representativity of Satyrinae observed in disturbed sites of all reserves corroborates previous studies in the Amazon (e.g. DeVries et al., 1999; Barlow et al., 2007b, 2008), Atlantic Forest (Uehara-Prado et al., 2007) and Cerrado (M Uehara-Prado, forthcoming), as well as studies done outside the Neotropics (e.g.; Fermon et al., 2005; Bossart et al., 2006). On the other hand, the higher proportion of Brassolinae individuals in undisturbed sites finds less correspondence in the literature, probably because the diversity of this group peaks in the coastal mountains near the Tropic of Capricorn in SE Brazil. Nevertheless, the only previous work in this region found that none brassoline species had higher abundance in fragmented habitats when compared to a continuous landscape, while the opposite was found for Biblidinae, Charaxinae and Satyrinae (Uehara-Prado et al., 2007). In fact, Brown & Freitas (2000) found strong habitat dissociation between Brassolinae and Satyrinae across several Atlantic Forest sites, and we expect this relationship to repeat across the distribution of the two subfamilies. Accordingly, Barlow et al. (2007b) found a negative correlation between the abundance of these subfamilies in primary and secondary forests and *Eucalyptus* plantations in the Brazilian Amazon. This habitat dissociation between Satyrinae and Brassolinae make them complementary in biological indication studies.

The relative abundance of Charaxinae was higher in disturbed areas of the two sites with old-growth vegetation, and did not differ between edge and interior in the site composed mostly by secondary vegetation, suggesting this subfamily, along with Satyrinae, as a good disturbance indicator. This finding may seem contradictory to the statement made by Brown & Freitas (2000, p. 950), who suggested the disappearance of forest-inhabiting Charaxinae from natural systems as among the best indicators of disturbance and pollution. However, while these authors deal with ‘species disappearance’, our result refers to the relative abundance of Charaxinae in the fruit-feeding butterfly assemblage, wich is driven by the commonest species. Therefore, both studies are complementary rather then contradictory: the disappearance of some charaxine species reflects large scale (reserve) disturbance, while the abundance of the ‘remnant’ species in relation to the other subfamilies in the assemblage reflects disturbance at smaller (habitat) scale.

IndVal results showed that no brassoline species were indicator of disturbed sites within different reserves, and three species in this subfamily were indicators of undisturbed sites (Fig.

6), corroborating results from relative abundance. Disturbed site indicators were butterflies from four subfamilies (Biblidinae, Charaxinae, Satyrinae and Morphinae), with no conspicuous common traits among them (e.g. body size, lifespan, behavior), except for their host plants, mostly typical of edges, gaps and secondary sites (see below).

Two species of the same genus, *Forsterinaria necys* and *F. quantius* (Satyrinae) were both indicators of disturbed sites in the same location (BBS). However, in PBR, where *F. necys* was also indicator of disturbance, as few as three individuals of *F. quantius* were caught (Appendix 1). Since PBR is composed mostly by secondary vegetation, while the opposite occur in BBS, it is probable that both species have different degrees of tolerance to disturbance, *F. necys* being more eurytopic than *F. quantius*. In fact, a previous study found that *F. necys* was more abundant in a fragmented landscape, while *F. quantius* was more abundant in a continuous landscape (Uehara-Prado et al., 2007). These are promising species to be investigated as ecological indicators in future studies in the Atlantic Forest. In contrast, the result for a large satyrine species, *Taygetis acuta* was incongruent. This species was indicator of undisturbed site in one reserve (SVN), while indicator of disturbed site in another (BBS). A testable hypothesis for this incongruency would only be available when more knowledge about natural history of *T. acuta* is accumulated. As previously stated (see Shahabuddin & Terborgh, 1999; Brown & Freitas, 2000; Barlow et al., 2007b), the subfamily Satyrinae includes species with a wide range of features, from small edge to large shade dwellers, which results in an equally wide range of responses to disturbance, making this subfamily a potential source of indicator species to different kinds of disturbance.

The Biblidinae *Myscelia orsis* was an indicator of disturbance in the present study, and appears among the most abundant species in two studies in fragmented landscapes in the Atlantic

Forest (Uehara-Prado et al., 2007; D.B. Ribeiro in prep.). Outside the Serra do Mar region, this subfamily is more representative within the fruit-feeding assemblage (Brown & Freitas, 2000), and species of Biblidinae are usually abundant. For example, species in the genus *Hamadryas*, which are very abundant in several different sites in the Neotropics (Pinheiro & Ortiz, 1992; Uehara-Prado et al., 2007; Barlow et al., 2008 and unpublished results of the authors), had the summed abundance always higher in disturbed sites of all reserves (SVN – D = 30, U = 1; BBS – D = 17, U = 0; PBR – D = 9, U = 3), despite the low abundance in the present study. These species seem to be promising indicators of disturbance *sensu latu*, and deserve additional studies.

Leaving sampling-related differences aside (see Hamer & Hill, 2000; Barlow et al., 2007b; Koh, 2007), and given that the same sampling protocol was applied in all reserves, several factors may generate these abundance-related patterns. Butterfly species presence, richness and abundance have been frequently related to the incidence and abundance in their host-plant (Shahabuddin & Terborgh, 1999; Brown & Freitas, 2000; Shahabuddin & Ponte, 2005; Barlow et al., 2008). This certainly applies to this study, since many of the species or subfamilies found with higher abundance/proportion in disturbed habitats (such as biblidines, and small satyrines and charaxines), have larvae that feed on plants typical of secondary Atlantic Forest sites (see Uehara-Prado et al., 2007).

On the other hand, host-plant specificity seems not to explain why brassolines are proportionally more abundant in less disturbed sites (see Uehara-Prado et al., 2007), since their larvae feed on Arecaceae (palms), Poaceae (bamboos and grasses), Musaceae (bananas) and Cyperaceae (sedges) (Penz et al., 1999; Beccaloni et al., 2008), usually found also in secondary, disturbed areas. One possible explanation is that some brassoline larvae may be adapted to cooler microclimates present in less disturbed sites (see Koh, 2007). Territoriality may also play an important role in the spatial distribution of adult brassolines (e.g. Freitas et al., 1997; Srygley & Penz, 1999). Individuals of territorial species may use environmental cues within a site to establish their territories, and these cues may be changed by disturbance. However, the use of environmental cues by butterflies is still an open question, deserving additional studies (see Peixoto & Benson, 2009). Finally, environmental disturbance may decouple phenological triggers from fruit-feeding butterflies and its main larval and adult resources, and these effects are more pronounced in larger species, like most Brassolinae (Ribeiro & Freitas, in prep.). These hypotheses concerning the responses of Brassolinae (and in part the other subfamilies) to disturbance are not mutually exclusive, and remain largely untested.

A note of caution should be made on using individual fruit-feeding species as biological indicators. Despite all 12 species with significant IndVal occurred in at least two reserves, only two species were indicators in two reserves, and none was indicator in the three reserves (Fig. 6). In other words, most individual species in this study may be good indicators for one type of disturbance, but not indicators of forest disturbance *sensu latu*. Also, the reserve with more indicator species (SVN) was that with the higher contrast in vegetation successional stage, suggesting that responses using this approach may need sites with elevated degree of differences, which, in turn, may not be useful in practical situations with low-contrasting disturbance. Additionally, Barlow et al. (2007b) point out the problem of achieving adequate sample sizes to quantify habitat preferences of rare species in Amazonian fruit-feeding butterflies, and the same may be true for other tropical forests.

Species composition

Previous studies have shown that parameters based on species identities are better in indicating anthropogenic disturbance than species numbers alone (Barlow et al. 2007a; Basset et al. 2008; Uehara-Prado et al., 2007, 2009). Corroborating such studies, species composition of fruit-feeding butterflies in this study was different between contrasting sites of all reserves, even when the degree of disturbance was not markedly contrasting, such as in BBS. The effort employed in the identification of fruit-feeding butterflies is smaller than for other invertebrate and also some vertebrate groups (see Gardner et al. 2008; Uehara-Prado et al. 2009), but even with this advantage, some practical situations (lack of time, money or taxonomic expertise - Mandelik et al., 2007) may require the use of lower taxonomic resolution (such as genera or subfamilies). Our results show that in these cases, subfamily composition may be good surrogate of species composition, at least in coarse disturbance assessment (e.g. disturbed vs. undisturbed).

Conclusions

Shifts in the species composition, total abundance, and relative proportion of subfamilies of fruit-feeding butterflies in response to Atlantic Forest disturbance were consistent in the three study areas with different disturbance types and degrees. Those responses may be related to ecological, physiological and behavioral traits for both larval and adult stages. Even if so far it is not possible to link responses to butterfly traits, the consistency of the present results validates this guild as an outstanding group of biological indicators.

Whatever the underlying factors causing the differences in occurrence recorded in this study, those species and groups showing consistent responses should be promptly employed by researchers who deal with the assessment and monitoring of anthropogenic disturbance in tropical forests. Meanwhile, the processes behind the patterns should be simultaneous and continuously investigated to improve our understanding in the ways management procedures would benefit butterflies and, consequently, other groups of vertebrates and invertebrates represented by them (Barlow et al., 2007a; Uehara-Prado et al., 2009).

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Captions

Figure 1. Study reserves in the Atlantic Forest (in grey, the Serra do Mar coastal forest ecoregion). PBR = Paranapiacaba Biological Reserve; BBS = Boracéia Biological Station; SVN = Santa Virginia Nucleus, Serra do Mar State Park.

Figure 2. Venn diagram showing overlap in species composition among reserves. BBS = Boracéia Biological Station; SVN = Santa Virgínia Nucleus; PBR = Paranapiacaba Biological Reserve. Species richness for each reserve in parentheses.

Figure 3. Individual-based rarefaction curves for fruit feeding butterfly assemblages sampled in three Atlantic Forest reserves with different disturbance contrasts. (A) Santa Virgínia Nucleus, (B) Boracéia Biological Station and (C) Paranapiacaba Biological Reserve. Grey lines represent disturbed sites. Dotted lines are the 95% confidence limits.

Figure 4. NMDS ordination of disturbed (open circles) and undisturbed (solid circles) sites within reserves, based on fruit-feeding butterfly assemblages. (A) Santa Virgínia Nucleus, (B) Boracéia Biological Station, (C) Paranapiacaba Biological Reserve. See specific disturbances in Table 1.

Figure 5. Proportion of individuals in the subfamilies of fruit-feeding nymphalid butterflies sampled in reserves with different disturbance contrasts. BIB = Biblidinae, BRA = Brassolinae, CHA = Charaxinae, MOR = Morphinae, NYM = Nymphalinae, SAT = Satyrinae. See Table 4 for significance values.

Figure 6. Abundance of fruit-feeding butterfly species with significant IndVal in at least one reserve. * = reserve where the IndVal was significant; black bars = undisturbed sites; white bars = disturbed sites; SVN = Santa Virgínia Nucleus; PBR = Paranapiacaba Biological Reserve; BBS = Boracéia Biological Station.

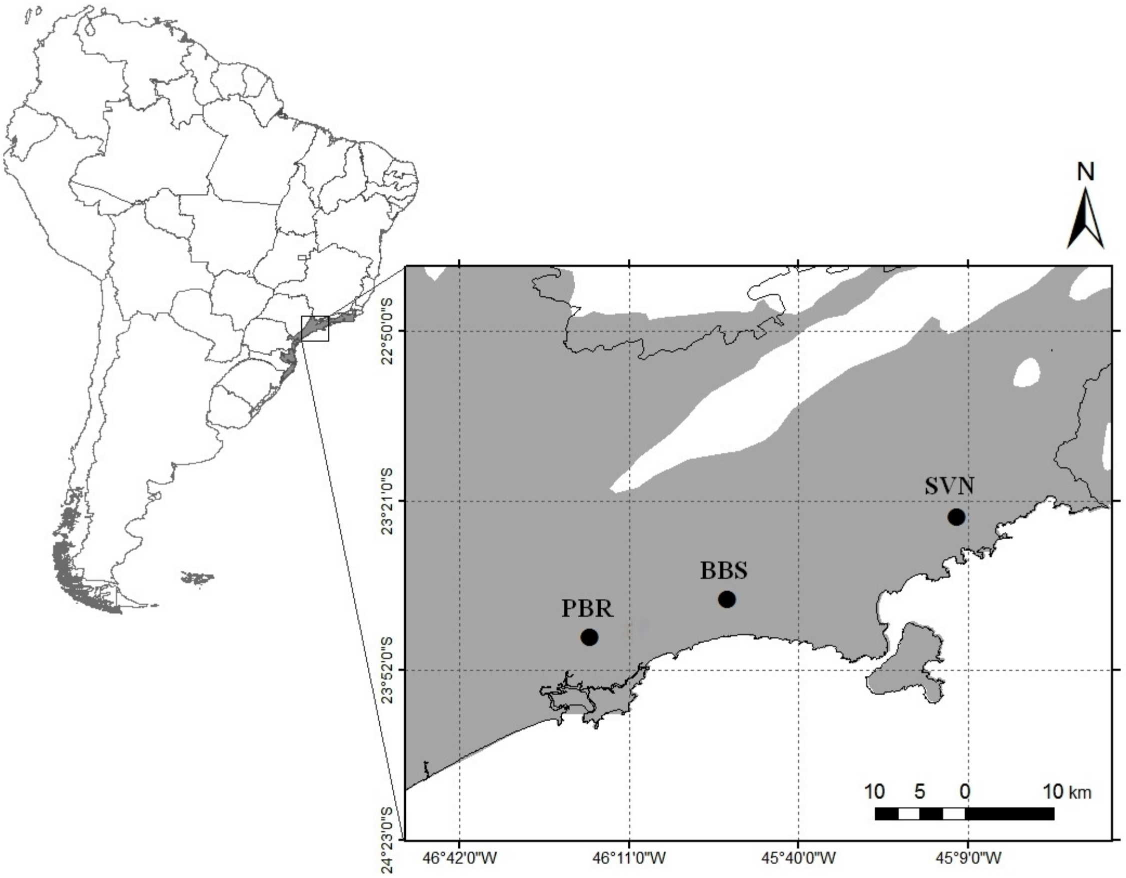

N
22°50'0"S
23°21'0"S
23°52'0"S
24°23'0"S
SVN
BBS
PBR
10 5 0 10 km
46°42'0"W
46°11'0"W
45°40'0"W
45°9'0"W

Figure 1.

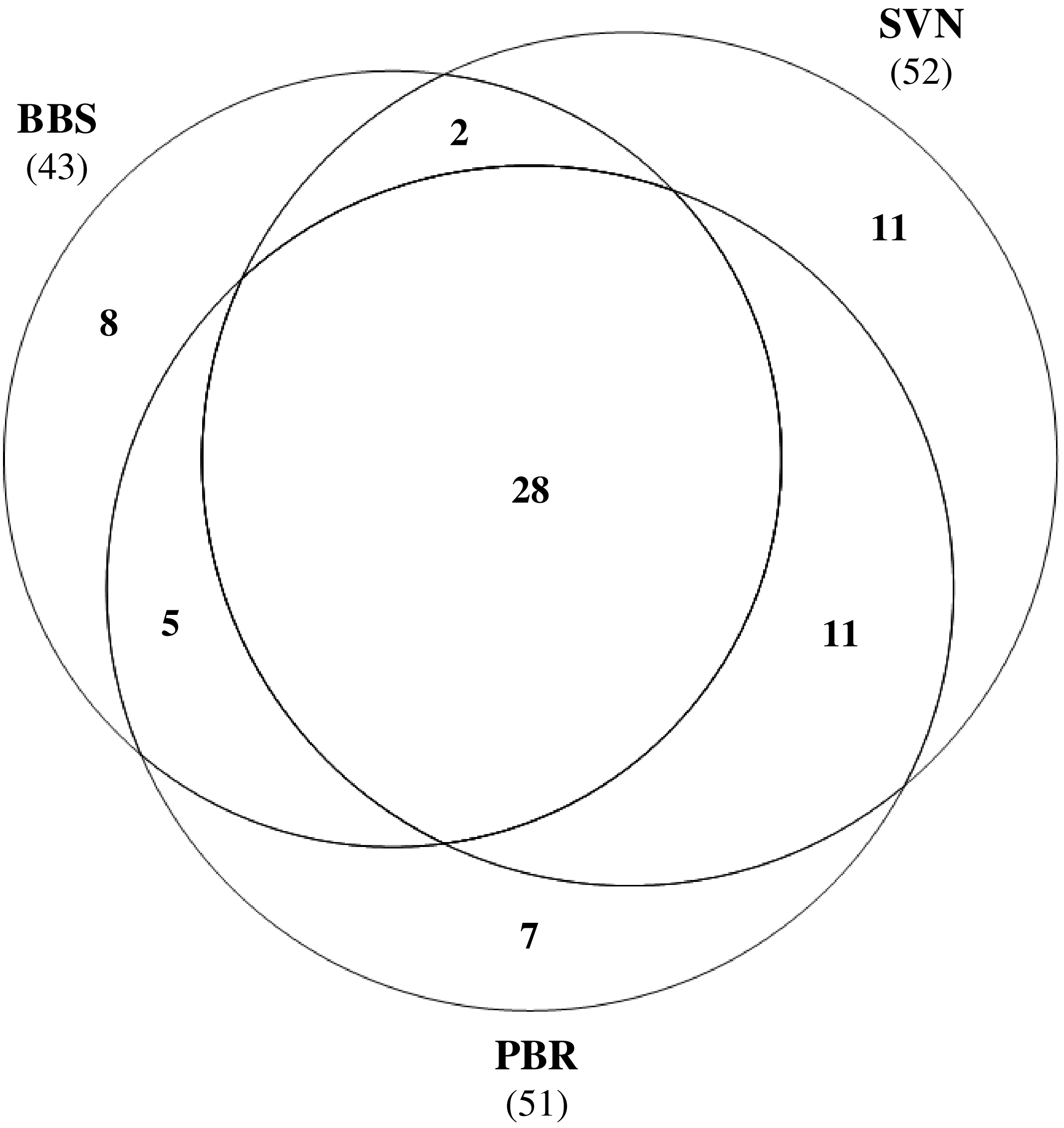


Figure 2.

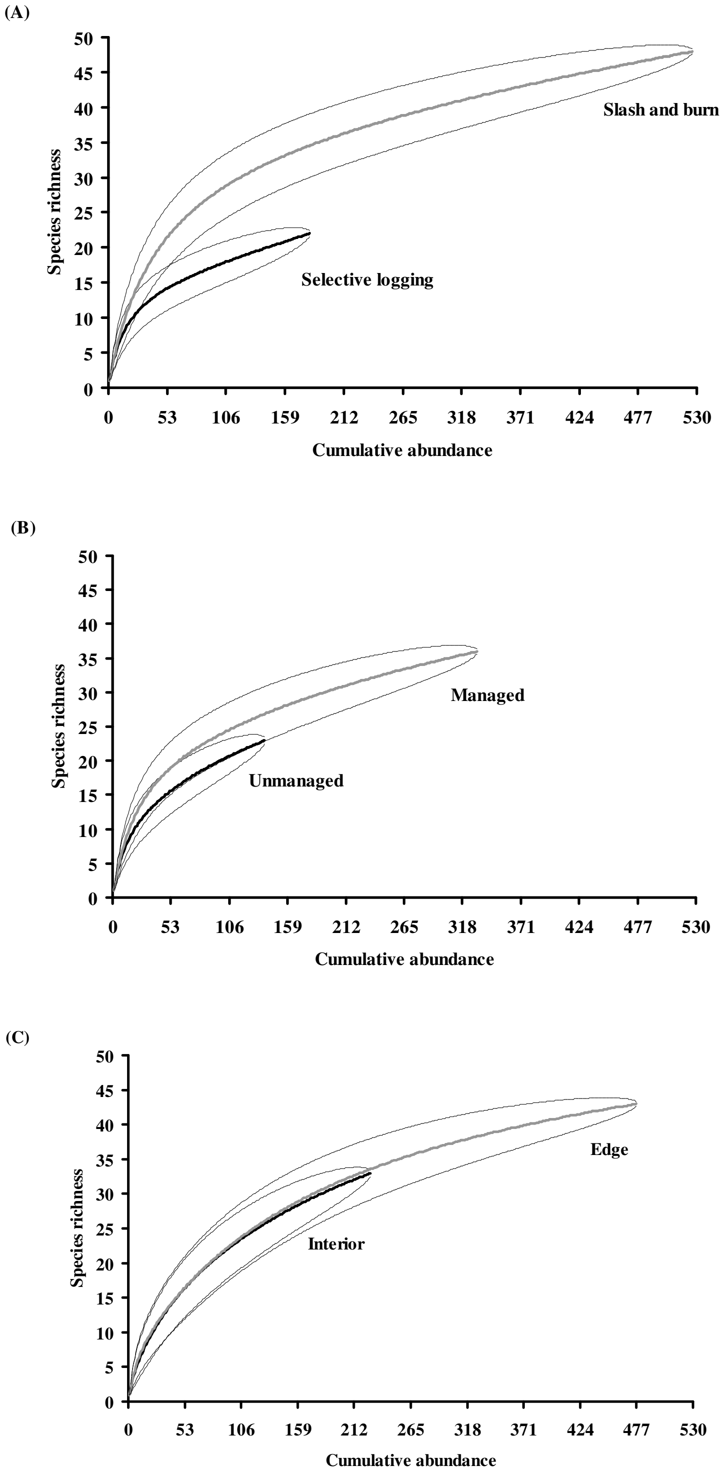

(A)
Species richness
50
45
40
35
30
25
20
15
10
5
0
0
53
106
159
212
265
318
371
424
477
530
Cumulative abundance
Slash and burn
Selective logging
(B)
Species richness
50
45
40
35
30
25
20
15
10
5
0
0
53
106
159
212
265
318
371
424
477
530
Cumulative abundance
Managed
Unmanaged
(C)
Species richness
50
45
40
35
30
25
20
15
10
5
0
0
53
106
159
212
265
318
371
424
477
530
Cumulative abundance
Edge
Interior

Figure 3.

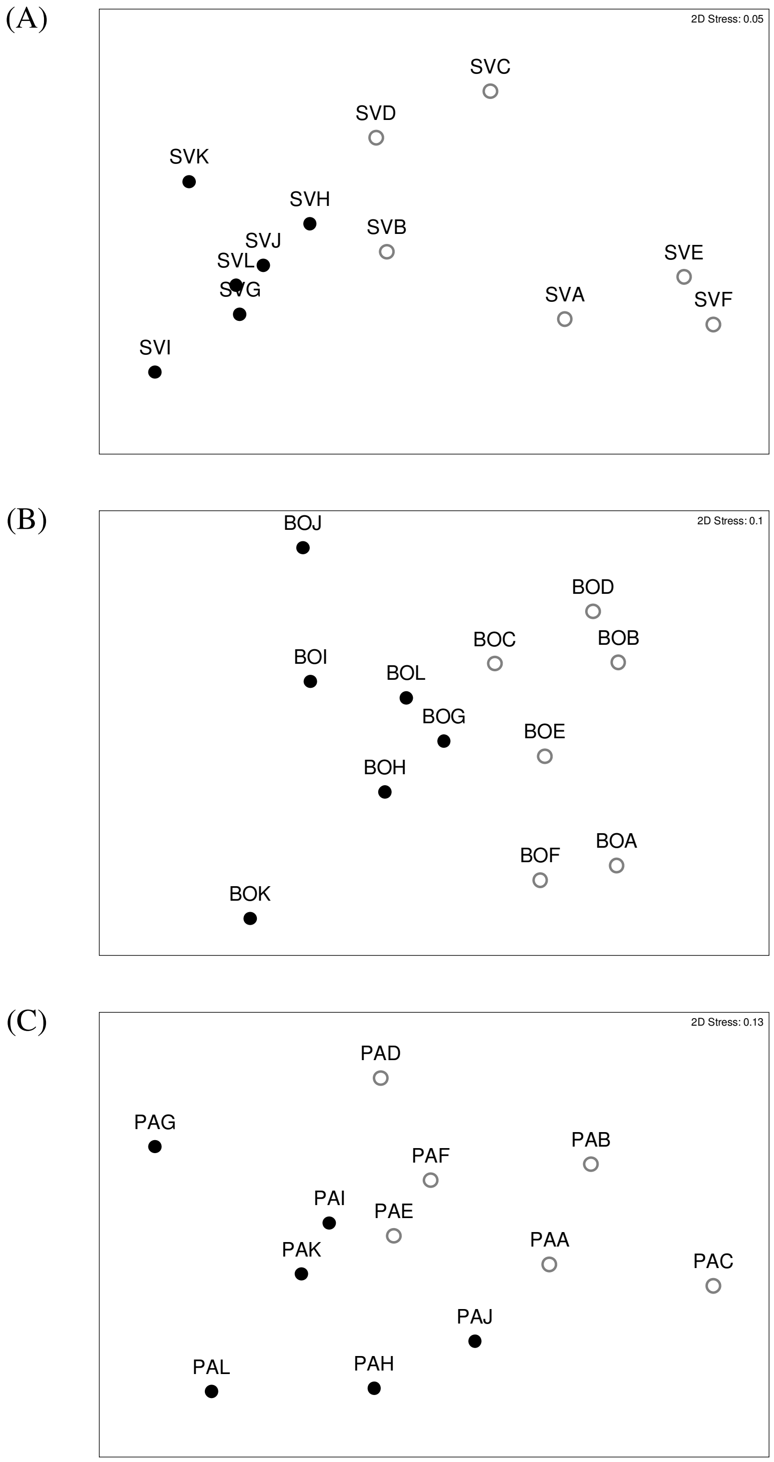
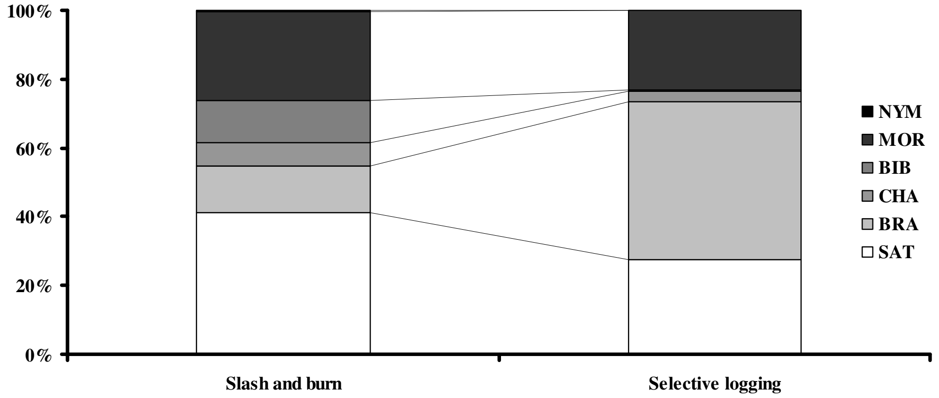
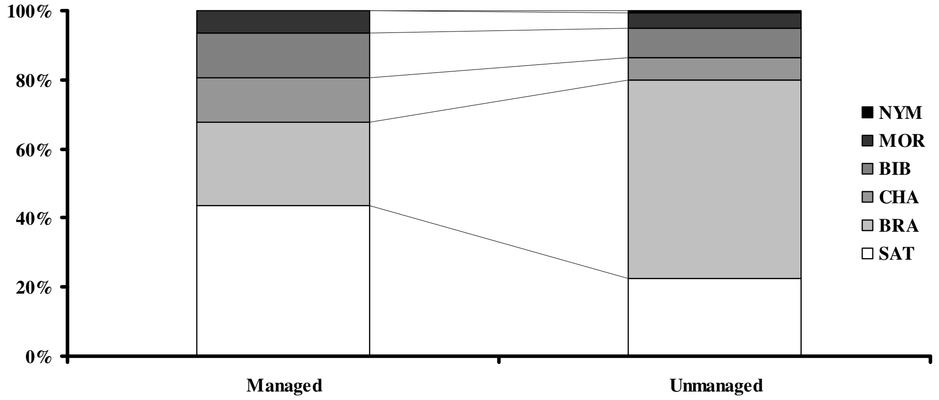

(A)
2D Stress: 0.05
SVC
SVD
SVK
SVH
SVB
SVJ
SVL
SVG
SVE
SVA
SVF
SVI
(B)
2D Stress: 0.1
BOJ
BOD
BOC
BOB
BOI
BOL
BOG
BOE
BOH
BOA
BOF
BOK
(C)
2D Stress: 0.13
PAD
PAG
PAB
PAF
PAI
PAE
PAK
PAA
PAC
PAJ
PAL
PAH

Figure 4.

Santa Virgínia Nucleus



Boracéia Biological Station



Paranapiacaba Biological Reserve

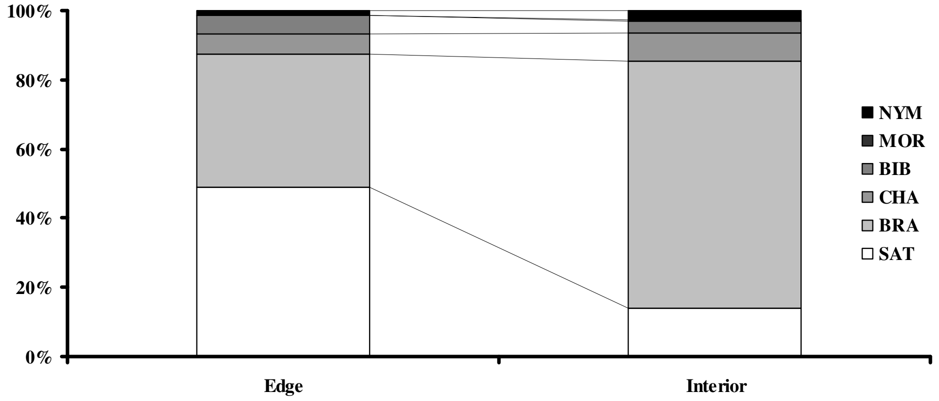


Figure 5.

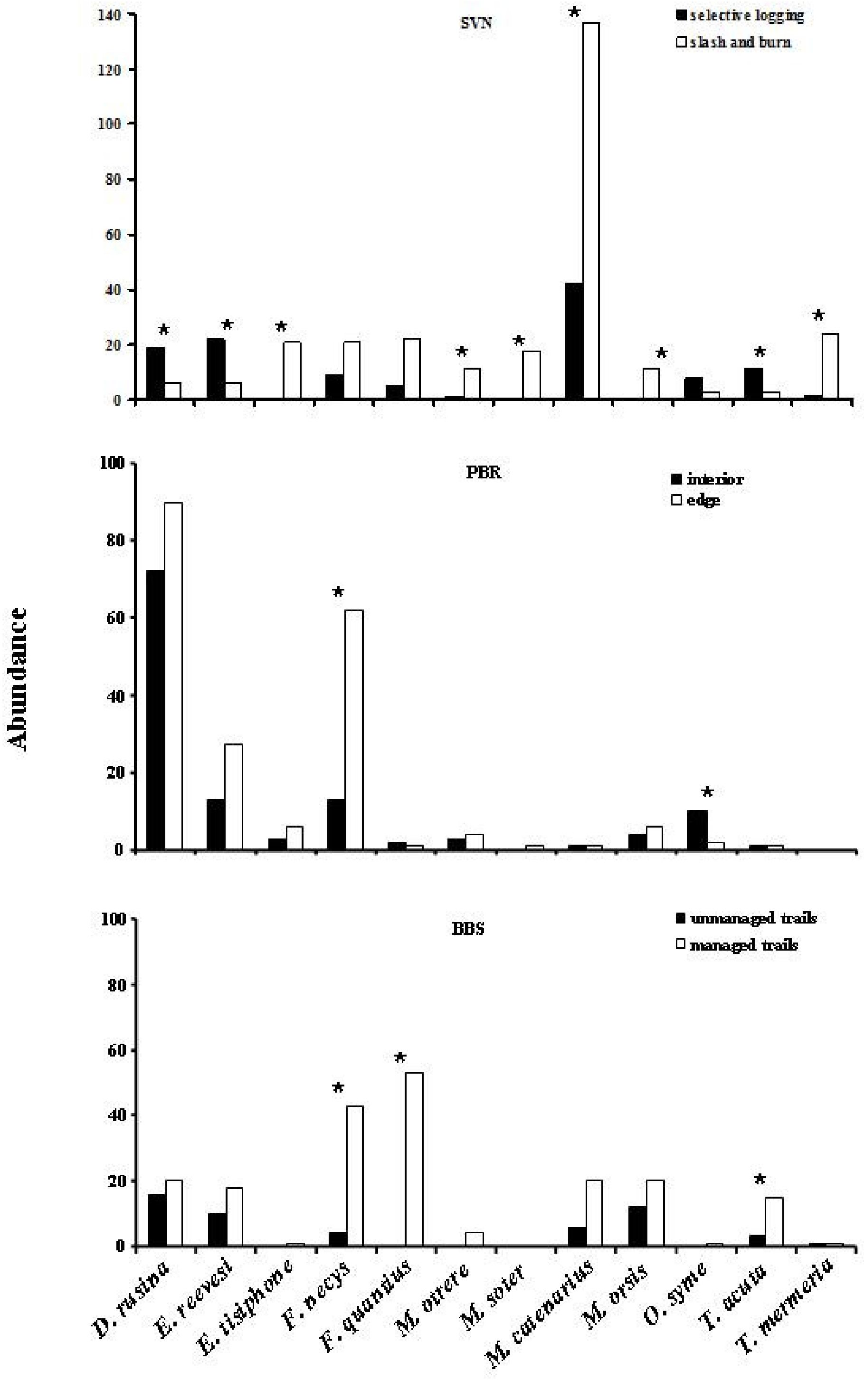

Abundance
SVN
selective logging
slash and burn
0
20
40
60
80
100
120
140
PBR
interior
edge
0
20
40
60
80
100
BBS
unmanaged trails
managed trails
0
20
40
60
80
100
*
D. rusina
E. reevesi
E. tisiphone
F. necys
F. quantius
M. ovrere
M. soter
M. catenarius
M. orsis
O. syme
T. acuta
T. mermeria

Figure 6.

Table 1. Characteristics of the forest reserves. See text for additional information.

Reserve	Legal area (ha)[1]	Altitude (m.a.s.l.)	Vegetation classification[2]	Contrasting areas in each reserve	
				Disturbed	Undisturbed
Santa Virgínia Nucleus (SVN)	17,000	740–1,620	Secondary(disturbed) and old growth (undisturbed)	History of slash-and-burn	History of selective logging
Boracéia Biological Station (BBS)	96	~800	Old growth	Managed trails	Unmanaged trails
Paranapiacaba Biological Reserve (PBR)	336	750-890	Secondary	Edge	Interior

[1] All reserves are embedded in a vegetation continuum.

[2] According to Clarke (1996).

Table 2. Abundance, observed and estimated species richness of fruit-feeding butterflies in reserves with different disturbance contrasts.

	Santa Virgínia			Boracéia			Paranapiacaba		
	Slash and burn	Logging	Total	Managed	Unmanaged	Total	Edge	Interior	Total
Abundance	527**	182	709	332**	139	471	477**	226	706
Observed species richness	48	22	52	36	23	43	43	33	51
Estimated species richness[1]	63.4	30.7	70.3	47.6	31.7	57.7	56.5	45.5	67.5

** = P < 0.01

[1] Jacknife 1

Table 3. NMDS and Anosim results for fruit-feeding butterfly species and subfamilies in the reserves with different contrasts of disturbance.

	Santa Virginia	Boracéia	Paranapiacaba
	Slash and burn vs. Selective logging	Managed vs. Unmanaged trails	Edge vs. Interior
Species			
Ordination stress	0.05	0.10	0.13
Anosim R	0.657*	0.504*	0.306**
Subfamilies			
Ordination stress	0.03	0.11	0.07
Anosim R	0.719*	0.406*	0.243*
Ordination quality[1]	maintained	maintained	maintained

* = $P < 0.05$, ** = $P < 0.01$

[1] Based on visual inspection of ordination diagrams.

Table 4. Representativity of fruit-feeding Nymphalidae subfamilies within disturbed and undisturbed sites of different reserves. Values in percentage.

	Santa Virginia		Boracéia		Paranapiacaba	
	Slash and burn	Selective logging	Managed	Unmanaged	Edge	Interior
Biblidinae	12.14**	0.55	12.95	8.63	5.49	3.45
Brassolinae	13.47	46.15**	24.40	57.55**	38.40	71.55**
Charaxinae	7.02*	2.75	12.95*	6.47	5.70	8.19
Morphinae	26.00	23.08	6.33	4.32	0.21	0.43
Nymphalinae	0.19	0.00	0.00	0.72	1.27	2.59
Satyrinae	41.18**	27.47	43.37**	22.30	48.95**	13.79

FDR corrected Binomial test, * = $P < 0.03$, ** = $P < 0.0001$

Appendix 1. Fruit-feeding butterfly species recorded in three reserves in the Atlantic Forest

	Boracéia Biological Station		Santa Virgínia Nucleus		Paranapiacaba Biological Reserve	
	Managed trails	Unmanaged trails	History of slash and burn	History of selective logging	Edge	Interior
Biblidinae						
Biblis hyperia	0	0	1	0	0	0
Catonephele acontius	2	0	1	0	2	0
Catonephele numilia	3	0	0	0	1	0
Catonephele sabrina	0	0	1	0	0	0
Diaethria candrena	0	0	1	0	0	0
Ectima thecla	0	0	10	0	0	1
Epiphile orea	1	0	7	0	7	0
Hamadryas amphinome	0	0	1	0	5	2
Hamadryas epinome	12	0	22	0	0	1
Hamadryas februa	0	0	0	0	1	0
Hamadryas feronia	1	0	1	0	2	0
Hamadryas fornax	4	0	6	1	1	0
Myscelia orsis	20	12	11	0	6	4
Temenis laothoe	0	0	1	0	1	0
Brassolinae						
Blepolenis batea	7	0	7	0	1	0
Caligo arisbe	2	1	42	21	3	0
Caligo beltrao	9	30	3	4	5	2
Caligo brasiliensis	0	0	1	0	0	0
Caligo illioneus	0	2	0	0	0	0

	Boracéia Biological Station		Santa Virgínia Nucleus		Paranapiacaba Biological Reserve	
	Managed trails	Unmanaged trails	History of slash and burn	History of selective logging	Edge	Interior
Catoblepia amphirrhoe	0	0	3	1	0	0
Dasyophthalma creusa	12	17	0	0	49	54
Dasyophthalma rusina	20	16	6	19	90	72
Eryphanis reevesi	18	10	6	22	27	13
Narope cyllarus	0	0	0	1	0	0
Narope cyllene	10	3	0	8	5	9
Opoptera aorsa	0	1	0	0	0	0
Opoptera syme	1	0	3	8	2	10
Opsiphanes invirae	1	0	0	0	2	2
Opsiphanes quiteria	0	0	0	0	0	2
Charaxinae						
Memphis appias	0	0	1	0	1	0
Memphis arginussa	0	0	6	0	0	0
Memphis morvus	1	0	1	1	10	5
Memphis otrere	4	0	11	1	4	3
Memphis philumena	0	0	1	0	0	4
Memphis ryphea	0	0	4	0	2	0
Prepona amphimachus	29	7	3	3	6	5
Prepona chalciope	0	0	1	0	0	0
Prepona demophon	7	2	7	0	3	1
Prepona demophoon	2	0	0	0	0	1
Zaretis itys	0	0	2	0	1	0

	Boracéia Biological Station		Santa Virgínia Nucleus		Paranapiacaba Biological Reserve	
	Managed trails	Unmanaged trails	History of slash and burn	History of selective logging	Edge	Interior
Morphinae						
Morpho aega	1	0	0	0	0	0
Morpho catenarius	20	6	137	42	1	1
Nymphalinae						
Colobura dirce	0	1	1	0	4	6
Smyrna blomfildia	0	0	0	0	2	0
Satyrinae						
Archeuptychia cluena	3	2	0	0	0	0
Carminda griseldis	1	1	13	0	5	0
Carminda paeon	0	1	1	0	112	2
Eteona tisiphone	1	0	21	0	6	3
Euptychia ernestina	0	1	0	0	0	0
Forsterinaria necys	43	4	21	9	62	13
Forsterinaria quantius	53	0	22	5	1	2
Godartiana muscosa	1	0	0	0	2	1
Guaianaza pronophila	0	0	0	0	3	1
Hermeuptychia hermes	4	0	23	0	23	1
Manataria hercina	0	0	1	0	0	0
Moneuptychia soter	0	0	18	0	1	0
Paryphthimoides interjecta	0	1	0	0	0	0
Paryphthimoides phronius	0	0	13	0	6	2
Paryphthimoides poltys	0	0	12	1	0	0

	Boracéia Biological Station		Santa Virgínia Nucleus		Paranapiacaba Biological Reserve	
	Managed trails	Unmanaged trails	History of slash and burn	History of selective logging	Edge	Interior
Pierella nereis	1	0	0	0	0	0
Praepedaliodes amusis	0	0	0	1	0	0
Praepedaliodes phanias	0	0	2	0	2	0
Pseudodebis euptychidia	0	0	0	0	1	0
Splendeuptychia doxes	0	0	0	0	0	1
Splendeuptychia hygina	2	0	0	1	0	1
Taydebis peculliaris	0	0	0	0	0	1
Taygetis acuta	15	3	3	11	1	1
Taygetis mermeria	1	1	24	2	0	0
Taygetis rectifascia	0	1	0	0	0	0
Taygetis ypthima	19	16	13	19	0	0
Yphthimoides castrensis	1	0	30	1	4	0
Yphthimoides grymon	0	0	1	0	5	1

CAPÍTULO 3 – Abundance of soil epigaeic arthropods in a Brazilian savanna under different fire frequencies

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Abstract

Fire is a major determinant of structure and dynamics in savannas, and the rapid occupation of this biome by human activities has changed the natural burning regime. The effects of fire on the fauna of the cerrado (Brazilian savanna) are still poorly understood, and studies comparing sites frequently and infrequently burned are scarce. In this study the abundance of epigaeic arthropod orders and trophic guilds was assessed in cerrado sites located in the Brazilian Central Plateau subjected to three burning frequencies: frequent (HighFi), intermediary (MidFi) and infrequent (LowFi). When arthropods were analyzed by orders, abundance of Collembola and Orthoptera was lower in the LowFi site, while for Hemiptera it was higher in the MidFi site. No significant differences were found for Hymenoptera, Coleoptera and Araneae. The abundance of detritivores and herbivores decreased from HighFi to LowFi, while it did not change significantly for omnivores and predators. These results indicate that some arthropod groups may not only be resilient to fire effects, but actually benefit from fire effect in cerrado. Arthropod responses to burning frequency at high taxonomic or functional levels are important for applied studies. Based on the results of the current study, springtails and ants seem to be particularly appropriate focal groups for further exploratory studies on the effects of fire at species level.

Key words: Insecta, Arachnida, burning, Cerrado, trophic guilds

Abundância de artrópodes epigéicos em uma área de cerrado sujeita a diferentes freqüências de queima

Resumo

O fogo é um importante determinante da estrutura e dinâmica das savanas, e a rápida ocupação desse bioma por atividades antrópicas tem mudado o regime natural de queima. Os efeitos do fogo na fauna do cerrado são pouco conhecidos, e estudos comparando áreas com diferentes freqüências de queima são escassos. No presente estudo comparamos a abundância de ordens e guildas tróficas de artrópodes em áreas de cerrado localizadas no Planalto Central do Brasil sujeitas a três regimes de queima: freqüente, intermediário e infreqüente. Quando a abundância dos artrópodes foi analisada por ordem, Collembola e Orthoptera foram menos abundantes na área com queimada infreqüente, enquanto Coleoptera foi menos abundante na área com freqüência intermediária de queima. Não houve diferença significativa entre os regimes de queima para Hymenoptera, Coleoptera e Araneae. Quando analisada por guildas tróficas, a abundância de artrópodes detritívoros e herbívoros decresceu da área com regime de queima freqüente para a área não queimada, mas não foi diferente para onívoros e predadores. Os resultados indicam que alguns grupos de artrópodes podem não apenas ser resilientes aos efeitos do fogo, mas de fato se beneficiar dele. A procura por padrões de resposta à freqüência de queima no cerrado em níveis taxonômicos superiores e em grupos funcionais pode ser importante para estudos aplicados. Baseado em nossos resultados, Collembola e formigas parecem ser grupos focais particularmente promissores para estudos adicionais.

Palavras-chave: insetos, aracnídeos, fogo, guildas tróficas.

INTRODUCTION

Originally covering about 2 million km^{2,} the Brazilian Cerrado is the largest savanna region in the Americas (Gottsberger and Silberbauer-Gottsberger 2006). Its fauna and flora are one of the most diverse amongst the savannas (Mittermeyer et al. 1999), comprising about 7,000 vascular plant species (Castro et al. 1999) and an estimated 90,000 insect species (Dias 1992). However, current threats to its biodiversity are also impressive, since 50% of the region was already converted into disturbed landscapes (WWF 1995).

Fire is a major determinant of cerrado structure and dynamics, influencing the vegetation physiognomy and composition (Moreira 2000), soil surface temperature (Miranda et al. 2002), and plant nutrient use efficiency (Nardoto et al. 2006). Fire stimulates the resprouting, germination, flowering and fruiting of many fire-adapted plant species (Coutinho 1990; Miranda et al. 2002; Gottsberger and Silberbauer-Gottsberger 2006), which may foster animal populations that are directly or indirectly related to these resources. However, the rapid human occupation of the Cerrado region has changed the natural fire regime (season and frequency of burning) with negative consequences for its flora and fauna (Ramos-Neto and Pivello 2000; Miranda et al. 2002). Frequent fires may be harmful to animals and plants through direct mortality or, indirectly, by changing local hydrology, nutrient availability and soil properties (Neary et al. 1999; Nardoto et al. 2006). For that reason, fire may also become a threat to Cerrado's biodiversity (Klink and Machado 2005; Durigan et al. 2007).

Arthropods are fundamental components of earth's biodiversity, occupying various niches and playing essential ecological roles in virtually every terrestrial ecosystem (Wilson 1987; York 1999; Lavelle et al. 2006). Arthropods are particularly important drivers of soil function and, therefore, likely to be affected by disruption in soil properties by burning (York 1999). Despite the importance of understanding the responses of arthropods to fire, only a few number of studies were done to date in the cerrado (see Oliveira and Marquis 2004), mostly involving one or few taxonomic groups (e.g. Morais and Benson 1988; Prada et al. 1995; Seyffarth et al. 1996; Vieira et al. 1996; Marini-Filho 2000; Morais et al. 2007; Knoechelmann and Morais 2008).

The aim of this study was to compare the abundance of epigaeic arthropod orders and trophic guilds under different fire frequencies in a Cerrado reserve. Most of the epigaeic fauna uses the leaf litter layer, a significant component of fuel in this ecosystem (Hoffmann 1996; Miranda et al. 2002), and therefore, their abundance are expected to be affected by fire (York 1999). Ultimately, this study provides information that may be usefull in exploring different ways in determining indicators of disturbance by fire in this cerrado reserve.

METHODS

Study site

The study was done in the Emas National Park, a Cerrado reserve located in the Brazilian Central Plateau (17°49'-18°28'S and 52°39'-53°10'W). This park is one of the largest and better preserved Cerrado reserves, and is a key area to the conservation of this ecosystem (Unesco 2001). The climate of the region is tropical humid with wet summer and dry winter (Aw of Köppen 1948). The dry season goes from June to August and the wet season from September to May. Annual rainfall varies from 1200 to 2000 mm, concentrated from September to March, and mean annual temperature is 24.6°C (Ramos-Neto and Pivello 2000). The relief is mostly flat, and altitude varies from 820 to 890 m (Ramos-Neto and Pivello 2000).

The area was used for cattle ranching in the past, and dry season burnings were used annually to promote pasture regrowth (Ramos-Neto and Pivello 2000). Since the park delimitation cattle are no longer allowed inside it and a fire exclusion policy was established (Ramos-Neto and Pivello 2000). As a consequence, uncontrolled wildfires occurred every 3-4 years, burning on average 80% of its total area (Ramos-Neto and Pivello 2000; França et al. 2007). Thus, since 1994, approximately 10 km² of preventive firebreaks (30 m wide) are burned annually in the dry season to avoid the spread of eventual fires (França et al. 2007).

Sampling and data analysis

In 1994, a lightning fire burned more than 90% of the Emas National Park (Ramos-Neto and Pivello 2002; França et al. 2007), so that year was considered the "ground zero" for burning effects on arthropods in this study. Arthropods were sampled in three sites with different burning frequencies from 1994 to 2006: a firebreak burned annually (12 fire events since 1994, last burning in 2005), another firebreak burned five times in this period (1996, 1999, 2001-2003) and a site unburned since 1994. Hereafter these sites will be referred as 'HighFi', 'MidFi' and 'LowFi', based on their burning frequency. Such fire management has been done every dry season when a fire brigade uses flamethrowers to burn all the biomass within the firebreaks. Except for the firebreaks, no burning ocurred in adjacent areas since 2003. Once true replication for burning areas was not possible in the study site, due to logistical, bureaucratic and ethical reasons, a natural experiment approach was adopted, with sampling being conducted in sites with well-documented history of burning (see Parr and Chown 2003). Additionally, the three sites were close enough to each other to reduce the probability of confounding factors (e.g., different land use in the past, soil type, vegetation composition). Although limiting the degree of generalization of the findings and not solving the statistical problem of a lack of true replicates for the fire treatments, this approach increases the likelihood that significant differences between sites are due to different fire frequencies (Pucheta et al. 1998), allowing us to discuss about patterns found within the reserve.

In each of these sites, twenty pitfall traps were randomly placed at least 10 m apart each other along 2.5 km straight lines (one per site). Pitfall traps were 500 ml plastic cups leveled with the soil surface, with 5.8 cm opening and 10.5 cm depth, protected from direct rainfall by a circular polystyrene shield placed above them. Traps were filled with ca. 200 ml of 30% propylene glycol, 0.1% formaldehyde, and a few drops of detergent. Pitfall traps were kept open from May 8 to May 12, 2006, the end of the rainy season and the beginning of the dry season. All collected arthropods were preserved in 70% ethanol.

Arthropods were sorted to different taxonomic levels from genera (e.g. ants and some Coleoptera) to order (e.g. Araneae and Scutigeromorpha), necessary to place them into four coarse trophic categories: detritivores, herbivores, omnivores and predators (based on Marinoni et al. 2001; Silvestre et al. 2003; Triplehorn and Johnson 2005). Leaf-cutting ants were assembled into herbivores. Ant abundance was based on species' frequency in the traps. Spider specimens were deposited in the collection of Instituto Butantan (São Paulo, Brazil), ants were deposited in the Museu de Zoologia, Universidade de São Paulo (São Paulo, Brazil) and the remaining taxa were deposited in the Museu de Zoologia, Universidade Estadual de Campinas (Campinas, Brazil).

To test the null hypothesis of no fire-induced abundance shift, differences in the abundance of each order and trophic group among sites were analyzed using a one-way randomized analysis of variance, appropriate for unreplicated designs (Payne, 2006). When significant differences were found, the Tukey post-hoc test was applied.

RESULTS

A total of 1,192 individuals from eight orders were captured. Collembola was the most abundant order, representing 33% of the arthropods in the sample, followed by Hymenoptera (mostly ants), Orthoptera, Hemiptera, Coleoptera, Araneae, Dyctioptera and Scutigeromorpha (Table 1). The most abundant trophic guild was the detritivores, with 38.5% of the individuals, followed by herbivores (27%), omnivores (17.5%) and predators (17%). The abundance of trophic guilds was highly skewed by one or two taxonomic groups: 85% of the detritivores were Collembola, 69.3% of herbivores were Orthoptera, 73.9% of predators were Araneae and Hymenoptera and 100% of the omnivores were Hymenoptera (ants) (Table 1).

When arthropods were analyzed by orders, the abundance of all but Hemiptera peaked in HighFi (Fig. 1). The abundance of Collembola was significantly higher in HighFi, while did not differ between MidFi and LowFi. For Orthoptera the abundance was significantly lower in LowFi, and did not differ between HighFi and MidFi. Hemiptera was the only order which abundance peaked in MidFi, with significant difference only between MidFi and LowFi (Fig. 1). The abundance of Coleoptera was lower in MidFi, and significantly different only between HighFi and MidFi. No significant differences were found for Araneae and Hymenoptera.

The abundance of all trophic guilds decreased from HighFi to LowFi (Figure 1). Detritivore abundance was significantly higher in HighFi and did not differ between MidFi and LowFi. The abundance of herbivores was significantly higher in HighFi and MidFi when compared to LowFi. Omnivores and predators also showed a tendency to become less abundant over time since last burning, yet this difference was not significant (Figure 1).

DISCUSSION

The general tendency found in this study - a lower abundance of epigaeic arthropods with decrease in fire frequency - corroborates some previous studies with fire effects on insects associated to cerrado plants. Prada et al. (1995) report a ca. 20-fold increase in the number of flowering plants of an Asteraceae species in a burned site followed by a higher abundance of herbivores associated to it. Ants visiting extrafloral nectaries also were more frequent in cerrado sites burned biennially than in unburned sites (Knoechelmann and Morais 2008). It may not be surprising that some organisms benefit from the vigorous regrowth of plants with which they interact in frequently burned sites (Marini-Filho 2000). Therefore, it should be expected an increase in the abundance of Orthoptera and the herbivore trophic guild in such sites. In South African savannas the abundance of grasshoppers also increased in frequently burned sites benefited by vegetation regrowth (Chambers and Samways 1998). Nonetheless, these relationships do not appear to be so obvious for other taxonomic or functional groups.

The lower abundance of detritivores in the MidFi and LowFi sites may be explained by the dominance of this trophic guild by Collembola, since some dominant springtail species may have greater frequency and density in burned than in unburned sites (Brand 2002). If species like these were numerically dominant among the springtails sampled in the Emas National Park, they would skew the response found for the order Collembola and consequently for detritivores, due to the dominance of springtails in this guild.

The abundance of omnivores did not differ among sites with different burning frequencies. The idiosyncratic nature of the omnivore guild in this study, composed exclusively by ants, may help us to understand their relationship with burning frequency. Almost 80% of capture frequency in this guild was composed by three dominant ant genera in

Cerrado, *Camponotus* (Formicinae), *Pheidole* (Myrmecinae) and *Linepithema* (Dolichoderinae) (data not shown), which present massive recruitment and aggressive interspecific interactions, even in disturbed sites (Silvestre et al. 2003). These characteristics, coupled with the ability to feed on a large range of items could explain the homogeneous response of omnivores to all burning frequencies. Morais and Benson (1988) reported a high mortality for cerrado arboreal ants caused by fire, and a reduction in their abundance at least 1.5 years after burning. They also postulated that ground ants would have higher survivorship to burning, due to a smaller effect of fire at the ground level. Their proposition is supported by the present study at least for omnivore ants. Few arboreal species were captured in this study (data not shown), and they did not affect the results. However, studies at species level are needed to verify whether there are shifts in the composition and species richness of omnivore ants in cerrado sites with different burning frequencies even when their abundance do not change.

The abundance of predators did not differ among sites with different burning frequencies. In this case, different responses by arthropod orders composing this guild homogenized the overall response (see Table 1, Figure 1 B). This also means that no directional functional response (i.e., predation) was observed in relation to fire frequency in this study. In fact, variation in responses to fire has been observed within and between arthropod orders (e.g. Warren et al. 1987). The assemblage of groups with different response at the ordinal level may also help to explain the responses of Coleoptera and Hemiptera (with several functional groups), which decreased and peaked in abundance in MidFi respectively (Figure 1).

Spider abundance did not differ among sites, contrasting with a previous study, which observed a significant reduction in spider abundance in a recently burned cerrado (Gomes et al. 2007). However, in that study spiders were collected using winkler extractors, which selectively sample spider species of small size, which could be either more susceptible to fire effects and/or slower in colonizing burned sites. On the other hand, the method used in the current study is more efficient for sampling surface active species (Churchill 1993), which are the species that are most likely to colonize burned sites.

The abundance of ground and grass-layer arthropods in tropical savanna woodlands and open forests in Australia were generally unaffected by different burning regimes, and this result was credited to an ordinal-level resilience of arthropod abundances (Andersen and Müller 2000 and references therein). This study indicates that some arthropod groups may not only be resilient to fire effect, but actually benefit from fire effect in cerrado. Additional studies should be conducted in this ecosystem to confirm the generality of this statement. Springtails and ants seem to be particularly appropriate focal groups for further exploratory studies at species level, since they are abundant in samples and, in the case of ants, relatively well known in the Cerrado (see Silvestre et al. 2003).

Final Remarks

The effects of fire on the cerrado fauna are still poorly understood, and studies comparing sites with different burning regimes are scarce (Morais et al. 2007). While long-term samplings and species-level identification are highly desirable in any assessment study, decision-making assessments are often made in time and money-constrained circumstances (particularly in Brazil), and consequently important decisions are based on snapshot samples and identifications at high taxonomic levels. In these unfavorable situations, the use of abundance in higher taxonomic categories may be the only alternative (Brennan et al. 2006).

Therefore, finding consistent patterns for arthropods at high taxonomic or functional level is important in a practical way.

It has been shown that the utility of higher taxonomic level as surrogate of lower levels will depend on how well documented the regional biodiversity is (Lovell et al., 2007). Therefore, this study should be considered a first assessment on high taxonomic level responses to fire regimes in cerrado arthropods, from which more detailed studies should be made. Ultimately, the information provided here may used to exploring different ways in the search for ecological indicators of disturbance by fire in cerrado.

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FIGURE LEGEND

Figure 1. Mean abundance (± sd) of arthropods in areas with different burning rates: HighFi (black bars), MidFi (dark gray bars), and LowFi (light gray bars). (A) orders and (B) trophic guilds. Different letters in the same sequence within an order or guild represent statistically significant differences in abundance (One-way randomized analysis of variance followed by a Tukey's post-hoc test, see Appendix 1).

Table 1. Abundance of epigaeic arthropod orders and trophic guilds in areas with different burning frequencies in the cerrado of Emas National Park, Brazil.

Order	Trophic guild	Burning rate[1]			Total
		HighFi	MidFi	LowFi	
Araneae	Predators	30	13	21	64
Collembola	Detritivores	225	115	57	397
Coleoptera	Detritivores	24	4	15	43
	Herbivores	1	1	1	3
	Predators	7	4	8	19
Dyctioptera	Detritivores	3	9	11	23
	Predators	0	1	0	1
Hemiptera	Herbivores	30	28	14	72
	Predators	8	19	6	33
Hymenoptera	Herbivores	6	5	8	19
	Omnivores	75	69	64	208
	Predators	34	36	16	86
Orthoptera	Herbivores	104	84	35	223
Scutigeromorpha	Predators	0	1	0	1

[1] HighFi – site burned annually from 1994 to 2006, MidFi – site burned five times in this period, LowFi – site unburned since 1994.

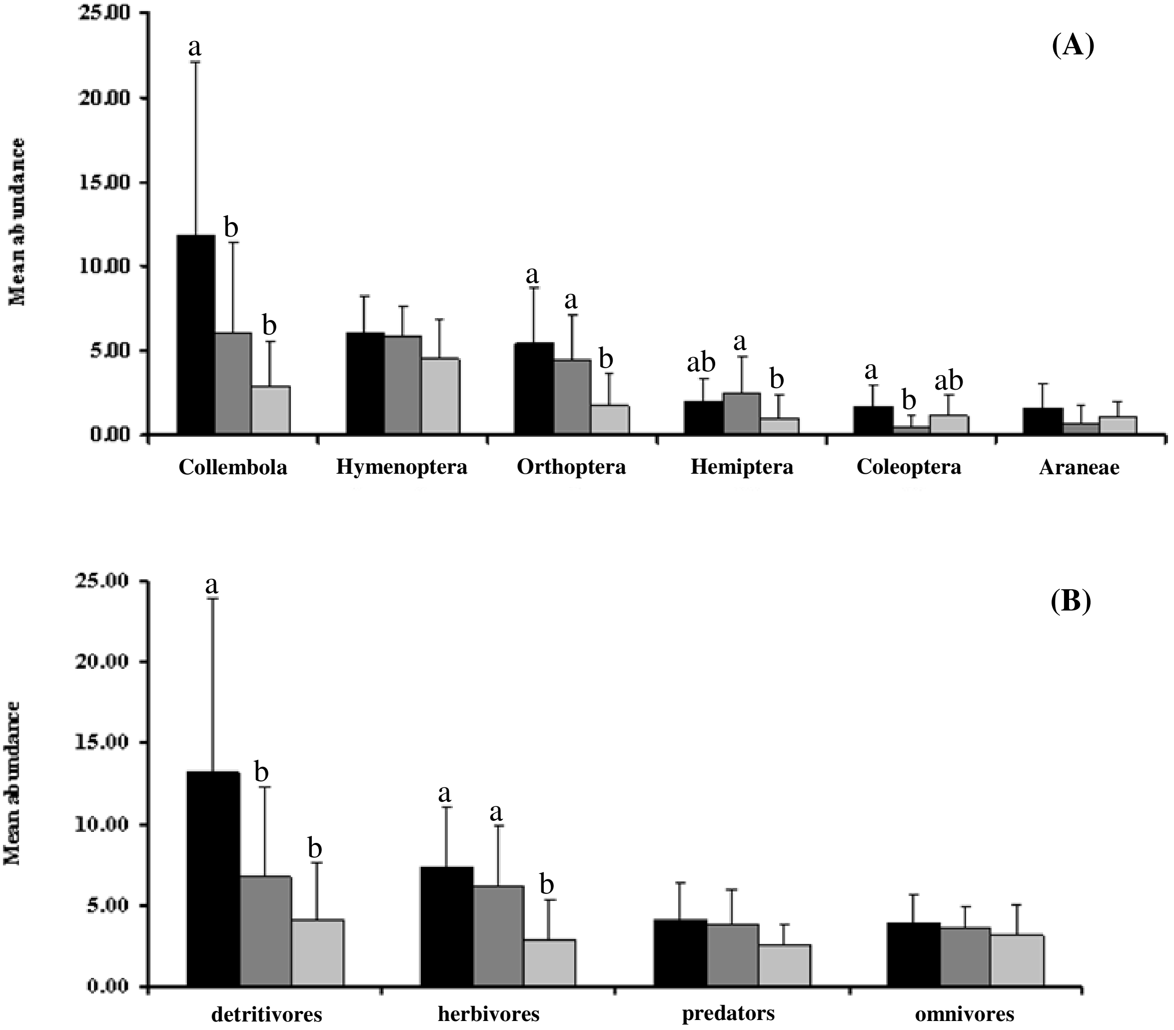

Figure 1. Mean abundance (± sd) of arthropods in areas with different burning rates: HighFi (black bars), MidFi (dark gray bars), and LowFi (light gray bars). (A) orders and (B) trophic guilds. Different letters in the same sequence within an order or guild represent statistically significant differences in abundance (One-way randomized analysis of variance followed by a Tukey's post-hoc test, see Appendix 1).

Appendix 1. Randomized analysis of variance and Tukey's pos-hoc test results for comparison of the abundance of arthropod orders and trophic guilds in areas with different burning frequencies in the cerrado of Emas National Park, Brazil. Significant values are in bold.

	Anova	Tukey's post hoc test *P*		
	P	HighFi x MidFi[1]	HighFi x LowFi	MidFi x LowFi
Araneae	0.0907	-	-	-
Coleoptera	**0.0329**	**0.003188**	0.4472	0.07429
Collembola	**0.0019**	**0.01935**	**0.0002989**	0.2869
Hemiptera	**0.0029**	0.9114	**0.01975**	**0.006551**
Hymenoptera	0.3616	-	-	-
Orthoptera	**0.0006**	0.8917	**0.000277**	**0.0008636**
Detritivores	**0.004**	**0.01732**	**0.0005546**	0.445
Herbivores	**0.0039**	0.7247	**0.0003568**	**0.002958**
Omnivores	0.2919	-	-	-
Predators	0.1745	-	-	-

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[1] HighFi – site burned annually from 1994 to 2006, MidFi – site burned five times in this period, LowFi – site unburned since 1994.

CONCLUSÃO GERAL

Estudos de diagnóstico e monitoramento de impacto ambiental conduzidos no Brasil raramente incluem invertebrados terrestres, os quais sabidamente estão entre os grupos que apresentam melhor custo-benefício em termos de indicação biológica (Gardner et al., 2008). Esse mesmo viés pode ser observado em estudos fora do Brasil (e.g. Dobson, 2005; Mendelik et al., 2005). Embora parte dessa ausência provavelmente se deva a questões 'vertebrocentristas' (Nash, 2004), no Brasil em particular isso se deve também a ausência de estudos e protocolos de avaliação e teste de indicadores.

Ao fim deste estudo fica claro que o emprego de indicadores ecológicos (sensu McGeoch, 1998) na prática está necessariamente relacionado ao tempo, recursos financeiros e à dificuldade taxonômica e logística imposta pelos diferentes *taxa* estudados. Os resultados encontrados empregando vários *taxa*, mas com diferentes resoluções taxonômicas e abordagens analíticas (Cap. 1) indicam que estudos que consideram apenas abundância total e/ou riqueza de espécies na avaliação de perturbação antrópica podem não detectar alterações no habitat, mesmo havendo um alto contraste entre uma área perturbada e uma não perturbada. A composição de espécies, por outro lado, mostrou-se um excelente parâmetro de comparação para vários grupos de artrópodes, e a composição agrupada em níveis taxonômicos superiores não influenciou a detectabilidade das alterações para besouros epigéicos (Cap. 1) e borboletas frugívoras (Cap. 1 e 2). Novos estudos são necessários para se testar a eficiência desses indicadores com menor resolução taxonômica em situações em que o contraste não é discreto (perturbado vs. conservado), mas contínuo.

Em muitos casos, estudos de diagnóstico ambiental ocorrem em situações de escassez de tempo, recursos financeiros e taxonômicos, e nesses casos a análise em escala ordinal ou o uso de grupos funcionais (Cap. 3) pode ser a única opção de avaliação de perturbação antrópica. Embora seja uma alternativa plausível, essa abordagem ainda necessita um grande aprofundamento a partir do que foi mostrado no presente estudo. No caso particular de frequencia de queima no cerrado, Collembola e formigas parecem ser grupos focais particularmente promissores para estudos exloratórios adicionais. A comparação com outros ecossistemas usando protocolos semelhantes pode esclarecer se existem padrões gerais e utilizáveis em indicação biológica.

Por fim, borboletas frugívoras são, indubitavelmente, o grupo de artrópodes com maior facilidade de aplicação imediata como indicadores biológicos em Floresta Atlântica (Cap. 1 e 2). Um protocolo de amostragem pode e deve ser criado (como o já existente para formigas – Agosti et al., 2000), a taxonomia da maioria das subfamílias (exceto por Satyrinae) é simples ou pode vir a ser facilitada por guias locais (e.g. Uehara-Prado et al., 2005), e respostas a perturbação aparentemente são consistentes ao longo da Floresta Atlântica (Uehara-Prado et al., 2007, 2009; Fonseca et al., 2009; Pardini et al., 2009). No entanto, o uso de indicadores com maior lastro em termos de informações biológicas básicas (como taxonomia e distribuição), não são garantia de que padrões bem definidos necessariamente resultem de processos bem explicados (Cap 2). Estudos básicos sobre história natural de borboletas frugívoras ainda são raros e extremamente necessários para aperfeiçoar e sofisticar seu uso como indicadores biológicos.

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APÊNDICE 1 – Some aspects of the population ecology of the exotic amphipod, Talitroides topitotum, in an Atlantic Forest reserve in Brazil

Crustaceana 82 (2009): 241-251

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Terrestrial amphipods live in forest litter and its interface with the soil, and they shelter under leaves and in fallen trees and other pieces of wood on the ground, i.e., habitats very similar to those of terrestrial isopods (Hurley, 1968). They feed on decomposing plant matter. When established in favourable environments, some species can replace native amphipods (Costello, 1993; Alvarez et al., 2000). They are usually nocturnal, a habit that minimizes dehydration and predation by birds (Friend & Richardson, 1986). Many species take an active part in soil dynamics, increasing oxygenation rates when moving within the soil and speeding up decomposition processes (Lam & Ma, 1989; Alvarez et al., 2000; Lopes & Masunari, 2004b).

Terrestrial amphipods are able to reproduce up to two times during their life time, with a brood size of 3 or 4 eggs and a mean life span of 10 months, giving rise to a mean of 3 to 4 generations per year (Lam & Ma, 1989). The sex ratio varies seasonally and is usually biased towards females (Wenner, 1972).

Talitroides topitotum (Burt, 1934) has its origins in the tropical and subtropical regions of the Indo-Pacific (Lemos de Castro, 1972; Lopes & Masunari, 2004a), and has become a cosmopolitan tropical and temperate species (Alvarez et al., 2000). It is usually associated with the introduction of non-native plants (sympatric spread) (Alvarez et al., 2000; Cowling et al., 2004). This species is always associated with high-humidity environments (Alvarez et al., 2000; Lopes & Masunari, 2004b), occurring at altitudes ranging from 120 m to over 2400 m a.s.l. (Lam & Ma, 1989; Richardson, 1992; Alvarez et al., 2000). In Brazil, T. topitotum was introduced with young trees imported for commercial purposes (Ulian & Mendes, 1987; Lopes & Masunari, 2004a), and has probably spread via human gardening and landscaping activities. The species seems closely associated with areas that were reforested with Eucalyptus spp., a culture that covers extensive areas in Brazil (Ulian & Mendes, 1988; Lopes & Masunari, 2004b). Initial records of the presence of T. topitotum in several countries appear to be related to the introduction of exotic species of plants, as is the case in Brazil (Lemos de Castro, 1972, Lemos de Castro & Pereira, 1978), Mexico (Alvarez et al., 2000), and the United States, where other terrestrial species amphipods of have also been introduced (Visscher, 1874; Medcof, 1939; Lazo-Wasem, 1984).

We studied some aspects of the population ecology of T. topitotum in an Atlantic forest area in southeastern Brazil. Some population studies on T. topitotum were performed earlier in Hong Kong by Lam & Ma (1989), in Mexico by Alvarez et al. (2000), and in southern Brazil by Lopes & Masunari (2004a, b, c). However, although it is an alien organism and its invasion may have unknown biotic consequences, few general studies exist on the population biology of this species (Lam & Ma, 1989; Alvarez et al., 2000; Lopes & Masunari, 2004a, b, c).

Fieldwork was carried out in the Parque Estadual da Serra do Mar (Serra do Mar State Park), Núcleo Santa Virginia (NSV) (23°17'-23°24'S45°03'-45°11'W), in the state of São Paulo, Brazil. The local geomorphological relief features steep escarpments with embedded valleys, ranging from 740 to 1620 m a.s.l. (Tabarelli & Mantovani, 1999). The climate is humid, with no dry season, and the mean yearly precipitation is 2180 mm (Setzer, 1949; Tabarelli & Mantovani, 1999). In the past, the original Atlantic forest of some parts of the area that currently forms the NSV underwent slash-and-burn management and subsequent pasture plantation, while hardwood was logged in other parts. Nowadays, the area is covered by dense ombrophilic montane forest, interspersed with patches of forest in several stages of regeneration, abandoned pastures, and eucalyptus plantations (Tabarelli & Mantovani, 1999; J.P. Villani, pers. comm.).

Sampling was carried out using pitfall traps made of 500 mL plastic cups with an 8.5 cm opening, set level with the soil surface and containing 30% propylene glycol, 0.1% formaldehyde, and a few drops of detergent to break the surface tension. The traps were protected from direct rainfall and falling leaves by a circular styrofoam shield placed above each cup. They were arranged in transects of 5 traps, 2 m apart, per area. A group of 5 traps was considered a sampling unit. The pitfall traps were kept open six days per month during the sampling period.

Twelve sampling units were installed in the study area, placed at least 100 m apart. Sampling was done from November 2004 to May 2005, encompassing late spring, summer, and early autumn, a period in which terrestrial amphipods are more active due to higher temperatures (Lopes & Masunari, 2004b). After each sampling event, the collected material was sorted, preserved in 70% ethanol, and labelled. All collected material has been deposited in the Museu de Zoologia, Instituto de Biologia, UNICAMP.

The number and sex of individuals in each sample were determined in all samples. Individuals were sexed following Lopes & Masunari (2004c; females have an oostegite and males have a penis). Mature individuals were based on size following Lopes & Masunari (2004c); one individual was considered mature when its size was bigger than 4.57 mm (the size of the smaller ovigerous female in all samples). The samples were analysed under a stereo-microscope fitted with a calibrated ocular micrometer. Individuals from each sampling unit were counted in a Petri dish filled with 70% ethanol to avoid dehydration, which could affect body size. For morphometric assessment, the individuals were placed in a standard position, with legs facing right in relation to the ruler. Two measures were done: 1) head length as the linear distance from the base of the antennae to beginning of the first thoracic segment; and 2) body length, as the linear distance from the base of the antennae to the last abdominal segment before the telson (following Leite & Wakabara, 1989). The presence of eggs was recorded, and the eggs were removed from the marsupium to be counted (number of eggs per female) (Lam & Ma, 1989; Alvarez et al., 2000; Lopes & Masunari, 2004c). Samples with N > 40 were re-sampled from the Petri dishes: after having been poured into the dishes, only one-fourth of the individuals (located in a predefined sector of the dish) was measured. Throughout the study, 3,593 individuals of T. topitotum were collected, all females. Abundance varied among sampling units, from zero to 1,602 individuals. Data about size were based on a subsample of 1,533 individuals following the methods described above. Based on this subsample, 87% of all individuals were of immatures (including juvenile and non ovigerous females), with only 13% of ovigerous females.

During the study period, two population peaks occurred, one in December, and the other in February (fig. 1). A peak of abundance of ovigerous females was observed in February. Two peaks of immatures abundance were also seen, in January and April (fig. 1).

Head length was positively correlated with total length (Spearman Coefficient, rs = 0.517; t = 16.32; $\underline{P} < 0.001$; $\underline{N} = 602$). Therefore, the former measurement can be used as a size indicator for this species (fig. 2). The total body length of T. topitotum individuals ranged from 1.48 to 10.12 mm, with the modal interval between 5.00 and 5.9 mm (fig. 3). Total body length of ovigerous females ranged from 4.57 to 9.02 mm. Mean egg production was 2.4 per female. The total number of eggs was positively correlated with total body length (Spearman Coefficient, rs = 0.2982; t = 2.88; $\underline{P} = 0.005$; $\underline{N} = 87$) (fig. 4).

Interactions among rainfall, relative air humidity, and temperature largely determine the population dynamics of terrestrial amphipods, both stimulating their activity (Lopes & Masunari, 2004b), and possibly also determining variations in fecundity and development time (Lindeman, 1991). In the study area, summer is the season that merges optimum levels of many of these factors for T. topitotum, probably leading to the observed population growth at this time of year, associated with the increase in immature (juvenile and non ovigerous females) recruitment. The same pattern was described in other studies, as was the decrease in abundance in winter and spring (Lam & Ma, 1989; Alvarez et al., 2000; Gonçalves et al., 2003). If, during summer, higher abundance is related to both population growth and higher individual activity, the winter drop may be related not only to the reduction in population size, but also to migration into more favourable environments, or displacement of individuals into deeper layers of the soil where microclimate conditions are more favourable (Gonçalves et al., 2003).

The body size of the individuals in this population ranged from 1.48 to 10.12 mm. This is within the expected range for the species, upon comparison with previous studies (Biernbaum, 1980; Lam & Ma, 1989; Alvarez et al., 2000; Lopes & Masunari, 2004c). The largest individual ever recorded was 14.43 mm long (Lopes & Masunari, 2004a). Mature females, however, show a great variation among the several studies that have been performed. In Hong Kong, females begin to produce eggs when they reach a length of 5.56 mm (Lam & Ma, 1989). In Brazil, the smallest ovigerous females ranged from 4.57 mm (present study) to 7.00 mm in the south of the country (Lopes & Masunari, 2004c). This difference in the minimum size of mature female may be related to differences in several factors regarding the various regions studied, such as mean temperature, food availability, and predation (O´Hanlon & Bolger, 1997a; Gonçalves et al., 2003).

Previous studies have shown that temperature greatly influences some population parameters of amphipods (Gonçalves et al., 2003; Ingólfsson et al., 2007), and may affect the reproduction period of T. topitotum throughout its geographical range. Gonçalves et al. (2003) showed that populations of the estuarine amphipod, Talorchestia brito (Stebbing, 1891), had longer reproductive periods in warmer areas, and Ingólfsson et al. (2007) showed that temperature was the most important factor in triggering the reproductive phase in the coastal amphipod, Orchestia gammarellus (Pallas, 1766). In the present study, the recruitment period of T. topitotum was relatively short, from January to April, and comparison with other populations at different latitudes may help to clarify how temperature affects recruitment in this species.

In the present study, no males were recorded throughout the total of sampling months, but other studies on T. topitotum have detected the presence of males in varying proportions (Lam & Ma, 1989; Alvarez et al., 2000). For crustaceans in general (Wenner, 1972), and amphipods in particular, sex-ratio biases seem to be common, especially toward an excess of females (Jones & Wigham, 1993; Cardoso & Veloso, 1996; Persson, 1999; Gonçalves et al., 2003, and references therein). In the literature, the main explanations for female predominance are: (1) shorter longevity of males; in some species, the males die immediately after copulation (Hastings, 1981; Carrasco & Arcos, 1984); (2) differences in the degree of catchability between the sexes, resulting from horizontal and vertical displacement (Williams, 1995); and (3) intersexuality (Ford & Fernandes, 2005). The reasons that lead to intersexuality are still little known, and parasitism seems to be one of the most common explanations (Ginsburger-Vogel, 1991; Lindeman, 1991; O´Hanlon & Bolger, 1997a; Ford & Fernandes, 2005). In the present work, intersexuality was not investigated, and future studies will be needed for a better understanding of the factors behind this bias in sex ratio in some T. topitotum populations.

Finally, if environmental factors influence the growth, recruitment, and fluctuation levels of populations of T. topitotum, then many factors have an indirect effect on the production of offspring. The present study shows that body size is positively correlated with female fecundity. Although this association was not found in a study carried out with the same species in southern Brazil (Lopes & Masunari, 2004c), the same pattern was detected for this species by Alvarez et al. (2000) in Mexico, and by Lam & Ma (1989) in Hong Kong, as well as for Arcitalitrus dorrieni (Hunt, 1925) by O´Hanlon & Bolger (1997b) in Ireland. Lam & Ma (1989) suggested that females may benefit from delaying the reproduction process until they reach a large body size, thus increasing their reproductive success. More, and more specific, studies are needed to test this hypothesis.

Talitroides topitotum as a potential bioindicator

Though Talitroides topitotum is a cosmopolitan species, few studies of its biology exist (Lopes & Masunari, 2004b). However, some conditions that favour its establishment are known, such as soil properties (high porosity and high organic-matter content) and climate (relative air humidity above 52%, temperature gradient from 13 to 30ºC, and abundant rainfall, at least about 100 mm per month) (Ulian & Mendes, 1987; Richardson, 1992; Alvarez et al., 2000; Cowling et al., 2003; Lopes & Masunari, 2004b). There is also evidence that anthropogenic disturbance favours this species, whose presence is especially associated with non-native plants (Alvarez et al., 2000), mainly Eucalyptus spp., in Brazil (Lemos de Castro, 1972; Lopes & Masunari, 2004b). NSV offers many of these properties, including high humidity year-round and Eucalyptus spp. plantations (see Tabarelli & Mantovani, 1999), making it especially favourable for the establishment of populations of this species. The same properties are shared by a large portion of the Atlantic forest throughout the Serra do Mar, a large mountain range along coastal southeastern Brazil. In the particular case of environments that have suffered human impact, the presence of introduced plants seems especially important for the establishment of T. topitotum populations. Additionally, when there is a mosaic of natural vegetation and plantation areas, the junction of different habitats may favour the movement of individuals among them, in search of a more suitable microhabitat. The invasion of these natural areas by T. topitotum and other exotic species may have consequences for the local biota that are still unknown. The presence and abundance of terrestrial amphipods may be a powerful tool in biomonitoring activities of these mosaics (see Lawes et al., 2005), and more studies on this subject are needed in the Brazilian Atlantic Forest.

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FIGURE CAPTIONS

Fig. 1. Talitroides topitotum (Burt, 1934): variation in population abundance during the sampling period at the Parque Estadual da Serra do Mar - Núcleo Santa Virgínia: Above, total population (▲); below, immatures (see text) (■) and ovigerous females (●).

Fig. 2. Correlation between head size and body size of Talitroides topitotum (Burt, 1934) collected in the Parque Estadual da Serra do Mar – Núcleo Santa Virgínia, Brazil.

Fig. 3. Number of individuals of Talitroides topitotum (Burt, 1934) in each body-size class.

Fig. 4. Ovigerous female body size vs. number of eggs produced in Talitroides topitotum (Burt, 1934).

FIGURE 1.

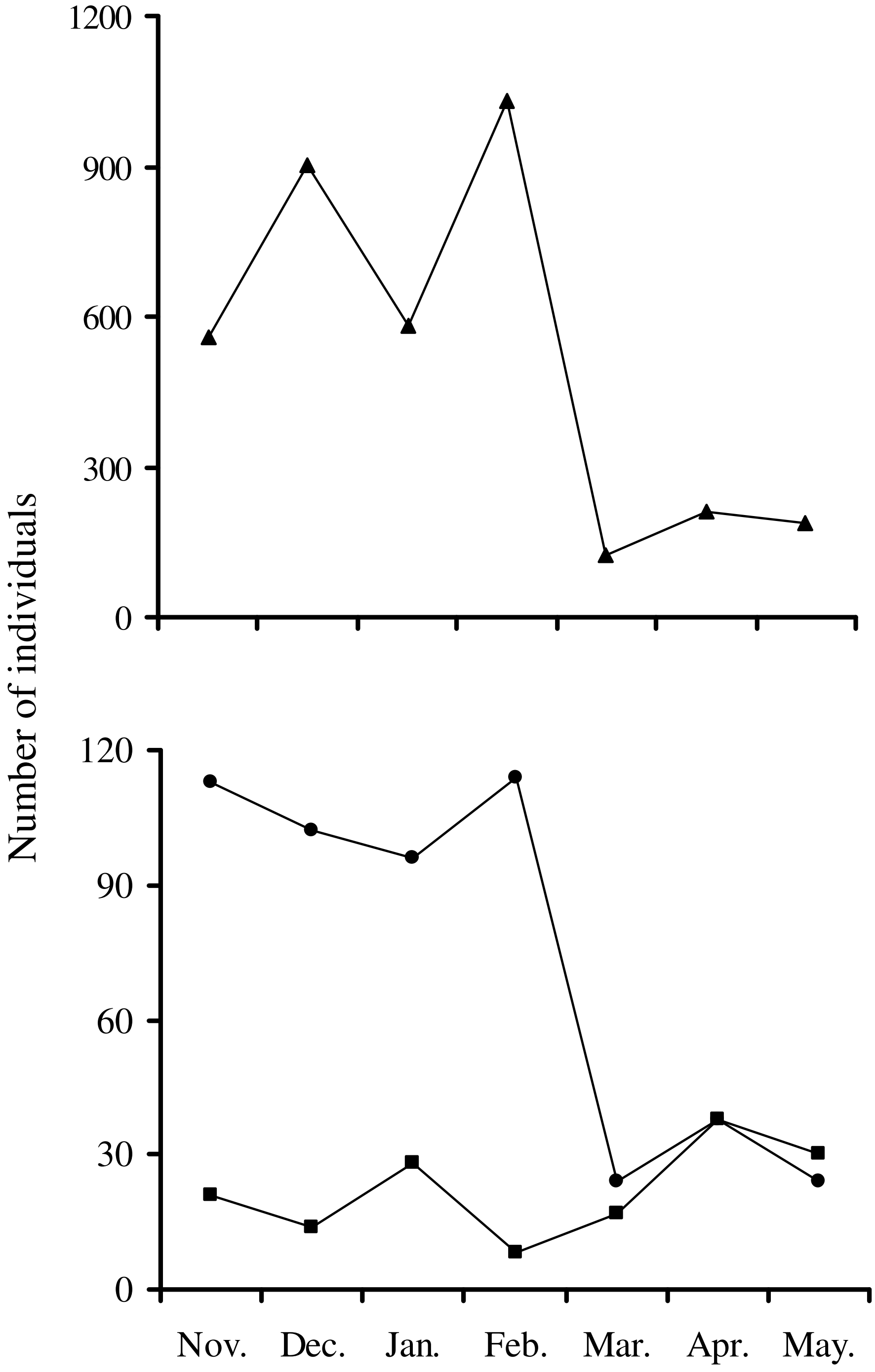

1200
900
600
300
0
Number of individuals
120
90
60
30
0
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
May.

FIGURE 2.

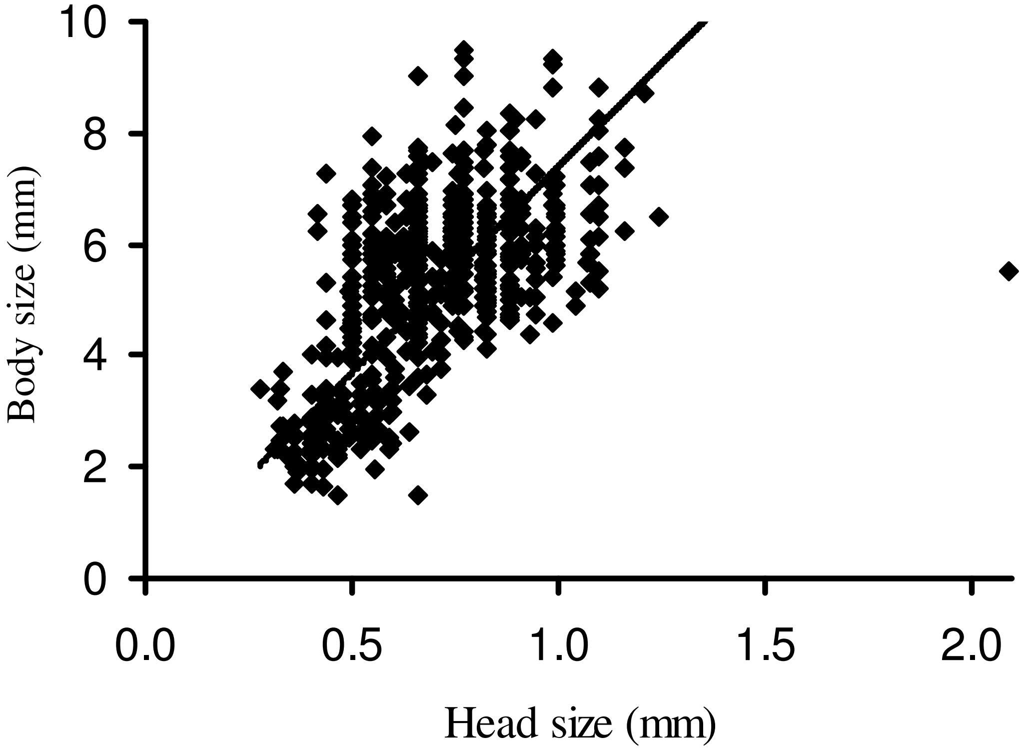


FIGURE 3.

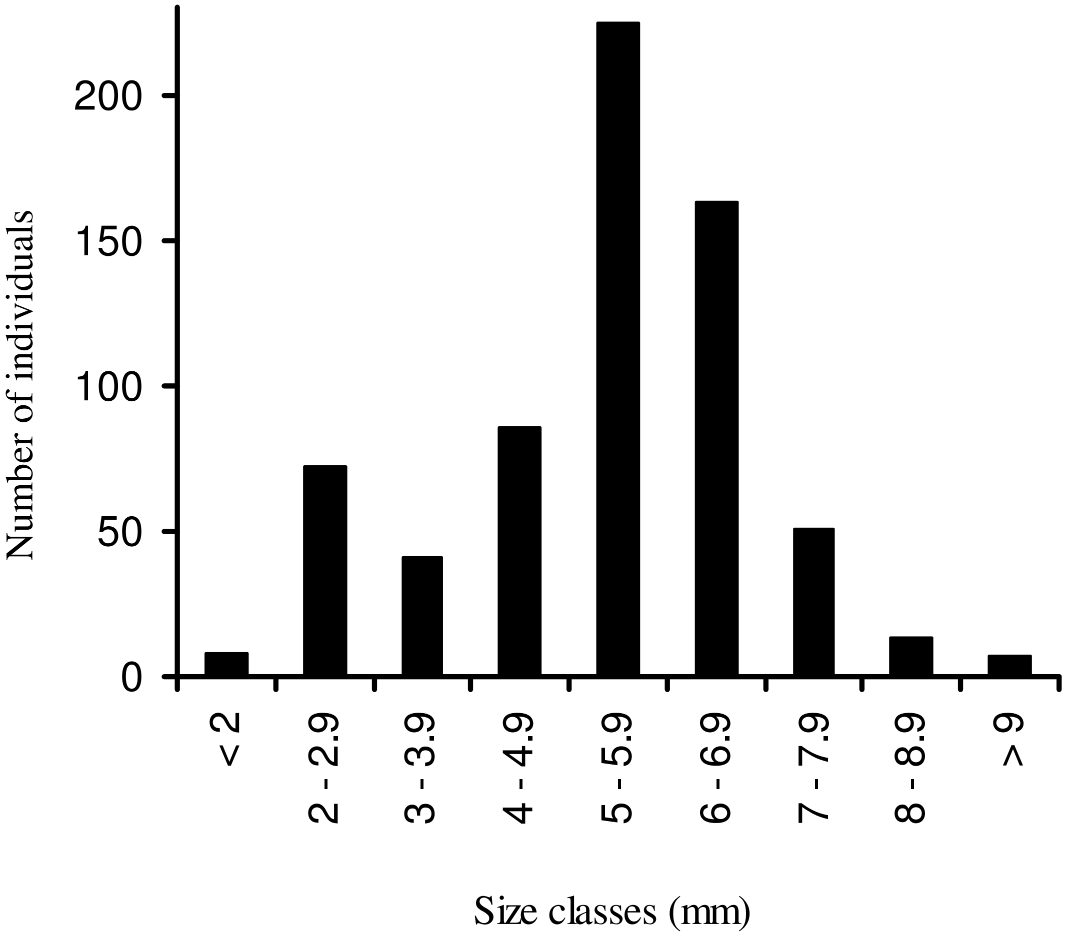
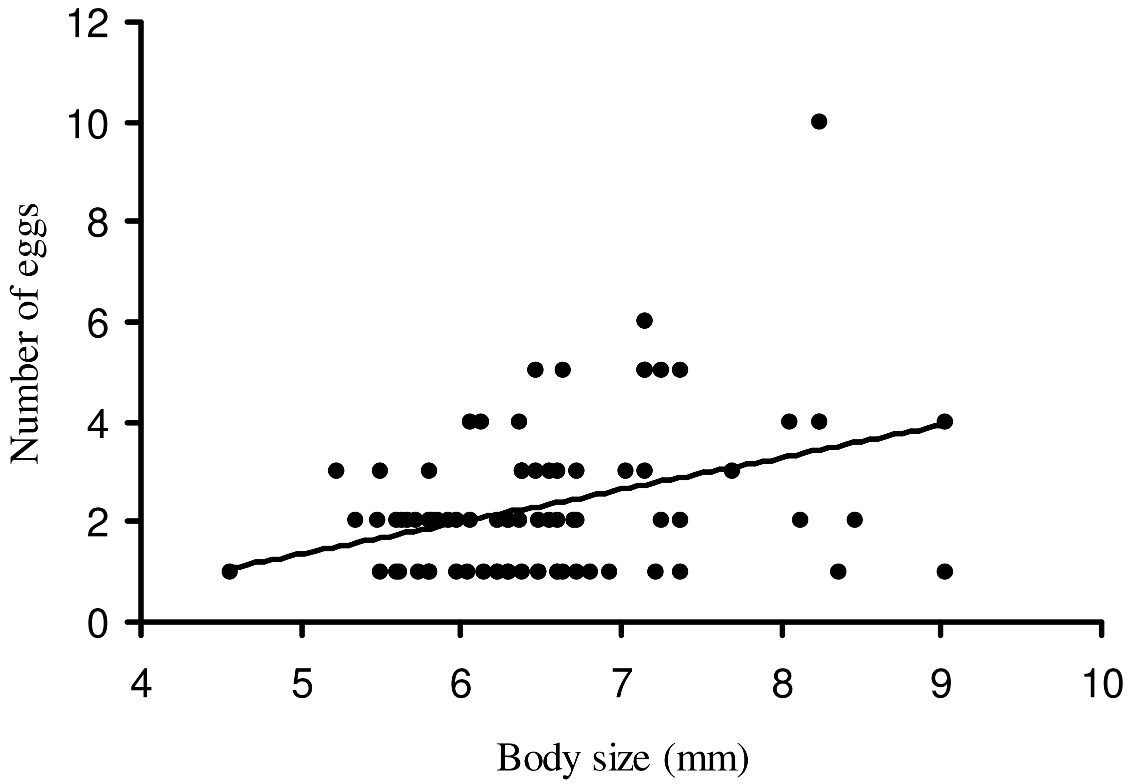

Number of individuals
0
50
100
150
200
< 2
2 - 2.9
3 - 3.9
4 - 4.9
5 - 5.9
6 - 6.9
7 - 7.9
8 - 8.9
> 9
Size classes (mm)

FIGURE 4.



APÊNDICE 2 - The effect of rainforest fragmentation on species diversity and mimicry ring composition of ithomiine butterflies

Insect Conservation and Diversity 2 (2009): 23–28

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Running title: Forest fragmentation and ithomiine butterflies

Abstract. 1. Subfamily Ithomiinae comprises about 370 species of Neotropical butterflies associated with humid forest habitats from Mexico to Northern Argentina. Adult Ithomiinae are central models in many mimicry rings throughout their range, and are assumed to have high potential as bio-indicators. Here we compare diversity and composition of Ithomiinae mimicry rings in continuous versus fragmented landscapes, and evaluate value these butterflies hold for ecological assessment and monitoring of anthropogenic disturbance. 2. Sampling was done at four sites inside a large forest block, the Morro Grande State Reserve, and in five forest fragments in a neighbor fragmented landscape. Butterflies were sampled with portable traps, baited with a fermented mixture of banana and sugar cane juice. Sampling was carried out during the period most favorable for the capture of ithomiine butterflies in south-eastern Brazil. 3. There was no difference between landscapes in species richness and diversity index, but dominance index, and the distributions of tribes and mimicry rings between them was clearly different. The higher average light intensity in the understory of fragments could explain in part the higher abundance there of mimicry patterns typical of open sunny habitats, and concomitant reduced abundance of clearwing mimicry patterns, typical of shaded habitats. These results confirm the potential of ithomiine assemblages as biological indicators of habitat quality.

Keywords: Atlantic rainforest, biological indicators, conservation, Ithomiinae

INTRODUCTION

The subfamily Ithomiinae (Lepidoptera: Nymphalidae) comprises a group of about 370 species of Neotropical butterflies distributed from Northern Argentina to Mexico (Lamas, 2004; Willmott & Freitas, 2006). Ithomiinae butterflies are usually associated with humid forest habitats, although some species can persist in small forest fragments and in urban or suburban systems (Brown & Freitas, 2003). Larvae are generally cryptic and feeds primarily on Solanaceae, with few species feeding on Apocynaceae and Gesneriaceae (Brown & Freitas, 1994; Freitas *et al.*, 1996), but the adults of all species are believed to be unpalatable and are aposematic, and are considered central models in many Neotropical butterfly mimicry rings (Brown & Benson, 1974; Beccaloni, 1997a,b).

Ithomiines were previously shown to have high potential as biological indicators for monitoring anthropogenic disturbance (Brown, 1991, 1997), and were considered good predictors of total lowland forest butterfly species richness (Beccaloni & Gaston, 1995, but see Brown & Freitas, 2000). Many species restricted to dense forests are sensitive to disturbance and pollution, and their absence from certain natural systems can be understood as a sign of anthropogenic effects (Brown & Freitas, 2000). Despite their importance and abundance in Neotropical forests, there are relatively few ecological studies focusing on Ithomiinae in comparison with their co-mimics in the Heliconiinae. Nonetheless, several recent studies have addressed ithomiine biology, chemical ecology and mimicry rings (see Brown, 1985, 1987; Beccaloni, 1997 a, b; DeVries *et al.*, 1999; Willmott & Freitas, 2006; Trigo, 2008).

Even though, ithomiine butterflies appear to be primarily nectar feeders (to obtain carbohydrates) they also visit certain Compositae and Boraginacae for pyrrolizidine alkaloids, bird droppings for nitrogen and are incidental visitors of fruit-baited butterfly traps (DeVries *et al.*, 1999; Uehara-Prado *et al.*, 2007; Trigo, 2008). Our study of ithomiines emerges from a broader study of fruit-feeding butterflies in which they are not the primary targets.

DeVries *et al.* (1999) showed that Müllerian co-mimicry associations can be measured on a fine scale in a tropical forest, and that these methods can be applied in studies on spatial and temporal organization of mimicry complexes. Since microhabitat use in ithomiines are linked with larval hostplant use (Beccaloni, 1997a) and there is evidence for microhabitat associations of different mimicry complexes (DeVries *et al.*, 1999; Willmott & Mallet, 2004) we hypothesize that mimicry rings composition could change as responses to disturbance related microhabitat modification. This study compares the diversity and the composition of Ithomiinae butterfly mimicry rings in a continuous and in a fragmented landscape, and examines whether these butterflies may be useful as a focal group in assessing and monitoring anthropogenic disturbance.

METHODS

Study area

The study area is located in the municipality of Cotia, São Paulo State, southeastern Brazil. The altitude in the study area varies from 800 to 1000 m, with climate Cwa (humid subtropical with a dry winter, Köppen, 1948). The annual mean temperature is 20.4ºC, ranging from 16.5ºC in July to 23.6ºC in February; mean annual rainfall is about 1340 mm (meteorological data for 1962-1992). The original vegetation in the region is classified as montane rainforest (Ururahy *et al.*, 1997), a constituent of the Atlantic rain forest system.

The field work was done in two distinct landscapes: in a 10 870 ha continuous forest block, the Morro Grande State Reserve (23°39′–23°50′S, 46°55′–47°01′W), mostly in advanced stages of succession and containing patches of well preserved old growth forest, and in a adjacent mosaic of forest fragments west of it. The fragmented landscape consists of a matrix mostly made up of small farms and orchards, mixed with vegetation in initial stages of regeneration (two to eight years) and reforestation with exotic eucalyptus and pine interspersed with about 35% native vegetation (data from 1:10 000 aerial photographs, April 2000) (Silva *et al.*, 2007). Additional details of the study area may be found in Uehara-Prado *et al.* (2005, 2007) and in Metzger *et al.* (2006).

Sampling procedures

Samples were collected in four independent sites within the Morro Grande State Reserve ("control" continuous forest) and five forest fragments, with ca. 14, 29, 52, 99 and 175 ha (Appendix 1). A sampling unit consisting of five portable bait traps was installed in each of the nine sites and kept in the field during periods of 12 to 14 days. The traps were disposed linearly along pre-existing trails in the understory of each site, hanged 1.8–2.2 m above the ground, with a minimum distance of 20 m between adjacent traps and at least 50 m from the forest edge. The average distance between adjacent traps did not differ between fragments and reserve (t = 0.54, P = 0.60, DF = 34). The sampling units were set at least 1400 m apart from each other (reserve: mean = 5961 m, SD = 3263.1 ; fragments: mean = 3849 m, SD = 1417.5), and the distance among sample units did not differ between landscapes (t = 1.31, P = 0.21, DF = 14).

A mixture of mashed banana with sugar cane juice, fermented for at least 48 hours, was used as attractant. The traps were checked every 48 hours, and the baits were substituted at each visit (see Uehara-Prado *et al.*, 2007 for detailed sampling procedures). Sampling was carried out six times from November 2001 to May 2002.

Analyses

The hypothesis that abundance would be equally distributed in the two landscapes was tested for species, subfamilies and mimicry rings with N > 5 individuals, through the G test with Williams' correction (Gotelli & Ellison, 2004). The same test was used to assess the species' sex ratio. Similarity between landscapes was calculated by the Sørensen qualitative index (C_S) (Magurran, 2004). Comparisons of species richness, Fisher's diversity index (α) and Berger-Parker dominance index (d) (Magurran, 2004) between landscapes were made by the bootstrapping procedure (Manly, 1991) implemented in the program PAST (Hammer *et al.*, 2001). In this procedure, data on species abundance from both landscapes were pooled and 1000 random pairs of samples taken from this pool, preserving the original abundance of both samples. For each pair, Fisher's index and Berger-Parker index were computed and the probability that the observed difference occurred by random sampling was calculated.

RESULTS

After 36 000 trap/hours, a total of 12 species and 217 individuals from six Ithomiinae tribes were captured in the bait traps. This corresponds to 48% of the total Ithomiinae diversity in the study area (25 species, A.V.L. Freitas unpublished data). Sex ratio was 1:1 in all species but *Aeria olena olena*, with 0.25 males/females (Table 1). The number of individuals collected in the fragments ($n = 152$) was higher than in the continuous forest ($n = 65$) (bootstrap $P < 0.001$).

Species richness and abundance were not stable along the sample period, with a marked peak in February (Fig. 1). The species accumulation curves had steep slopes for both landscapes, but was steeper in fragmented landscape (Fig. 2). Seven species were captured in the reserve and 11 species in the fragments (bootstrap $P = 0.067$), with six species shared by the two landscapes ($C_S = 66.7\%$) (Table 1). Fisher's α was slightly higher in the fragments ($\alpha = 2.72$) than in the continuous forest ($\alpha = 1.99$), but the two values were not significantly different (bootstrap $P = 0.318$). Berger-Parker dominance index was significantly higher in the continuous forest (Continuous forest, d = 0.539; Fragments, d = 0.421; bootstrap $P = 0.026$).

A large proportion of species in the continuous forest were of the tribe Godyridini (90.8%) while in the fragments species richness was fairly evenly distributed among tribes (G test = 84.3, $df = 4$, $P < 0.001$). When the abundance of individual ithomiine species was compared between landscapes, *Pseudoscada acilla acilla* was more abundant in the reserve, *Ithomia drymo* Hübner, *A. olena olena*, *Pseudoscada erruca, Epityches eupompe* and *Hypothyris ninonia daeta* were all more abundant in the fragments, and *Hypoleria adasa adasa* occurred at equal abundance in both landscapes (Table 1).

Most Ithomiinae sampled in this study belonged to the clear-wing mimicry ring, with 98.5% of the individuals in the continuous forest (all but one individual) and 72.4% of the individuals in the fragments (Table 1). The response of these species to forest fragmentation varied from negatively affected (*P. acilla acilla*), not affected (*H. adasa adasa*), to positively affected (*I. drymo* and *P. erruca*). Individuals in the yellow-transparent and tiger mimicry rings occurred almost exclusively in the fragmented landscape (42 of 43 butterflies) (G test = 36.5, $df = 1$, $P < 0.001$).

DISCUSSION

The temporal variation in individual abundance in the present study is similar to that observed in other ithomiine population studies in the region (Freitas, 1993, 1996; Freitas *et al.*, 2001). Additionally, the periods of maximum abundance of individuals were the ones with higher species richness, as previously recorded for Ithomiinae by Freitas (1996) and DeVries *et al.* (1999), and in other butterfly groups such as fruit-feeding butterflies (DeVries *et al.*, 1999). DeVries *et al.* (1999) propose that abundance of trapped Ithomiinae could be related to rainfall, but in the present study our sampling scheme does not permit us to test this hypothesis. The few population studies of Ithomiinae have reported male biased sex ratios (Freitas, 1993, 1996; Freitas *et al.*, 2001), while the present study showed that, for most species, males and females were sampled in equal proportions in bait traps. For several Ithomiinae species, sex ratio in the laboratory is usually 1:1 (Freitas, 1993; Freitas *et al.*, 2001, and unpublished results for 12 species), and male-biased sex ratios in field captures have been attributed to behavioral differences between sexes, especially the strong attraction of males to sources of pyrrolizidine alkaloids (Brown, 1985; Freitas, 1996; Trigo *et al.*, 1996; Trigo, 2008). The results of the present study shows that the use of fruit-baited traps may overcome this bias for some species (see also Uehara-Prado *et al.*, 2005) and could give a more realistic evaluation of sex ratios in nature.

The species richness of Ithomiinae sampled in the present study – 48% of the total richness – was higher than that recorded by DeVries *et al.* (1999), which sampled 39% of the total richness in Jatun Sacha, Ecuador with an equivalent sampling effort. It is interesting to note, however, that the sampling was taxonomically similar in both studies, capturing only species of few genera in the tribes Tithoreini (specifically the genus *Aeria*), Napeogenini, Oleriini, Dircennini and Godyridini, and no individuals of the equally abundant tribes Mechanitini and Melinaeini. This shows that, even in two unrelated biomes, the taxonomic composition of the fauna sampled by this method is equivalent, resulting in comparable results in studies of community ecology and ecological monitoring.

Apparently, the differences in taxonomic composition are related to differences in flight heights, with the species attracted by fruits being those found in the lower strata of the forest (DeVries *et al*., 1999). For example, the tiger mimicry ring has been shown to preferentially fly above 1 m (Papageorgis, 1975; Medina *et al*., 1996; Beccaloni, 1997a), perhaps as a result of host plant use and mate seeking behavior (Beccaloni, 1997a), and so, they might be less attracted to rotting fruits on the forest floor. This could explain the near absence of species in the tiger mimicry ring, which were fairly abundant in the two landscapes based on hand-netting (A.V.L. Freitas, unpublished data), but represented by only seven individuals in the present study. It should also be considered that differences in species abundance could reflect in part differences in bait preference among species, and this should be better investigated in the future.

Since microhabitat characteristics influence the distribution of species of Solanaceae in the forest understory, differences in taxonomic and mimicry ring composition could be a result of availability of host plants in a given place (Beccaloni, 1997a, b). The clear-wing species from SE Brazil (mostly in tribe Godyridini) are restricted predominantly to microhabitats with low light levels, flying below 1 m high. The higher light incidence in the forest understory due to fragmentation could explain in part the decrease in the dominance of the clearwing pattern in the fragments, and the higher contribution of mimicry patterns typical of open sunny habitats (such as the yellow transparent pattern). Although species accumulation curves were not asymptotic, the results should not change with additional sampling effort, since the main differences were due to common species in each habitat (see Table 1). It is worth noting that ithomiines are not a guild in the same sense of the fruit-feeding butterflies, and some species will always be rare in the sample due to low attraction to the bait. These species contributed to the steep slope of accumulation curves in studies like this.

The results of the present study showed that the ithomiine assemblage, as indicated by mimicry ring composition, is different between the two landscapes, and supports past assertions that these butterflies could be used as biological indicators of forest disturbance. In this study, Ithomiinae are collateral captures since the study was primarily designed to sample fruit-feeding nymphalids. However, the taxonomic consistency and differences in community structure and mimicry rings between the two landscapes demonstrated that Ithomiinae attracted by baits may be an adequate group for biological monitoring.

Ithomiines have long been proposed as good indicators of habitat integrity (Brown, 1991, 1997; Beccaloni & Gaston, 1995). However, this potential has not been demonstrated in large scale studies (Brown & Freitas, 2000, 2003; but see DeVries *et al.*, 1999 to a small scale approach). This study demonstrate that forest fragmentation affects the composition of the ithomiine mimicry rings, which are considered to be the central models for mimicry rings in the Neotropics. Beyond indicating alteration in forest structure, shifts in predominant ithomiine color patterns may impact other taxonomic groups that rely on the umbrella of protection from certain model species (Beccaloni, 1997b), thus changing the equilibrium of mimicry complexes in these habitats.

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Table 1. Mimicry rings, abundance in each landscape, and sex ratio of ithomiine butterflies species. Mimicry ring (MR) abbreviations (after Beccaloni 1997a, b; DeVries et al. 1999, in part): C = clear-wing, YT = yellow-transparent, T = tiger.

Figure 1. Species richness (black line) and mean abundance ± s.e. (gray line) of ithomiine butterflies along the sample period (November 2001 to May 2002).

Figure 2. Species accumulation curves (± sd) of ithomiine butterflies in the continuous forest (black line) and forest fragments (grey line).

Appendix 1. Size, altitude and geographical coordinates of sampled sites.

Table 1.

	Tribe	MR	Abundance		P*	Sex ratio (♂/♀)	P*
			Continuous Forest	Fragments			
Ithomia drymo	Ithomiini	C	3	64	**< 0.0001**	1.31	0.2726
Hypoleria adasa adasa	Godyridini	C	35	31	0.1636	1.00	-
Pseudoscada acilla acilla	Godyridini	C	18	1	**< 0.0001**	0.58	0.2547
Aeria olena olena	Tithoreini	YT	1	16	**0.0004**	0.25	**0.018**
Epityches eupompe	Napeogenini	YT	0	17	**< 0.0001**	1.13	0.811
Pseudoscada erruca	Godyridini	C	3	11	**0.0006**	1.33	0.5988
Hypothyris ninonia daeta	Napeogenini	T	0	7	**0.0056**	0.40	0.2655
Hypoleria lavinia proxima	Godyridini	C	3	2	-	-	-
Pteronymia carlia	Dircennini	C	2	0	-	-	-
Mcclungia cymo salonina	Godyridini	YT	0	1	-	-	-
Oleria aquata	Oleriini	C	0	1	-	-	-
Episcada hymenaea hymenaea	Dircennini	YT	0	1	-	-	-

*G-test, with Williams' correction.

Figure 1.

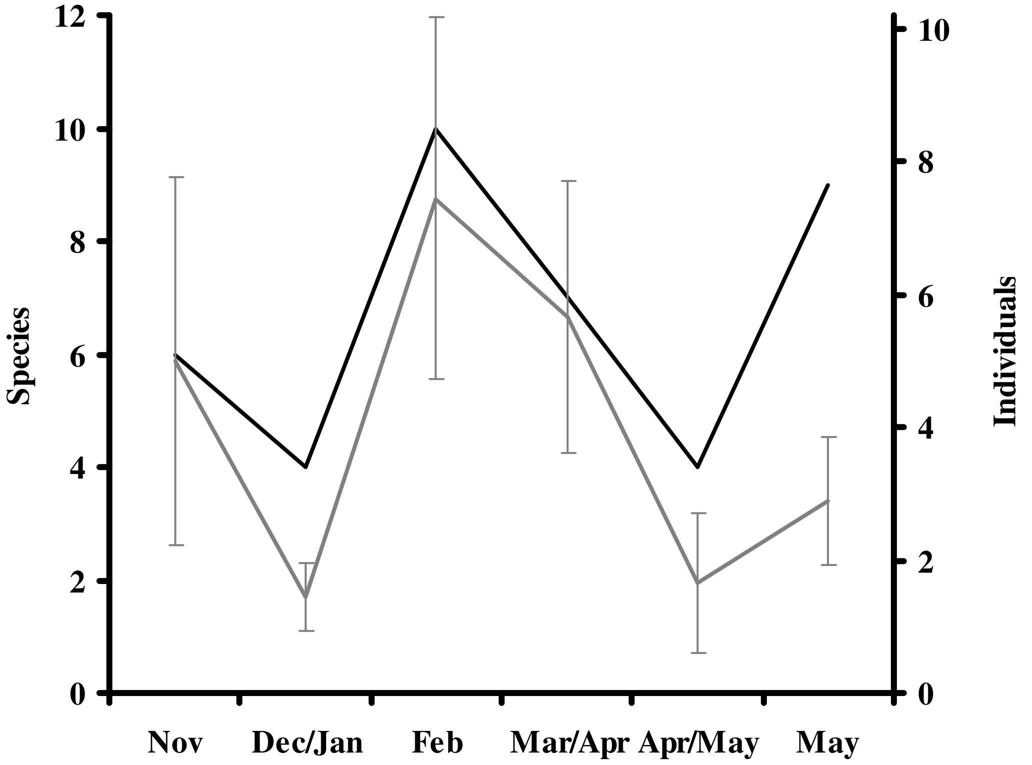
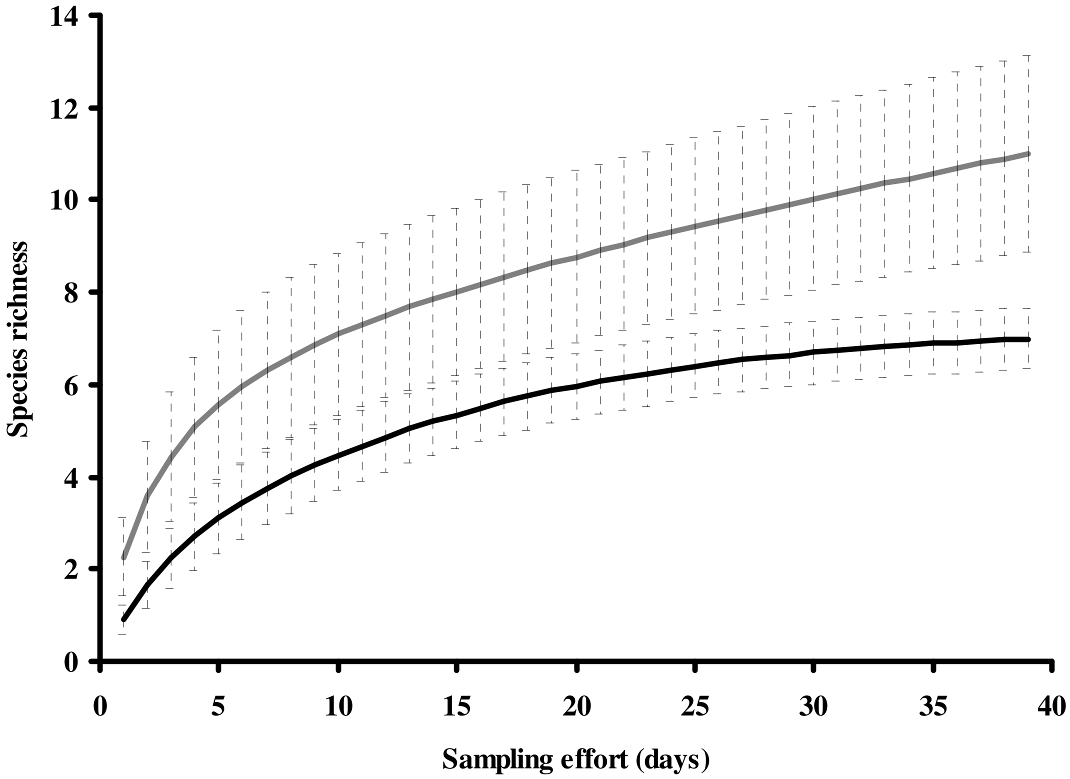

12
10
8
6
4
2
0
Species
10
8
6
4
2
0
Individuals
Nov
Dec/Jan
Feb
Mar/Apr
Apr/May
May

Figure 2


14
12
10
8
6
4
2
0
Species richness
0
5
10
15
20
25
30
35
40
Sampling effort (days)

Appendix 1.

	Site code[1]	Area	Altitude (m)	Geographical coordinates
Reserve	A	continuous[2]	890	46º 57' 38.049"W, 23º 40' 27.924"S
	B	continuous	900	46º 57' 25.066"W, 23º 41' 39.272"S
	C	continuous	920	46º 56' 43.837"W, 23º 42' 55.201"S
	D	continuous	985	47º 0'15.869"W, 23º 45'21.424"S
Fragments	E	14.00 ha	930	47º 6' 46.346"W, 23º 42' 57.339"S
	F	28.88 ha	940	47º 6' 58.213"W, 23º 43' 43.655"S
	G	52.17 ha	935	47º 3' 51.879"W, 23º 43' 36.716"S
	H	99.39 ha	930	47º 4' 58.05"W, 23º 42' 4.172"S
	I	175.10 ha	950	47º 4' 19.819"W, 23º 44' 13.395"S

[1] See Figure 1 in Uehara-Prado *et al*. (2007)

[2] Total area of the Morro Grande State Reserve: 10 870 ha