

**UNIVERSIDADE ESTADUAL DE CAMPINAS**



Danilo Bandini Ribeiro

**“EFEITOS DO CORTE SELETIVO COM IMPACTO  
REDUZIDO NA ASSEMBLEIA DE BORBOLETAS  
FRUGÍVORAS DA PLANÍCIE AMAZÔNICA”**

Este exemplar corresponde à redação final  
da tese defendida pelo(a) candidato (a)  
DANILO BANDINI RIBEIRO  
e aprovada pela Comissão Julgadora.

Tese apresentada ao Instituto de  
Biologia para obtenção do título  
de Doutor em Ecologia.

A handwritten signature in blue ink, consisting of a stylized 'A' followed by a long horizontal stroke.

ORIENTADOR: Prof. Dr. André Victor Lucci Freitas

FICHA CATALOGRÁFICA ELABORADA POR  
ROBERTA CRISTINA DAL' EVEDOVE TARTAROTTI – CRB8/7430  
BIBLIOTECA DO INSTITUTO DE BIOLOGIA - UNICAMP

R354e	<p>Ribeiro, Danilo Bandini, 1980- Efeitos do corte seletivo com impacto reduzido na assembleia de borboletas frugívoras da planície amazônica / Danilo Bandini Ribeiro. – Campinas, SP: [s.n.], 2011.</p> <p>Orientador: André Victor Lucci Freitas. Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.</p> <p>1. Mariposa. 2. Estrutura da vegetação. 3. Teoria do Escalonamento Metabólico. 4. Detectabilidade. 5. Estratificação vertical. I. Freitas, André Victor Lucci, 1971-. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.</p>
-------	---

Informações para Biblioteca Digital

**Título em Inglês:** The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil

**Palavras-chave em Inglês:**

Moths

Vegetation structure

Metabolic Scaling Theory (MST)

Detectability

Vertical stratification

**Área de concentração:** Ecologia

**Titulação:** Doutor em Ecologia

**Banca examinadora:**

André Victor Lucci Freitas [Orientador]

Thomas Michael Lewinsohn

Ronaldo Bastos Francini

Flávio Nunes Ramos

Helena Romanowski

**Data da defesa:** 08-07-2011

**Programa de Pós Graduação:** Ecologia

## Banca Examinadora

Prof. Dr. André Victor Lucci Freitas



Prof. Dr. Thomas Michael Lewinsohn



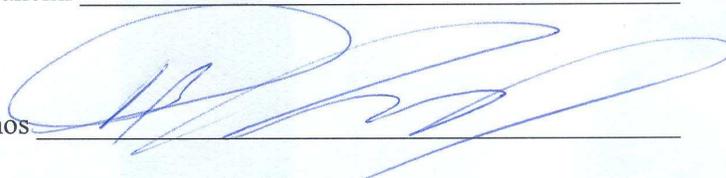
Prof. Dra. Helena Romanowski



Prof. Dr. Ronaldo Bastos Francini



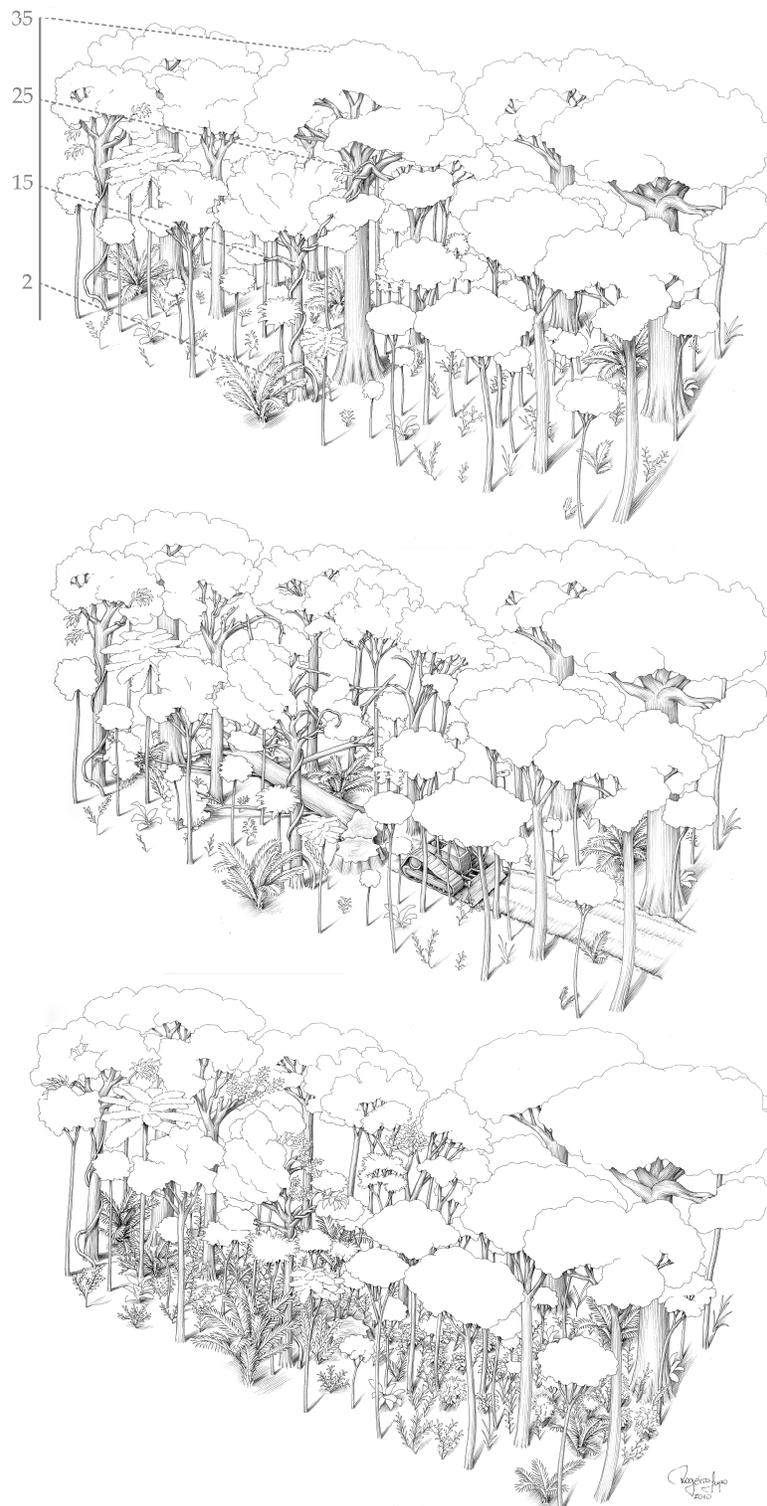
Prof. Dr. Flávio Nunes Ramos



Prof. Dr. Cristiano Agra Iserhard

Prof. Dr. Paulo Inácio K. L. Prado

Prof. Dr. Gustavo Quevedo Romero



Dedico este trabalho a minha esposa Letícia , pelo apoio incondicional e pelo carinho que foram fundamentais durante todos esses anos.

## AGRADECIMENTOS

Gostaria de agradecer a todos que contribuíram de alguma forma com o meu trabalho e especialmente a:

Prof. Keith S. Brown pela sua contribuição na formação de duas gerações de biólogos e pela sua inspiradora paixão pela Ciência.

André Vitor Lucci Freitas pela orientação e amizade durante a realização deste trabalho, que foram essenciais para a sua realização.

Ao Dr. Matthew R. Williams pela orientação e amizade durante o meu período de “Sanduíche” em Perth.

Ao assessor da Fapesp por suas valiosas colaborações durante a realização do trabalho.

Ao Prof. Dr. Marcelo Duarte e ao Prof. Dr. Martín Pareja pela leitura crítica dos manuscritos da tese.

Aos Membros da banca: Profa. Dra. Helena Piccoli Romanowski, Prof. Dr. Thomaz Michael Lewinsohn, Prof. Dr. Ronaldo Bastos Francini, Prof. Dr. Flavio Nunes Ramos e Dr. Cristiano Agra Iserhard.

Ao pessoal do Departamento de Biologia Animal: Edu, Luiza, Lucas, Marcio, Cris, Daniela, Tina e Jessie, pela amizade.

Aos meus companheiros do “Arena Bio” que caridosamente cederam suas canelas e joelhos para que eu me desestressa-se.

Aos velhos amigos Shima, Andrey, Ana e Fabiano. Aos meus pais Edelcio e Neuza, e aos meus irmãos Fábio e Sabrina, por todo apoio durante estes anos.

As pessoas que tanto me ajudaram durante minha estadia em Perth, Bruno Buzzatto, Mariana Cruz Campos, Troy, Danilo e Stephie.

Aos novos amigos Antoine, Johanna, Dario, Alescia, Monica, Martin, Jos, Tim e Carly.

A Fundação de Amparo a Pesquisa do Estado de São Paulo pela bolsa concedida (07/50896-0). A “Lepidoptera Research Foundation” pelo apoio financeiro.

A empresa Mil Madeiras pelo apoio logístico e por permitir a coleta dos dados em sua propriedade.

Ao “Department of Environment and Conservation, Western Australia” por todo o suporte durante o meu período de Doutorado “sanduíche” na Austrália.

## Índice Remissivo

RESUMO.....	1
ABSTRACT.....	3
INTRODUÇÃO GERAL.....	5
Bibliografia citada.....	9
CAPÍTULO 1 “Differences in vegetation structure caused by the Reduced Impact Logging (RIL) in Central Amazon”.....	13
Abstract.....	14
Introduction.....	15
Methods.....	17
Results.....	20
Discussion.....	21
Acknowledgments.....	24
References.....	25
Tables.....	28
Figure Captions.....	29
Figures.....	30
Appendix.....	34
CAPÍTULO 2 “The effect of Reduced-Impact Logging on Fruit-feeding butterflies in Central Amazon, Brazil”.....	35
Abstract.....	36
Introduction.....	37
Materials and Methods.....	40
Results.....	45
Discussion.....	46
Acknowledgments.....	50
References.....	51
Tables.....	56
Figure Captions.....	57
Figures.....	58
Appendix.....	62
CAPÍTULO 3. “Stratigraphic and temporal variability in the detectability of fruit-feeding butterflies and moths in tropical forest”.....	64
Abstract.....	65
Introduction.....	67
Materials and Methods.....	69
Results.....	72
Discussion.....	73
Acknowledgments.....	77
Literature Cited.....	77
Figure Captions.....	81
Figures.....	82
Appendix.....	87
CONCLUSÕES GERAIS.....	93

## **RESUMO**

A Amazônia representa mais da metade da área de todas as florestas tropicais do mundo, e vem sendo ameaçada por diversas atividades antrópicas, incluindo vários tipos de extração de madeira. O corte seletivo de impacto reduzido (em inglês “Reduced Impact Logging – RIL”) é considerado um método menos destrutivo de exploração madeireira que promove uma menor alteração na estrutura da floresta comparado com métodos convencionais. No entanto, existem poucas informações sobre os efeitos do RIL em invertebrados, incluindo borboletas. Desta forma, investigamos o efeito do RIL na estrutura da vegetação florestal e sobre as borboletas frugívoras, comparando a fauna do dossel e do sub-bosque entre uma área explorada (RIL) e uma área não explorada (controle).

Devido à pouca informação disponível sobre protocolos de amostragem para as borboletas tropicais, alguns aspectos metodológicos relativos à amostragem dos ninfalídeos frugívoros foram investigados. Analisamos como a detectabilidade varia entre diferentes espécies, habitats (Amazônia x Mata Atlântica), estratos da floresta e também qual o esforço adequado de amostragem para detectar uma certa quantidade espécies em uma determinada área, no presente estudo esta quantidade foi estabelecida como 25% do total de espécies estimado no local.

### **Implicações biológicas**

Uma floresta não explorada apresenta árvores adultas e juvenis maiores do que as de uma floresta explorada (RIL). O número de plântulas e mudas é maior na floresta explorada (RIL) e a distribuição de frequências de tamanhos (SDFslope) não foi diferente entre as áreas de RIL (-2,61) e não explorada (-2,31). A abertura do dossel foi maior na floresta não explorada, provavelmente devido a um aumento das plantas do sub-bosque na floresta RIL. A área basal e altura das árvores foram maiores na floresta não explorada.

Em relação às borboletas frugívoras, a fauna do dossel é diferente e significativamente mais rica do que a fauna do sub-bosque, mostrando que amostrar apenas o estrato mais baixo pode subestimar a diversidade de borboletas. Os efeitos do RIL foram detectados principalmente na assembleia de borboletas do sub-bosque, onde foram observadas diferenças significativas na composição de espécies entre as áreas. Os impactos do RIL, que incluem o corte de árvores, a abertura de trilhas de arraste e de estradas, são mais intensos no sub-bosque do que no dossel. Estas diferentes intensidades de impacto no

dossel e no sub-bosque podem explicar os diferentes efeitos do RIL nas borboletas presentes nesses estratos. Considerando o grande potencial das borboletas frugívoras para prever as respostas de vários outros grupos taxonômicos à perturbação da floresta na Amazônia, esperamos que padrões semelhantes sejam encontrados em outros táxons. No entanto, apesar dos efeitos detectáveis do RIL em borboletas frugívoras, não pudemos perceber espécies que foram excluídas ou que invadiram a área de RIL, os nossos resultados mostram principalmente diferenças nas abundâncias das espécies entre as áreas. Este resultado é similar ao encontrado em estudos feitos com outros *taxa* mostra que o RIL em geral não altera a diversidade de espécies podendo ser uma alternativa para preservar uma parcela significativa da fauna em áreas com este tipo de exploração. A criação de áreas protegidas na Amazônia apesar de desejável é bastante complicada e nem sempre é efetiva na preservação da cobertura vegetal, assim sendo o corte seletivo de impacto reduzido pode ser considerado uma boa alternativa para preservar borboletas frugívoras na floresta amazônica e, certamente, muitos outros táxons. Além disso, devido ao alto valor da madeira produzida neste sistema, esta poderia ser uma alternativa econômica desejável para a região.

### **Implicações metodológicas**

Quase todas as borboletas e mariposas amostrados no presente estudo foram mais facilmente amostradas em um estrato específico (dossel ou sub-bosque). No presente estudo, mesmo as espécies mais comuns do dossel raramente foram amostradas no sub-bosque. Assim, fazer uso de um protocolo de amostragem que não utiliza armadilhas em ambos os estratos irá aumentar os erros de detecção de muitas borboletas e pode conduzir a inferências incorretas sobre a riqueza e diversidade em uma determinada área. As diferenças na detectabilidade entre os meses no conjunto de dados da Amazônia mostraram que mesmo quando as borboletas são amostradas durante o período do ano com maior probabilidade de captura, existem diferenças importantes na detectabilidade entre os meses. A baixa detectabilidade e a grande variação entre os estratos e meses nos levam a propor que, para borboletas frugívoras, a amostragem deve ser feita na época correta e em florestas altas os diferentes estratos devem ser considerados de modo a reduzir os erros de detecção e possíveis vieses nos resultados. O esforço amostral mínimo para a detecção de 25% das espécies presentes nas florestas tropicais é de 130 armadilhas / dia para a Mata Atlântica e

510 dias para Amazônia Central. Além disso, a amostragem deve ser feita com réplicas temporais em um curto espaço de tempo para aumentar o poder de interpretação dos dados coletados.

#### ABSTRACT

The Amazon region represents more than half of the area of all tropical forests in the world, and has been threatened by many anthropogenic activities, including several kinds of timber harvesting. Reduced-Impact Logging (RIL) is considered a less destructive method of timber harvesting that promotes a smaller change in forest structure than conventional logging. However, there is a general lack of information about the effects of RIL on Amazonian invertebrates, including butterflies. We therefore investigated the effect of RIL on forest vegetation structure and on fruit-feeding butterflies by comparing their distribution on canopy and understory between an area under RIL and a control area without RIL.

Because of the relative lack of information about sampling protocols for tropical butterflies, some methodological aspects of fruit-feeding Nymphalidae sampling were investigated. We analyzed the variation in detectability among species, habitats (Amazon x Atlantic Forest), layers and the adequate sampling effort need for detect an specific amount of species in a given area were analyzed in this thesis, in the present study this amount was established as 25% of the total estimated species richness. **Biological implications**

An unlogged forest has bigger juveniles and adult trees, and less seedlings and saplings than a RIL forest, and the Size Frequency Distribution (SDF) slope was not different from those of logged (-2.61) and unlogged (-2.31) areas. The canopy openness was greater in the unlogged forest, probably due to an increase of understory plants in the RIL forest. The basal area was wider and the height was taller in unlogged forest trees. In relation to the fruit-feeding butterflies, the canopy fauna is different and significantly richer than the understory fauna, showing that sampling only the lower strata underestimates the diversity of fruit-feeding butterflies. The effects of RIL were mainly detected in the understory butterfly assemblage, as significant differences were observed in species composition within this stratum. Effects of the RIL regime, which include tree cutting, skid trails and road openings, are stronger in the understory than in the canopy, explaining the reported differences. Despite the detectable effects of RIL on the composition of fruit-feeding

butterfly's assemblages the overall diversity was not affected, this pattern is very similar for many other *taxa* indicating that a noticeable part of the diversity of many *taxa* could be preserved in areas under RIL management. Given the problems of creating protected areas in the Amazon, RIL is a good alternatives to preserve fruit-feeding butterflies and surely many other *taxa*, and it might be a desirable economic alternative for the region.

### **Methodological implications**

Almost all butterflies and moths sampled in the present study were more readily trapped in one specific stratum. Indeed, in the present study, even the most common canopy species were rarely sampled in the understory. Thus, using a sampling protocol that does not locate traps in both layers will increase the imperfect detection of many butterflies and could lead to incorrect inferences about the richness and diversity in a given area. The differences in detectability between months in the Amazon dataset showed that even with an experimental design planned for sampling butterflies during the period that enhances capture probability, there are important differences in butterfly detectability across months. The low detectability and great variation among strata and months in fruit-feeding butterflies lead us to assume that sampling designs must address sampling effort to the correct season and strata reducing imperfect detections and biases in the results. The minimal sampling effort for detecting 25% of the species present in tropical forests is 130 trap/days in Atlantic Forest and 510 days in Central Amazon.

Additionally, such sampling should use temporal replication over a short period to improve the interpretability of the data collected.

## INTRODUÇÃO GERAL

A Amazônia compreende 60% de toda a cobertura de florestas tropicais do mundo, e só considerando-se os últimos 30 anos a área desmatada foi maior do que a soma dos primeiros 450 anos de colonização européia nos Neotrópicos (Lovejoy 1999). Entre agosto de 2009 e agosto de 2010, um total de 6.451 km<sup>2</sup> de mata foi destruído na região amazônica (com base nos dados do Projeto PRODES - (INPE 2010). Além da área que sofreu corte raso outros 13.301 km<sup>2</sup> sofreram atividades de extração de madeira de diferentes intensidades (Sist 2000; INPE 2010).

A extração de Madeira é a maior causa de degradação da Floresta amazônica, e pode ser realizada, sem corte raso, de duas maneiras: 1) Corte seletivo convencional, onde a maior parte das árvores de alto valor econômico são removidas sem planejamento prévio, sem se preocupar com o impacto na floresta remanescente e 2) Corte seletivo de impacto reduzido (em inglês “Reduced-Impact logging” - RIL) onde apenas poucos indivíduos são retirados por hectare utilizando técnicas que visam diminuir o impacto das atividades de corte na vegetação remanescente como o corte direcional das árvores e a retirada das lianas para evitar que outras árvores sejam afetadas na hora da queda e o planejamento prévio das trilhas que serão abertas para a extração das toras com intuito de diminuir o impacto na vegetação remanescente e a quantidade de solo compactado pelos tratores que arrastam as toras (Sist 2000; Laurance *et al.* 2005).

O corte seletivo convencional afeta diversos grupos de organismos (Johns 1985; Azevedo-Ramos, Carvalho Jr & do Amaral 2006) e altera a estrutura da floresta remanescente (Gerwing 2002). Esta atividade causa mudanças físicas no ambiente aumentando a compactação do solo e a incidência de luz no sub-bosque (Rab 1994; Whitman, Brokaw & Hagan 1997), levando a um aumento nas taxas de erosão e na

deposição de sedimentos no solo (Megahan & Kidd 1972). Este processo também aumenta a temperatura de riachos e causa assoreamento dos mesmos (Holtby 1988). Outro importante efeito do corte seletivo convencional é o aumento da incidência de incêndios florestais (Gerwing 2002). Todos estes fatores alteram a estrutura da vegetação na floresta (Johns, Barreto & Uhl. 1996; Aström *et al.* 2005), as taxas de recrutamento das árvores, a sobrevivência de plântulas (Whitman, Brokaw & Hagan 1997) e o fluxo gênico entre populações de árvores (Murawski, Gunatilleke & Bawa 1994), e conseqüentemente, afeta os níveis tróficos superiores (veja a seguir).

A fauna de vertebrados é afetada diretamente pela extração de madeira através da degradação do habitat causada por esse processo (Johns 1992; Kavanagh & Stanton 2005), e indiretamente pelo aumento da caça ilegal em decorrência desta atividade (Wilkie, Sidle & Boundzanga 1992). A comunidade de peixes pode ser afetada (Wright & Flecker 2004), fazendo com que as populações de espécies de valor econômico sejam alteradas (Nislow & Lowe 2006). A estrutura, composição e diversidade de diversos grupos de vertebrados são também afetadas pelo corte seletivo convencional; esses efeitos foram registrados em aves (Lambert 1992; Thiollay 1992; Marsden 1998; Robinson & Robinson 1999; Vidaurre, Pacheco & Roldán 2006), pequenos mamíferos (Penn *et al.* 2003; Simard & Fryxell 2003), grandes felinos (Dyke *et al.* 1986), primatas (Chapman *et al.* 2000) e lagartos (Penn *et al.* 2003).

O corte seletivo convencional pode afetar os invertebrados presentes em todos os ambientes da floresta, alterando a fauna dos riachos (Davies *et al.* 2005, Herlihy *et al.* 2005, Nislow & Lowe 2006), do solo (Seastedt & Crossley 1981, Holloway *et al.* 1991, Grove 2002, Baker *et al.* 2006) e as comunidades de insetos que vivem sobre a vegetação (Holloway *et al.* 1992, DeVries 1997, Devy & Davidar 2001, Dumbrell & Hill 2005,

Forkner *et al.* 2006).

Tendo em vista o grande impacto do corte seletivo convencional na floresta, o corte seletivo de impacto reduzido (“Reduced-impact logging” – RIL) foi proposto com o objetivo principal de reduzir substancialmente os distúrbios causados ao solo e à vegetação remanescente em comparação com a extração convencional. Esta técnica (RIL) é principalmente baseada no planejamento e controle de todas as operações de colheita (Embrapa-CIFOR 2000). As mudanças causadas pelo RIL em alguns grupos de vertebrados e artrópodes parecem ser pequenas (Lewis 2001; Azevedo-Ramos, Carvalho Jr & do Amaral 2006) porém, ainda não se sabe o seu efeito sobre as borboletas frugívoras na amazônia.

Dentre os grupos de invertebrados que são afetados pelo corte seletivo de impacto reduzido, as borboletas podem ser consideradas um ótimo modelo de estudo. Devido ao seu tamanho relativamente grande, sua aparência colorida, facilidade de amostragem e taxonomia bem resolvida, as borboletas estão entre os grupos de insetos mais bem conhecidos, mostrando um grande potencial para elucidar os padrões de diversidade e para estudos de conservação de insetos e de seus habitats (Brown 1991; DeVries, Murray & Lande 1997).

Borboletas são normalmente divididas em duas guildas, segundo os hábitos alimentares dos adultos (DeVries 1987): as nectarívoras, que se alimentam de néctar durante a vida adulta e incluem a maior parte das espécies das famílias Papilionidae, Lycaenidae, Riodinidae, e alguns grupos de Nymphalidae (DeVries, Murray & Lande 1997), e as frugívoras, que obtêm a maior parte de seus nutrientes de frutas fermentadas e seiva de plantas. Na região neotropical esta guilda é composta principalmente pela linhagem satiróide de Nymphalidae (segundo (Wahlberg *et al.* 2009), compreendendo as

subfamílias Satyrinae (tribos Brassolini, Morphini e Satyrini), Charaxinae e Biblidinae, e a tribo Coeini (Nymphalinae).

Borboletas frugívoras são facilmente amostradas com armadilhas contendo iscas de frutas fermentadas, o que possibilita que duas ou mais áreas sejam amostradas simultaneamente com o mesmo esforço amostral. Além disto, este grupo compreende entre 50 e 75% da riqueza total dos Nymphalidae Neotropicais (DeVries 1987; Brown 2005) e sua diversidade esta correlacionada com a diversidade total de borboletas e aves (Brown & Freitas 2000; Schulze, Linsenmaier & Fiedler 2001; Horner-Devine *et al.* 2003). Borboletas frugívoras são consideradas boas preditoras das respostas de vários grupos de organismos à perturbação como alguns artrópodes, vertebrados, árvores e lianas (Barlow *et al.* 2007b; Gardner *et al.* 2007).

A amostragem de borboletas frugívoras oferece muitas vantagens, porém não resolve completamente o problema da detectabilidade (*sensu* MacKenzie *et al.* 2002). Poucas espécies são consistentemente detectadas quando presentes, e a não detecção de uma espécie não implica que a mesma esteja ausente (MacKenzie *et al.* 2002). Falsas ausências acontecem quando uma espécie está presente mas passa despercebida, o que leva a elaboração de listas de espécies incompletas e a subestimativa da distribuição geográfica de uma espécie (Pellet 2008). Esta é uma questão importante para os *taxa* amplamente utilizados como indicadores ambientais como é o caso das borboletas, pois inferências enviesadas podem estender o erro a outros grupos taxonômicos de interesse (Thomas 2005; Barlow *et al.* 2007a). Conhecer o esforço amostral adequado para elaboração de listas de espécies é importante para evitar conclusões errôneas e assegurar inferências corretas sobre

os grupos estudados (Dorazio *et al.* 2006; Kery & Plattner 2007; Kery *et al.* 2009; Longcore *et al.* 2010).

O uso de armadilhas com iscas pode evitar o problema da influência do pesquisador na detectabilidade, problema comum em transectos com redes entomológicas (Kery & Plattner 2007; Schlicht, Swengel & Swengel 2009), e a detecção enviesada de espécies mais ativas ou conspícuas (Dennis *et al.* 2006; Zheng *et al.* 2007). Estas armadilhas também permitem a captura de mariposas frugívoras, que raramente são estudadas. Porém, uma questão ainda não resolvida quando utilizamos este método é como a detectabilidade varia entre diferentes espécies e habitats e qual o esforço amostral necessário para amostrar de maneira adequada a assembleia de lepidópteros frugívoros em uma determinada área.

Assim sendo, esta tese se propõe a responder três perguntas principais:

- 1- Quais são as diferenças na estrutura da vegetação de uma floresta que sofreu corte seletivo de impacto reduzido quando comparada a uma floresta que nunca foi explorada?
- 2- Como as borboletas frugívoras são afetadas pelo corte seletivo de baixo impacto?
- 3- Como a detectabilidade varia entre diferentes espécies de mariposas e borboletas frugívoras em diferentes ambientes?

## **BIBLIOGRAFIA CITADA**

- Aström, M., Dynesius, M., Hylander, K. & Nilsson, C. (2005) Effects of slash harvest on bryophytes and vascular plants in Southern Boreal Forest clear-cuts. *Journal of Applied Ecology*, **42**, 1194-1202.
- Azevedo-Ramos, C., Carvalho Jr, O. & do Amaral, B.D. (2006) Short-term effects of reduced-impact logging on eastern Amazon fauna. *Forest Ecology and Management*, **232**, 26-35.
- Barlow, J., Gardner, T.A., Araujo, I.S., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Leite, R.N., Lo-Man-Hung, N.F., Malcolm,

- J.R., Martins, M.B., Mestre, L.A.M., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, L., Ribeiro-Junior, M.A., Motta, C.d.S., Silva, M.N.F.d. & Peres, C.A. (2007a) Quantifying the biodiversity value of tropical primary, secondary and plantation forests. *Proceedings of the National Academy of Science of the United States of America*, **104**, 18555-18560.
- Barlow, J., Overal, W.L., Araujo, I.S., Gardner, T.A. & Peres, C.A. (2007b) The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *Journal of Applied Ecology*, **44**, 1001-1012.
- Brown, K.S. (1991) Conservation of the Neotropical environments: insects as indicators. *The Conservation of Insects and their Habitats* (eds N.M. Collins & J.A. Thomas), pp. 350-404. Academic Press, San Diego.
- Brown, K.S. (2005) Geologic, evolutionary, and ecological bases of the diversification of neotropical butterflies: Implications for conservation. *Tropical Rainforest: Past, Present, and Future* (eds C.W. Dick & G. Moritz), pp. 166-201. The University of Chicago Press, Chicago.
- Brown, K.S. & Freitas, A.V.L. (2000) Atlantic forest butterflies: Indicators for Landscape Conservation. *Biotropica*, **32**, 934-956.
- Chapman, C.A., Balcomb, S.R., Gillespie, T., Skorupa, J. & Struhsaker, T.T. (2000) Longterm effects of logging on African primate communities: A 28 year comparison from Kibale National Park, Uganda. *Conservation Biology*, **14**, 207-217.
- Dennis, R.L.H., Shreeve, T.G., Isaac, N.J.B., Roy, D.B., Hardy, P.B., Fox, R. & Asher, J. (2006) The effects of visual apparency on bias in butterfly recording and monitoring. *Biological Conservation*, **128**, 486-492.
- DeVries, P.J. (1987) *The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, and Nymphalidae*. Princeton University Press, Princeton.
- DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, **62**, 343-364.
- Dorazio, R.M., Royle, J.A., Soderstrom, B. & Glimskar, A. (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, **87**, 842-854.
- Dyke, F.G., Brocke, R.H., Shaw, H.G., Ackerman, B.B., Hemker, T.P. & Lindzey, F.G. (1986) Reactions of mountain lions to logging and human activity. *Journal of Wildlife Management*, **50**, 94-102.
- Embrapa-CIFOR, P. (2000) *Diretrizes técnicas para a exploração de impacto reduzido em operações florestais de terra firme na Amazonia brasileira*. . CIFOR, Belem.
- Gardner, T.A., Barlow, J., Araujo, I.S., Avila-Pires, T.C.S., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernández, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santas, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Gunior, M.A., Silva, M.N.F.d., Motta, C.d.S. & Peres, C. (2007) The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters*, **11**, 139-150.
- Gerwing, J.J. (2002) Degradation of forests through logging and fire in the eastern Brazilian Amazon. *Forest Ecology and Management*, **157**, 131-150.

- Holtby, L.B. (1988) Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the Coho salmon (*Oncorhynchus kisutch*) *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 502-515.
- Horner-Devine, M.C., Daily, G.C., Ehrlich, P.R. & Boggs, C.L. (2003) Countryside biogeography of tropical butterflies. *Conservation Biology*, **17**, 168-177.
- INPE (2010) MAPEAMENTO DA DEGRADAÇÃO FLORESTAL NA AMAZÔNIA BRASILEIRA (ed. I.N.d.P. Espaciais).
- Johns, A.D. (1985) Selective logging and wildlife conservation in tropical rain-forest: problems and recommendations. . *Biological Conservation*, **31**, 355-375.
- Johns, A.D. (1992) Vertebrate responses to selective logging: implications for the design of logging systems. *Philosophical Transactions: Biological Sciences*, **335**, 437-442.
- Johns, J.S., Barreto, P. & Uhl., C. (1996) Logging damage during planned and unplanned logging operations in the eastern Amazon. *Forest Ecology and Management*, **89**, 59-77.
- Kavanagh, R.P. & Stanton, M.A. (2005) Vertebrate species assemblages and species sensitivity to logging in the forests of north-eastern New South Wales *Forest Ecology and Management*, **209**, 309-341.
- Kery, M. & Plattner, M. (2007) Species richness estimation and determinants of species detectability in butterfly monitoring programmes. *Ecological Entomology*, **32**, 53-61.
- Kery, M., Royle, J.A., Plattner, M. & Dorazio, R.M. (2009) Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, **90**, 1279-1290.
- Lambert, F.R. (1992) The consequences of selective logging for lowlands forest bird. *Philosophical Transactions of the Royal Society of London B*, **335**, 443-457.
- Laurance, W.F., Bergen, S., Cochrane, M.A., Fearnside, P.M., Delamônica, P., d'Angelo, S., Barber, C. & Fernandes, T. (2005) The future of the Amazon. *Tropical Rainforest: Past, Present, and Future*. (eds E. Bermingham, C.W. Dick & G. Moritz), pp. 583-609. The University of Chicago Press, Chicago.
- Lewis, O.T. (2001) Effect of experimental selective logging on tropical butterflies. *Conservation Biology*, **15**, 389-400.
- Longcore, T., Lam, C.S., Kobernus, P., Polk, E. & Wilson, J.P. (2010) Extracting useful data from imperfect monitoring schemes: endangered butterflies at San Bruno Mountain, San Mateo County, California (1982-2000) and implications for habitat management. *Journal of Insect Conservation*, **14**, 335-346.
- Lovejoy, T.E. (1999) Preface. *Biological Conservation*, **91**, 100.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy when detection probabilities are less than one. *Ecology*, **83**, 2248-2255.
- Marsden, S.J. (1998) Changes in bird abundance following selective logging on Seram, Indonesia. *Conservation Biology*, **12**, 605-611.
- Megahan, W.F. & Kidd, W.J. (1972) Effects of logging and logging roads on erosion and sediment deposition from steep terrain. *Journal of Forestry*, **70**, 136-141.
- Murawski, D.A., Gunatilleke, I.A.U.N. & Bawa, K.S. (1994) The Effects of Selective Logging on Inbreeding in *Shorea megistophylla* (Dipterocarpaceae) from Sri Lanka. *Conservation Biology*, **8**, 997-1002.

- Nislow, K.H. & Lowe, W.H. (2006) Influences of logging history and riparian forest characteristics on macroinvertebrates and brook trout (*Salvelinus fontinalis*) in headwater streams (New Hampshire, U.S.A.). *Freshwater Biology*, **51**, 388-397.
- Pellet, J. (2008) Seasonal variation in detectability of butterflies surveyed with Pollard walks *Journal of Insect Behaviour*, **12**, 155-162.
- Penn, A.M., Sherwin, W.B., Lunney, D. & Banks, P.B. (2003) The effects of a low-intensity fire on small mammals and lizards in a logged, burnt forest. *Wildlife Research*, **30**, 477-486.
- Rab, M.A. (1994) Changes in physical properties of a soil associated with logging of *Eucalyptus regnans* forest in southeastern Australia. *Forest Ecology and Management*, **70**, 215-229.
- Robinson, W.D. & Robinson, S.K. (1999) Effects of selective logging on forest bird populations in a fragmented landscape. **13**, 58-66.
- Schlicht, D., Swengel, A. & Swengel, S. (2009) Meta-analysis of survey data to assess trends of prairie butterflies in Minnesota, USA during 1979-2005. *Journal of Insect Conservation*, **13**, 429-447.
- Schulze, C.H., Linsenmaier, K.E. & Fiedler, K. (2001) Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology*, **153**, 133-152.
- Simard, J.R. & Fryxell, J.M. (2003) Effects of selective logging on terrestrial small mammals and arthropods. *Canadian Journal of Zoology*, **81**, 1318-1326.
- Sist, P. (2000) Reduced-impact logging in the tropics. Objectives, principles and impacts. *International forestry review*, **2**, 3-10.
- Thiollay, J.M. (1992) Influence of selective logging on bird species diversity in Guianan Rain Forest. *Conservation Biology*, **6**, 294-302.
- Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 339-357.
- Vidaurre, M., Pacheco, L.F. & Roldán, A.I. (2006) Composition and abundance of birds in Andean alder (*Alnus acuminata*) patches with past and present harvest in Bolivia. *Biological Conservation*, **132**, 12-21.
- Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V.L. & Brower, A.V.Z. (2009) Nymphalid butterflies diversify following near demise at the cretaceous/tertiary boundary. *Proceedings of the Royal Society B*, **276**, 4295-4302.
- Whitman, A.A., Brokaw, N.V.L. & Hagan, J.M. (1997) Forest damage caused by selection logging of mahogany (*Swietenia macrophylla*) in northern Belize. *Forest Ecology and Management*, **92**, 87-96.
- Wilkie, D.S., Sidle, J.G. & Boundzanga, G.C. (1992) Mechanized logging, market hunting, and a bank loan in Congo. *Conservation Biology*, **6**, 570-580.
- Wright, J.P. & Flecker, A.S. (2004) Deforesting the riverscape: the effects of wood on fish diversity in a Venezuelan piedmont stream. *Biological Conservation*, **120**, 439-447.
- Zheng, C., Ovaskainen, O., Saastamoinen, M. & Hanski, I. (2007) Age-dependent survival analyzed with Bayesian models of mark-recapture data. *Ecology Letters*, **88**, 1970-1976.

# Differences in vegetation structure caused by the Reduced Impact Logging (RIL) in Central Amazon

Danilo B. Ribeiro<sup>1</sup>; Leticia C. Garcia<sup>2</sup>

<sup>1</sup> Programa de Pós-Graduação em Ecologia. Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas. CP 6109, 13083-970 Campinas, São Paulo State, Brazil, tel. +5519 -3521-6386. <sup>1</sup>.

<sup>2</sup> Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas. Brazil; Laboratório de Ecologia e Restauração Florestal, Escola Superior de Agricultura “Luiz de Queiroz” – ESALQ, Universidade de São Paulo – USP.

<sup>1</sup>Corresponding author; e-mail: [biodbr@yahoo.com.br](mailto:biodbr@yahoo.com.br)

**ABSTRACT**

A less impacting alternative to conventional logging and clear cutting, known as Reduced Impact Logging (RIL), has been proposed for the Brazilian Amazon. However, it is important to understand better how this strategy affects forest vegetation structure.

Therefore, we analyzed the differences between vegetation traits and the Size Frequency Distribution (SDF) of the trees (DBH>10cm) of a RIL forest versus an unlogged forest. An unlogged forest has higher juveniles and adult trees, wider basal area, and smaller seedling and sapling densities than a RIL forest. The SDF slope was not different between RIL (-2.61) and unlogged (-2.31) areas. The canopy openness was greater in the unlogged forest (12%), probably due to an increase of understory plants in the RIL forest (11%). RIL forest 3 years after exploitation keeps some structure traits of the original forest such as a similar density of trees, juveniles and herbs and near values of canopy coverage. The simple measures used in the present study are able to detect differences in vegetation structure and could be a useful tool to analyze other forest impacts. Therefore, even if the RIL changes some vegetation traits in the forest, it could preserve some aspects of the original forest structure. It possibly will be a low impact alternative for Amazon economic exploitation.

**Keywords:** Brazil; Forest Certification; Metabolic Scaling Theory; Selective Logging; Treefall Gaps; Tropical Wet Forest.

## INTRODUCTION

At present, large areas of primary forest in the tropical Americas are being logged at an increasing rate (Rice et al., 2001). This unsustainable economic practice, also called conventional logging, often involves the swift cutting of a limited number of highly valued species with no investment in regeneration (Rice et al., 2001). Aside from this, little attention has been given to the condition of the remaining vegetation, which includes a large number of damaged trees (Nepstad et al., 2001; Rice et al., 2001). This practice often precedes deforestation to make way for fields of crops and cattle pastures in an old practice usually called “slash and burn” (Zarin et al., 2007). As a result, conventional logging reduces future timber production and may be the first step in the deforestation process in tropical forests (Uhl & Buschbacher, 1985; Veríssimo et al., 1995; Nepstad et al., 2001; Laurance et al., 2005). At present, there is little understanding of the extent or the impact of selective logging throughout the tropical forests of the world, including the Amazon Basin (Asner et al., 2005).

In Brazil, 85% of Amazon wood comes from illegal timber harvesting (Zarin et al., 2007; FSC, 2009), and in 2008, 11,968 km<sup>2</sup> of this biome were completely cleared, beyond more 24,932 km<sup>2</sup> suffering some kind of logging activities (INPE, 2010). However, in view of the growing concern about deforestation and its consequences on the global environment, several timber harvesting companies are looking for certifications of sustainable exploitation. According to the Forest Stewardship Council (FSC, 2009), an international non-profit forest certification and labeling system, the total FSC certificated Brazilian forest area consists of only 0.01% of the total Brazilian Amazon. The number of companies selling certified wood has recently increased as a result of the rising demand for

certificated wood and its higher value in the international market (up to 15% higher than non-certified wood).

Certified lumber mills are required to use a policy of “Reduced Impact Logging” (RIL), a less impacting alternative to traditional logging activities (Vidal, Viana & Batista, 2002; Zarin et al., 2007; Putz et al., 2008). The techniques applied in RIL, also referred to as low-impact logging, aim to reduce the impact of wood extraction in the forest and involve cutting climbers, planning skid trails and limiting the number of the trees extracted per hectare.

RIL is certainly a less impacting alternative to traditional unplanned logging and clear cutting, and Brazilian law suggests a thirty year cutting cycle of exploitation, which should be enough to allow the forest to regenerate by natural processes. However, some authors suggest that thirty years is too short time to guarantee forest recovery, since RIL reduces seed availability, changes population densities and affects gene flow in several tree species (Silva et al., 1995; Lobo et al., 2007; Kukkonen et al., 2008; Peña-Claros et al., 2008).

In this context, the objective of the present study was to investigate what differences in forest structure there are between a pristine area and RIL areas in the Brazilian Amazon. As measures of vegetation structure, we used the size and density of forest plants, canopy openness and the size-frequency distribution of trees. According to West et al. (2009), the size-frequency distribution (SFD) of trees in an undisturbed forest can be predicted by the Metabolic Scaling Theory. The observed deviations of this expected distribution could be used as measures of disturbance (Enquist, West & Brown, 2009). In this way, we expected to find differences in SDF and vegetation measures (size and density of forest plants, canopy openness) between RIL and unlogged areas.

## METHODS

### STUDY SITE

The study site is located in the Amazon River Basin, Itacoatiara Municipality, Amazon State, Brazil (located at 2°53'39" S and 58°42'58" W, Fig.1). The altitude is *ca.* 18 m above sea level and the climate is hot, rainy and humid, without dry season, the average mean temperature of 26°C and the average annual rainfall of about 2,250 mm (MME, 1983). In the present study, we compared the vegetation structure of a primary forest with an area that was logged tree years before the beginning of this study (hereafter called unlogged forest and RIL forest, respectively). Both areas are within a continuum of forest but separated from each other by 25 km (Fig. 1).

This study was conducted in an upland forest, which is commonly more open than other Amazon vegetations, with greater spacing among trees and not subject to flooding. There are many rare plant species and no clear dominance of any single species (Rizzini, Coimbra Filho & A., 1988). The most common commercial species are Abiurana vermelha (*Pouteria* spp.), Cupiuba (*Goupia glabra*), Acariquara (*Minquartia guianensis*), Louro gamela (*Nectandra rubra*), Castanharana (*Lecythis prancei*), Uchi torrado (*Sacoglottis guianensis*), Arura vermelho (*Iryanthera grandis*) and Massaranduba (*Manilkara huberi*) (Wellhöfer, 2002).

### MANAGEMENT SYSTEM

The company owns several areas of wood extraction based on the Celos Management System described by De Graaf and Poels (1990) and has an unlogged forest of 7,500 hectares with no extraction. The low-impact standard operation is based on an inventory that selects trees with more than 50 cm DBH (Diameter at Breast Height) from among 70

valuable species. A system of roads and skill trails is implemented, and trees are cut using directional felling practices. Around 15-20 m<sup>3</sup> of roundwood were extracted per hectare (with a maximum of six trees extracted per hectare) during the first rotation cycle, which lasted 30 years. The trees that were cut are then locally processed providing employment opportunities and other services to the local community, and the products are sold to the USA, Europe and Asia.

#### MEASURES OF VEGETATION STRUCTURE

One hundred sampling points were marked, with 50 located in the logged and 50 in the unlogged forest. The points sampled were disposed in a 10 km “U” transect (Appendix I), ignoring topography, and comprising a representative range of variation in forest structure within each habitat. The points sampled were located within five blocks 900 m apart along the track. The sampling method used at each point was the “point centered quarter method”. The sampling points were separated from each other by 100 m and were 10 m apart from the track used to access the areas. Each section around the point was split into four 90° quarters, and the nearest tree in each quarter with a diameter at breast height (DBH) greater than 10 cm was measured with a total of 200 adult trees per area. We recorded the distance from the point to the tree, the DBH and an estimate of the stem and total height. The DBH was used to calculate the basal area of trees. At each point, a quadrant (1x1 m) was established where we counted the number of seedlings and saplings (seedlings = 16-35 cm; saplings = 36-200 cm, adapted from Environmental Canada, 2004), the number, height and DBH of Juveniles (>200 cm in height and <10 cm DBH) and abundance of herbaceous plants.

## CANOPY COVERAGE

To measure the canopy openness, a hemispheric fisheye lens was used. The hemispherical fisheye photographs (hemiphotographs) were taken with a camera at 100 cm above the ground at the same locations as the vegetation samples. The hemiphotographs were analyzed using the Gap Light Analyzer 2.0 computer software (Frazer, Canham & Lertzman, 1999). I

## DATA ANALYSES

Analyses were conducted by grouping the samples by areas (RIL and unlogged). We used the Mann-Whitney non-parametric test to analyze the differences between logged and unlogged for number of herbaceous plants, number of seedlings and saplings, number of juvenile individuals, DBH, average distance from the point centered quarter to the nearest tree, stem and total height of understory and canopy individuals. We performed a logit transformation ( $\log(y/1-y)$ ) (Zar, 1999; Warton & Hui, 2011) in the data of canopy openness before perform a one-way Anova test between areas.

To test how samples are distributed in an ordination space, a Correspondence Analysis (CA) was performed using all variables (vegetation structure measures and canopy openness). Before undergoing this analysis, all variables were range transformed. Analysis of similarities (ANOSIM) was conducted to compare vegetation traits between RIL and Unlogged areas using  $\chi^2$  distance by Past software (Hammer, Harper & Ryan, 2001).

## SIZE DISTRIBUTION FREQUENCY

According to Enquist et al. (2009), the size distribution frequency of trees in a forest without disturbance can be predicted by the Metabolic Scaling Theory (MST). The MST predicts that, following an exponential curve, the slope ( $\alpha$ ) of the size distribution frequency curve should be -2 in a pristine forest, and deviations from this slope could be used as measures of disturbance. In this way, we calculated the slope of the size distribution frequency curve in the RIL and Unlogged areas using the method of Maximum Likelihood with the formula presented by Clauset et al. (2007):

$$\hat{\alpha} = 1 + n \left[ \sum_{i=1}^n \ln \frac{x_i}{x_{\min}} \right]^{-1}$$

where  $x_i$ ,  $i = 1 \dots n$  are the observed values of  $x$  such that  $x_i \geq x_{\min}$  and  $x$  is the stem radii of the trees measured. To analyze if the slopes are significantly different, we calculated the 95% Confidence Interval according to Clark et al. (1999) and verified the overlap between them.

## RESULTS

The density of seedlings (16 to 35cm of height) and saplings (36 to 200 cm) were greater in the RIL forest than in Unlogged area (seedlings –  $Z = 2.41$ ;  $P = 0.01$ ; saplings  $Z = 1.89$ ;  $P = 0.058$ ) (Figure 2). The density of juvenile individuals was not significantly different between sites ( $Z = 0.48$ ;  $P = 0.31$ ); however, they were significantly higher ( $Z = 2.71$ ;  $P = 0.007$ ) and wider ( $Z = 2.50$ ;  $P = 0.01$ ) in the unlogged forest (Table I, Figure 2).

Density of adult trees was similar between areas ( $Z = 0.61$ ;  $P = 0.53$ ), but basal area and tree height were both significantly greater in the unlogged forest than RIL area ( $Z =$

2.18;  $P = 0.03$ ;  $Z = 3.84$ ;  $P = 0.0001$ , respectively) (Fig. 2). Average stem height was significantly higher in the unlogged forest ( $Z = 4.07$ ;  $P < 0.01$ ) (Table 1). Finally, the canopy was significantly more open in the unlogged forest ( $12.06 \pm 2.2$  %) than in the RIL forest ( $11.07 \pm 2.13$  %) ( $F = 5.41$ ;  $P = 0.02$ ) (Figure 2).

There was a great overlap between the SDF slopes of RIL and Unlogged forests. The slope of the size distribution frequency curve for the RIL area was -2.61 with a 95% confidence interval between -2.40 and -2.86; and for the unlogged area it was -2.37 with a 95% confidence interval between -2.20 and -2.58 (Figure 4).

Comparisons of the pattern in vegetation structure measures and canopy openness of the RIL and unlogged forests showed a large overlap among the samples examined by the Correspondence Analysis (Figure 3). The first three axes explained 80 percent of the total variation. Despite the samples have been superimposed in the Correspondence Analysis, RIL and Unlogged samples were significant different in the ANOSIM test ( $R = 0.023$ ;  $P = 0.03$ ).

## DISCUSSION

There was a significant difference in the vegetation structure between the RIL and unlogged forests. The basal area was wider and the trees were taller in the unlogged forest, as a possible consequence of the management system that removes the tallest and largest trees. Additionally, this procedure effectively decreases the density of the largest and tallest individuals in the logged area, because these trees usually belong to the emergent strata.

Reduction in mean basal area and tree height was reported in several areas that underwent timber harvest (see Veríssimo et al., 1995; Vidal, Viana & Batista, 2002; Sist & Ferreira, 2007; Zarin et al., 2007), and this pattern can be observed even a decade after RIL

activities (Silva et al., 1995; Carvalho, Silva & Lopes, 2004). After logging, the new recruitment seedlings and saplings increased their density probably due an increase of light availability. A similar result was found by Felton et al. (2006) in the Bolivian Amazon. D'Oliveira & Braz (2006) reported a reduction of juveniles (DBH 5 - 10 cm) after RIL in the Brazilian Amazon, and Macedo & Arderson (1993) detected a great decrease of seedlings in the Amazon floodplain after conventional logging activities. These results showed that there is a wide variety of responses to logging due to management techniques and vegetation type. More studies are needed to determine the effect of RIL in the Brazilian Amazon.

In our study, the canopy openness of the RIL area was smaller than that in the unlogged area, probably because cutting the biggest trees opens gaps and promotes the growth of the lower strata (Fig. 2). According to Thiollay (1997), the structure of the upland Amazon forest is composed by seven strata: low (< 2 m) and mid (2 - 14 m) understory, upper understory and lower canopy (15 - 24 m), upper canopy (25 - 35 m) and emergent trees (> 35 m), with the lower strata growing mainly in gaps left after large trees fell (de Graaf, Poels & Van Rompaey, 1999). Species of the lower strata, that had their growth limited by low levels of radiation before logging, are benefitted greatly from the removal of emergent trees due to the immediately increased light availability.

Canopy openness values change as a result of elapsed time after RIL and in face of RIL intensity. For instance, Sist & Ferreira (2007), in a study reporting the immediate effect (three months later) of RIL in two transects in the Eastern Amazon forest, found mean values of canopy openness higher than in unlogged areas. This could be explained as a result of the short interval after tree removal in that study, where three months were not enough to allow significant growth of the lower strata as we found in the present study. On

the other hand, several additional studies also reported higher values of canopy openness in logged areas compared with unlogged areas (Silva et al., 1995; Webb, 1997; Pereira et al., 2002). However these sites suffered a more intense logging ( $70\text{m}^3 \text{ha}^{-1} - 12 \text{trees ha}^{-1}$ ) (Silva et al., 1995; Webb, 1997) compared with those in the present study ( $\sim 20\text{m}^3 \text{ha}^{-1} - 6 \text{trees ha}^{-1}$ ). In another forest with similar logging intensity (Pereira et al., 2002), the unlogged forest had a canopy substantially closer (3% of canopy openness) (Pereira et al., 2002) than the present studied sites ( $\sim 11\%$ ). Hence, the variation in the RIL techniques and in the forest structure before logging prevents us to generalize the effect of the RIL in this vegetation trait.

The SDF slopes of the unlogged and RIL areas were different from the -2 predicted for an undisturbed forest by the Metabolic Scaling Theory (MST). These different slopes, even found in the present studied unlogged pristine area, could reveal that the predictions of this theory are not broad enough to describe the Size Distribution Frequency of trees in Amazon forest. Additionally, despite the visible differences in SDF of unlogged and RIL sites (Fig. 4), the SDF slope of both sites were not significant different. This result suggests that the SDF measure don't have enough power to be used in comparisons between forests under small disturbance managements such as RIL system.

The present study has demonstrated that RIL caused significant effects on several vegetation traits and forest structure such as in the canopy openness, in an increasing number of seedlings and saplings, and a decrease by 47% of the tree basal area ( $\text{DBH} < 10\text{cm}$ ). Nevertheless, after 3 years old of exploitation, the RIL forest has a similar density of trees, juveniles and herbs and near values of canopy coverage. So, the RIL forest keeps some structure traits of the original forest and maybe after the 30 years proposed by Brazilian laws the forest would be recovered. More studies about the RIL influence on

forest structure will be required in order to clarify this exploitation age effect. In view of the high rates of destruction in the Brazilian Amazon (Zarin et al., 2007; Putz et al., 2008), RIL is yet an alternative to maintain many traits of the forest structure similar to an unlogged area. Therefore, even if the RIL changes some vegetation traits in the forest, it is still a good option as an economic activity in Amazon that does not change the vegetation cover. We believe that RIL probably helps at least some part of the local biota to be preserved. Whether some actions like gap enrichment (Schulze, 2008) or the further explored woods and other silviculture practices (Zarin et al., 2007; Forshed et al., 2008; Peña-Claros et al., 2008) are adopted in RIL areas, in the future, we could maintain several areas of sustainable forest management (Sist & Ferreira, 2007) that will keep the Amazon vegetation cover. We found significant differences between the vegetation structure of a three-year-old RIL forest and an unlogged forest, and this methodology could be a useful tool to analyze impacts of logging in the forest. Finally, we highlight that it is important to study other RIL forests in order to investigate whether the outputs observed in the present studied sites will be similar to forests with different RIL activity backgrounds and exploitation ages.

## **ACKNOWLEDGEMENTS**

This research was supported by the Fapesp (grant #07/50896-0 and #07/50885-8) and the Lepidoptera Research Foundation. We express our sincere acknowledge to Dr. Sérgio Gandolfi, who lent the lens and tripod, and to Dr. Thomas Lewinsohn, who lent the camera. We also thank Dr. Brian Enquist for providing the literature about Metabolic Scaling Theory. Comments on early versions of the manuscript were provided by Dr. André V.L. Freitas, Dr. Martín Pareja, Dr. Flávio A.M. Santos and Dr. Flávio Nunes Ramos, Dr.

Thomas Lewinsohn and Dr. Ricardo R. Rodrigues. We thank Rogério Lupo for preparing detailed illustrations.

## REFERENCES

- Asner, G. P., D. E. Knapp, E. N. Broadbent, P. J. C. Oliveira, M. Keller & J. N. Silva, 2005. Selective Logging in the Brazilian Amazon. *Science*, 310: 480-481.
- Carvalho, J. O. P., J. N. M. Silva & J. C. A. Lopes, 2004. Growth rate of a terra firme rain forest in Brazilian Amazonia over an eight-year period in response to logging. *Acta Amazonica*, 34: 209-217.
- Clark, R. M., S. J. D. Cox & G. M. Laslett, 1999. Generalizations of power-law distributions applicable to sampled fault-trace length: Model choice, parameter estimation and caveats. *Geophysical Journal International*, 136: 357-372.
- Clauset, A., C. R. Shalizi & M. E. J. Newman, 2007 Power-law distributions in empirical data. *Physics*.
- D'Oliveira, M. V. N. & E. M. Braz., 2006. Forest dynamics study of the managed forest of the PC Peixoto Communit forest management project in western Amazon. *Acta Amazonica*, 36: 177-182.
- de Graaf, N. R. & R. L. H. Poels 1990. The Celos Management System: a polycyclic method for sustained timber production in South American rain forest. pages 116-127 in A. B. Anderson (eds). *Alternatives to deforestation: steps towards sustainable use of the Amazon rain forest*. Columbia University Press, New York.
- de Graaf, N. R., R. L. H. Poels & R. S. A. R. Van Rompaey, 1999. Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. *Forest Ecology and Management*, 124: 123-135.
- Enquist, B. J., G. B. West & J. H. Brown, 2009. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences USA*, 106: 7046-7051.
- Environmental Canada, C. F. S. (2004). "Terrestrial Monitoring Protocol: Regeneration and Sapling Survey." 2007, from <http://www.ec.gc.ca/Publications/A6D9405D-2A2F-4B1D-9572-0552DFB384DC/TerrestrialMonitoringProtocolRegenerationAndSaplingSurvey.pdf>
- Forshed, O., A. Karlsson, F. J. & C. J., 2008. Stand development after two modes of selective logging and pre-felling climber cutting in a dipterocarp rainforest in Sabah, Malaysia. *Forest Ecology and Management*, 255: 993-1001.
- Frazer, G. W., C. D. Canham & K. P. Lertzman, 1999. *Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from truecolour fisheye photographs, users manual and program documentation*. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- FSC. (2009). "Forest Stewardship Council ", 2009, from [www.fsc.org](http://www.fsc.org).
- Hammer, O., D. A. T. Harper & P. D. Ryan, 2001 Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4.

- INPE, 2010. Mapeamento da degradação florestal na amazônia brasileira I. N. d. P. Espaciais.
- Kukkonen, M., H. Rita, S. Hohnwald & A. Nygren, 2008. Treefall gaps of certified, conventionally managed and natural forests as regeneration sites for Neotropical timber trees in northern Honduras. *Forest Ecology and Management*, 255: 2163-2176.
- Laurance, W. F., S. Bergen, M. A. Cochrane, P. M. Fearnside, P. Delamônica, S. d'Angelo, C. Barber & T. Fernandes 2005. The future of the Amazon. pages 583-609 in E. Bermingham, C. W. Dick & G. Moritz (eds). *Tropical Rainforest: Past, Present, and Future*. The University of Chicago Press, Chicago.
- Lobo, J., G. Barrantes, M. Castillo, R. Quesada, T. Maldonado, E. J. Fuchs, S. Solís & M. Quesada, 2007. Effects of selective logging on the abundance, regeneration and short-term survival of *Caryocar costaricense* (Caryocaceae) and *Peltogyne purpurea* (Caesalpinaceae), two endemic timber species of southern Central America. *Forest Ecology and Management*, 245: 88-95.
- Macedo, D. S. & A. B. Anderson, 1993. Early ecological changes associated with logging in an Amazonian floodplain. *Biotropica*, 25: 151-163.
- MME, 1983. Ministério das Minas e Energia. Projeto Radam Brasil. Programa de Integração Nacional. Levantamento de Recursos Naturais. Publication Division, Rio de Janeiro.
- Nepstad, D., G. Carvalho, A. C. Barros, A. Alencar, J. P. Capobianco, J. Bishop, P. Moutinho, P. Lefebvre & U. L. Silva Jr, 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. *Forest Ecology and Management*: 395-407.
- Peña-Claros, M., T. S. Fredericksen, A. Alarcón, G. M. Blate, U. Choque, C. Leño, J. C. Licona, B. Mostacedo, W. Pariona, Z. Villegas & F. E. Putz, 2008. Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, 256: 1458-1467.
- Pereira, R., J. Zweede, G. P. Asner & M. Keller, 2002. Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. *Forest Ecology and Management*, 168: 77-89.
- Putz, F. E., P. Sist, T. Fredericksen & D. Dykstra, 2008. Reduced-impact logging: Challenges and opportunities. *Forest Ecology and Management*, 256: 1427-1433.
- Rice, R. E., C. A. Sugal, S. M. Ratay & G. A. Fonseca, 2001. Sustainable forest management: A review of conventional wisdom. *Advances in Applied Biodiversity Science*: 1-29.
- Rizzini, C. T., A. F. Coimbra Filho & H. A., 1988. *Ecosistemas brasileiros*. Index Editora, Rio de Janeiro.
- Schulze, M., 2008. Technical and financial analysis of enrichment planting in logging gaps as a potential component of forest management in the eastern Amazon. *Forest Ecology and Management*, 255: 866-879.
- Silva, J. N. M., J. O. P. d. Carvalho, J. C. A. Lopes, B. F. d. Almeida, D. H. M. Costa, L. C. d. Oliveira, J. K. Vanclay & J. P. Skovsgaard, 1995. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. *Forest Ecology and Management*, 71: 267-274.
- Sist, P. & F. N. Ferreira, 2007. Sustainability of reduced-impact logging in the Eastern Amazon. *Forest Ecology and Management*, 243: 199-209.

- Thiollay, J. M., 1997. Disturbance, selective logging and bird diversity: a neotropical forest study. *Biodiversity and Conservation*, 6: 1155-1173.
- Uhl, C. & R. Buschbacher, 1985. A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the eastern Amazon. *Biotropica*, 17: 265-268.
- Veríssimo, A., P. Barreto, R. Tarifa & C. Uhl, 1995. Extraction of a high-value natural resource in Amazonia. The case of Mahogany. *Forest Ecology and Management*, 72: 39-60.
- Vidal, E., V. M. Viana & J. L. F. Batista, 2002. Regrowth of a tropical rain forest in Eastern Amazonia three years after planned and unplanned logging. *Scientia Forestalis*, 61: 133-143.
- Warton, D. I. & F. K. C. Hui, 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92: 3-10.
- Webb, E. L., 1997. Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of northeast Costa Rica. *Forest Ecology and Management*, 95: 117-129.
- Wellhöfer, S., 2002. Environmentally sound forest harvesting in Brazil Assessment regeneration and environmental impacts four years after harvesting. Food and Agricultural Organization of the United Nations (FAO), Rome.
- West, G. B., B. J. Enquist & J. H. Brown, 2009. A general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences USA*, 106: 7040-7045.
- Zar, J. H., 1999. *Biostatistical analysis*. Prentice Hall, Bergen.
- Zarin, D. J., M. D. Schulze, E. Vidal & M. Lentini, 2007. Beyond reaping the first harvest: Management objectives for timber production in the Brazilian Amazon. *Conservation Biology*, 21: 916-925.

**TABLE I.** Comparison between vegetation traits of a forest three years after a reduced impact logging and an unlogged forest in the Brazilian Amazon (Itacoatiara Municipality, Amazonas State). The values in the second and third columns are mean  $\pm$  standard deviation of each vegetation trait. Values in bold are significantly different in the Mann-Whitney U test.

	<b>Logged</b>	<b>Unlogged</b>	<b><i>P</i></b>
<b>Canopy openness (%)*</b>	<b>11.07 <math>\pm</math> 2.13</b>	<b>12.06 <math>\pm</math> 2.2</b>	<b>&lt;0.01</b>
<b>Herbaceous density (n.m<sup>-2</sup>)</b>	1.96 $\pm$ 5.19	1.96 $\pm$ 5.14	ns
<b>Seedling (height 16-35 cm) density (n.m<sup>-2</sup>)</b>	<b>4.14 <math>\pm</math> 3.08</b>	<b>2.96 <math>\pm</math> 3.63</b>	<b>0.01</b>
<b>Sapling (height 36-200 cm) density (n.m<sup>-2</sup>)</b>	<b>2.78 <math>\pm</math> 2.46</b>	<b>1.92 <math>\pm</math> 1.86</b>	<b>0.058</b>
<b>Juvenile (&gt;200 cm in height and &lt;10 cm DBH)</b>			
<b>Density (n.m<sup>-2</sup>)</b>	0.56 $\pm$ 0.31	0.57 $\pm$ 0.78	ns
<b>DBH (cm)</b>	<b>2.44 <math>\pm</math> 0.97</b>	<b>3.26 <math>\pm</math> 2.18</b>	<b>&lt;0.001</b>
<b>Height (m)</b>	<b>4.01 <math>\pm</math> 0.70</b>	<b>5.85 <math>\pm</math> 4.19</b>	<b>0.01</b>
<b>Adult trees</b>			
<b>Basal area (cm<sup>2</sup>)</b>	<b>444 <math>\pm</math> 611</b>	<b>703 <math>\pm</math> 1213</b>	<b>0.04</b>
<b>DBH (cm)</b>	<b>20.79 <math>\pm</math> 11.59</b>	<b>24.77 <math>\pm</math> 16.94</b>	<b>0.03</b>
<b>Total height (m)</b>	<b>12.88 <math>\pm</math> 3.89</b>	<b>14.87 <math>\pm</math> 5.51</b>	<b>&lt;0.001</b>
<b>Stem height (m)</b>	<b>9.01 <math>\pm</math> 3.66</b>	<b>11.09 <math>\pm</math> 5.13</b>	<b>&lt;0.001</b>
<b>Average distance (m)</b>	3.80 $\pm$ 2.13	3.66 $\pm$ 2.02	ns
<b>Density (trees.ha<sup>-1</sup>)</b>	693	747	ns

\* Data of canopy openness was logit transformed before perform the one-way Anova test.

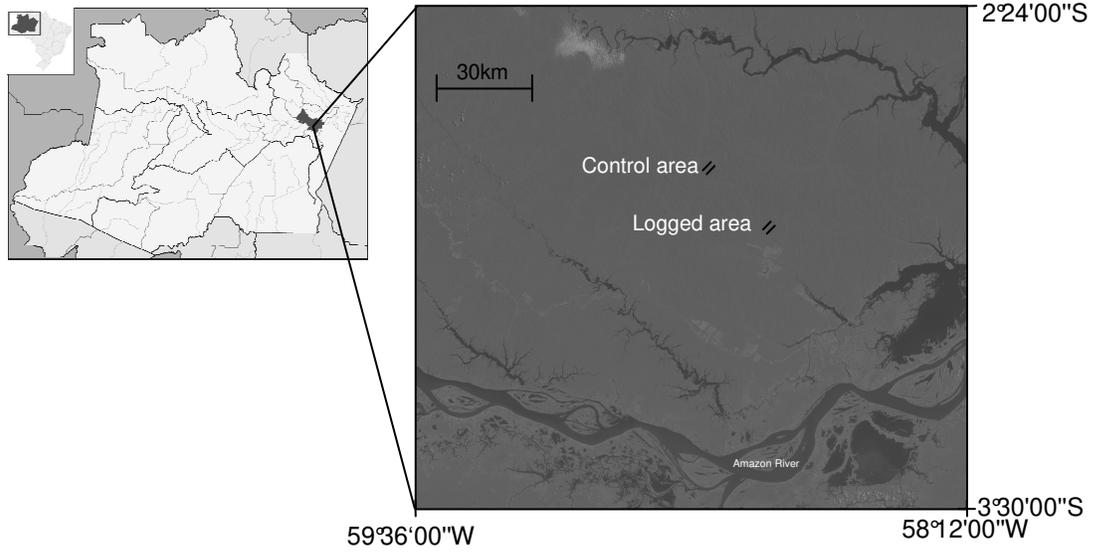
**Figure captions**

**FIGURE 1** - Localization of the study area, Itacoatiara Municipality, Amazon State, Brazil (2°53'39" S e 58°42'58" W).

**FIGURE 2** – Profile diagrams of vegetation in Itacoatiara Municipality, Amazonas State, Brazil. A- Unlogged Forest, B- Forest during wood extraction, C- Forest three years after a reduced impact logging. The scale in profile A shows the height of the forest in meters.

**FIGURE 3** - Correspondence analyses of vegetation traits of an unlogged and a forest three years after a reduced impact logging (RIL) in the Brazilian Amazon (Itacoatiara Municipality, Amazonas State). The open dots represent RIL areas and the filled dots represent unlogged areas. The *R* and *P* in the plot concern to Anosim analyses performed with  $\chi^2$  distance.

**FIGURE 1.**



**FIGURE 2.**

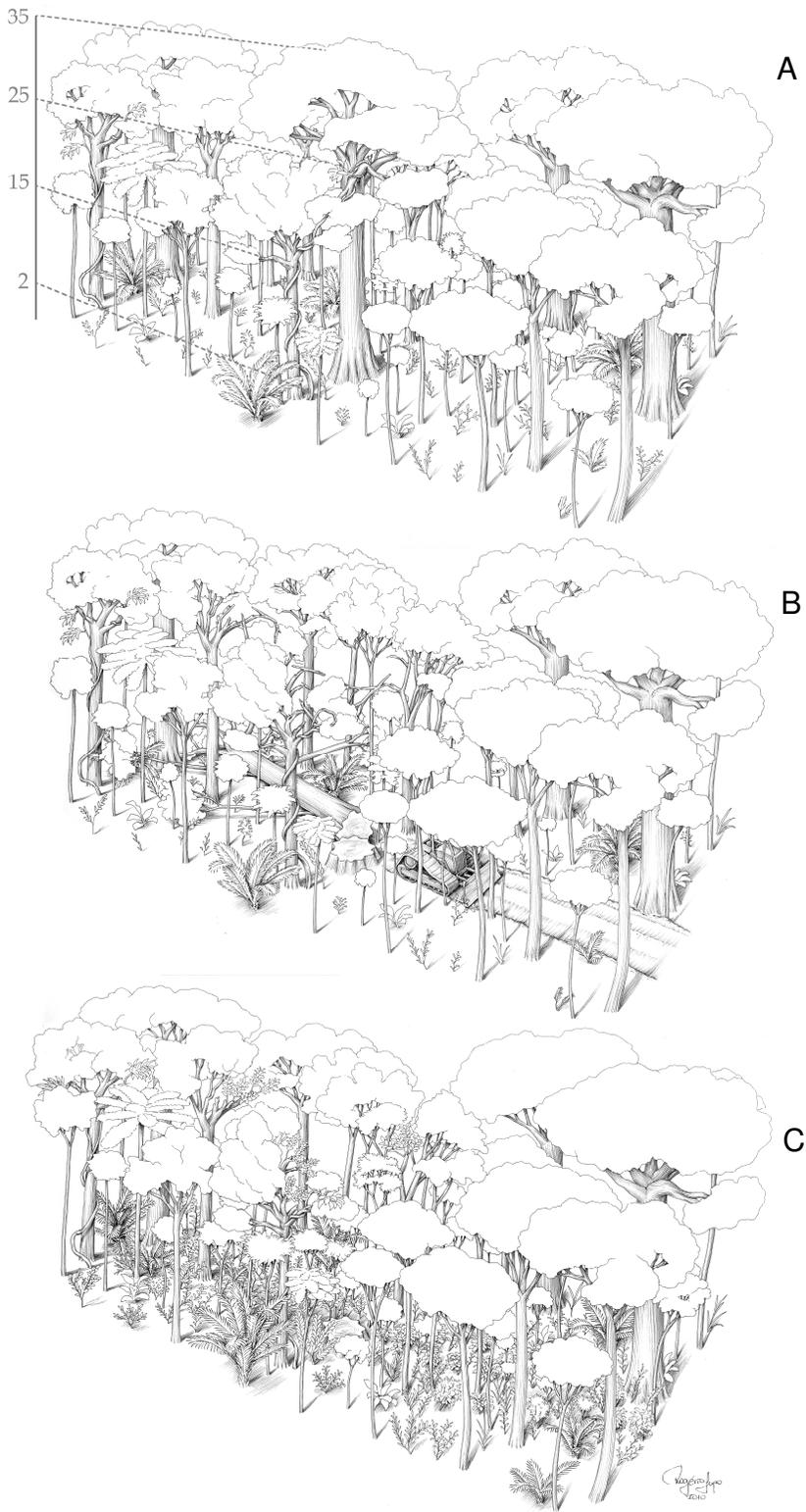


FIGURE 3.

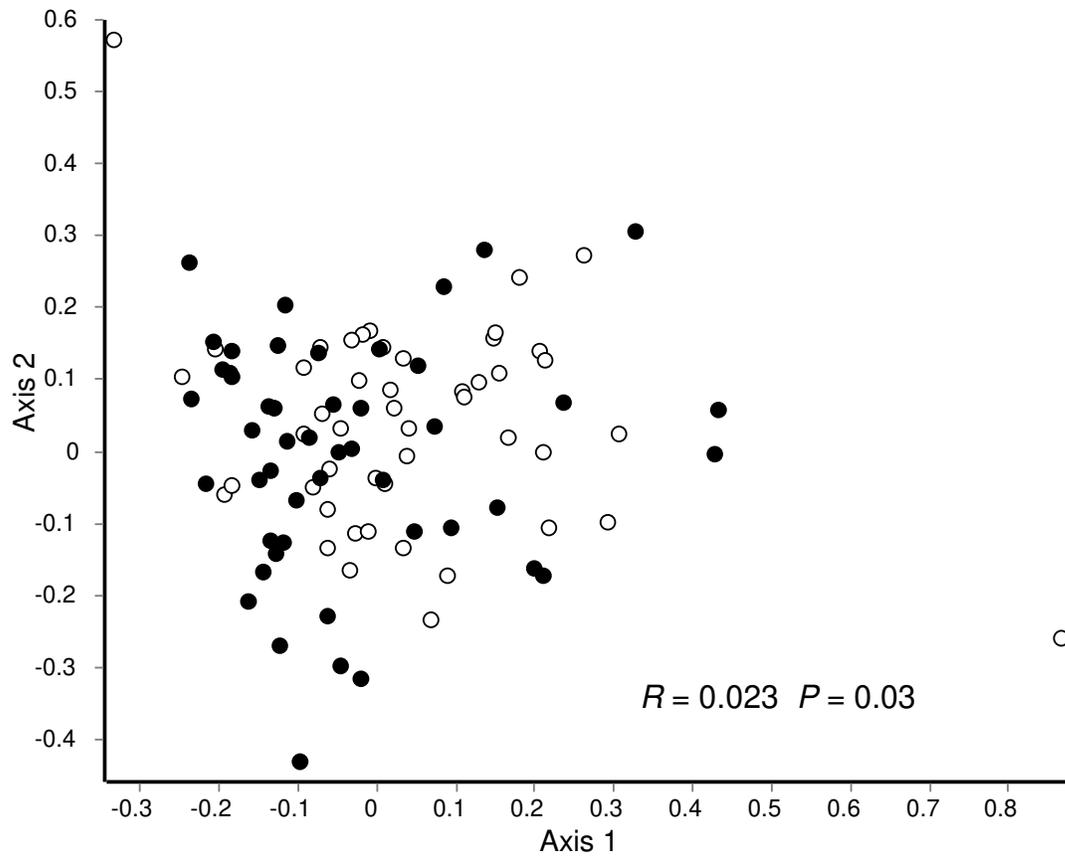
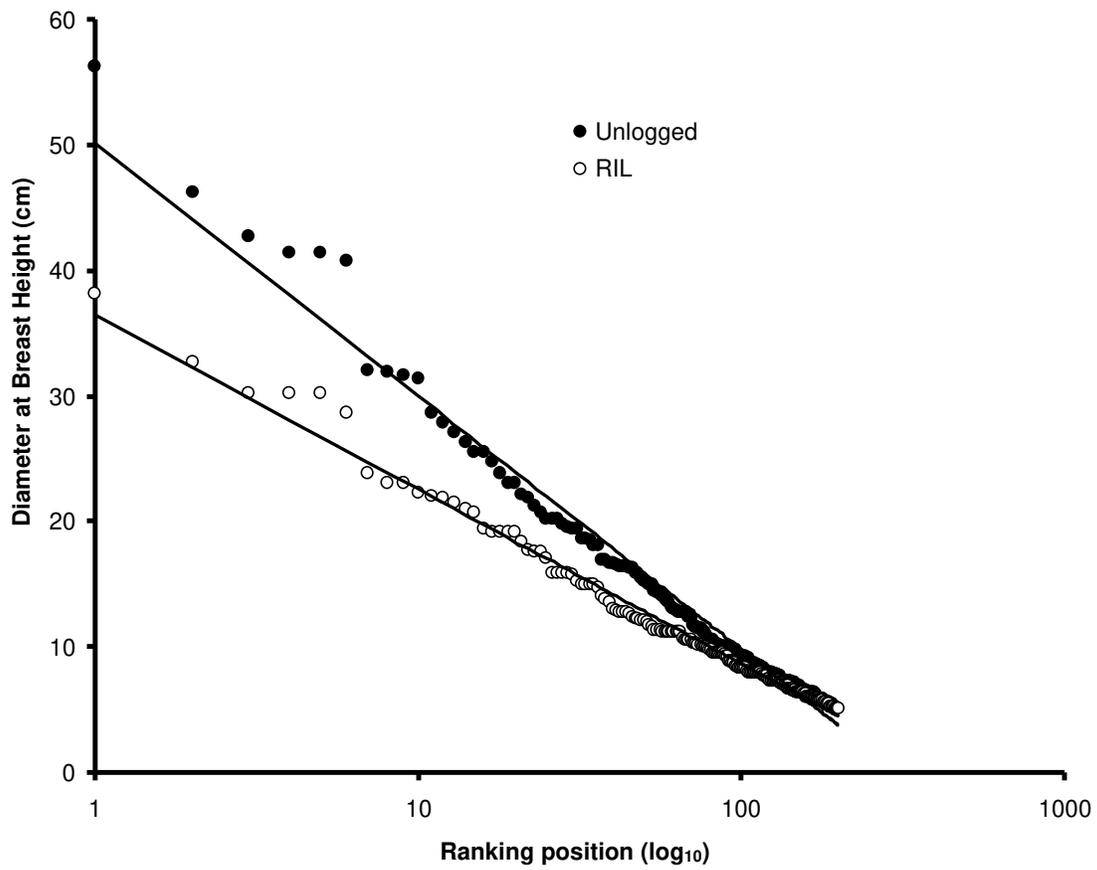
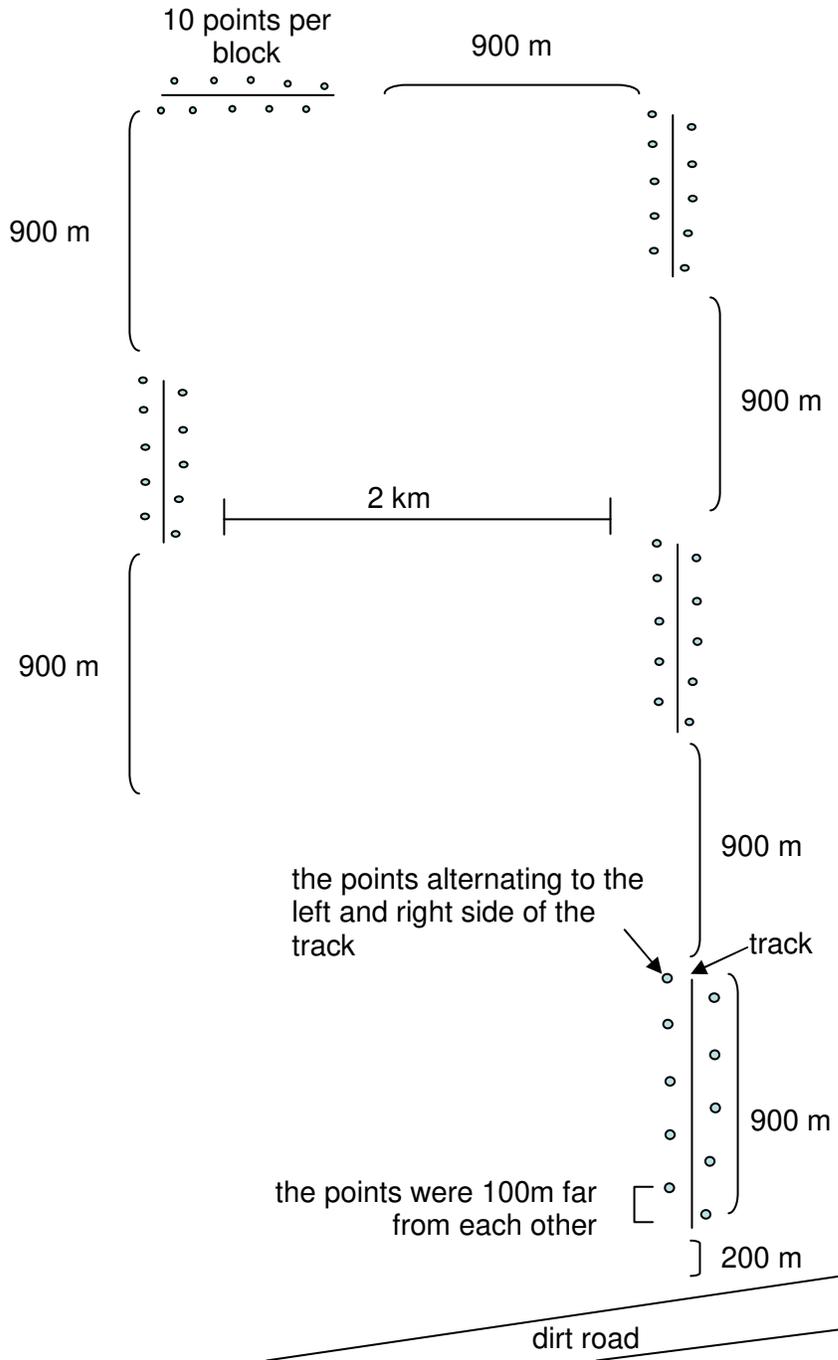


FIGURE 4.



**Appendix I** - Distribution of sampling points throughout the sampled areas. Sampling points were distributed in five blocks with ten points each one in both sides of the track (see below). Blocks were disposed 900m far from each other and sampling points were separated by 100m.



**The effect of Reduced-Impact Logging on Fruit-feeding butterflies in Central Amazon, Brazil**

**Danilo B. Ribeiro<sup>a\*</sup> & André V. L. Freitas<sup>b</sup>**

\* **corresponding author:** Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas. P.O.Box 6109, 13083-970 Campinas, São Paulo State, Brazil, tel. +5519 -3521-6386. e-mail: biodbr@yahoo.com.br

<sup>a</sup> Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas. Brazil

<sup>b</sup> Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas. P.O.Box 6109, 13083-970 Campinas, São Paulo State, Brazil. e-mail: baku@unicamp.br

## **ABSTRACT**

The Amazon region represents more than a half of all tropical forests in the world, and has been threatened by many anthropogenic activities, including several kinds of timber harvesting. The Reduced-Impact Logging (RIL) is considered a less destructive method of timber harvesting, but there is a general lack of information about the effects on Amazonian invertebrates, including butterflies. We investigated the effect of RIL on fruit-feeding butterflies by comparing canopy and understory between an area under RIL and a control area without RIL. The canopy fauna is different and significantly richer than the understory fauna, showing that sampling only the lower strata underestimates the diversity of fruit-feeding butterflies. The effects of RIL were mainly detected in the understory butterfly assemblage, as significant differences were observed in species composition within this stratum. Effects of the RIL regime, which include tree cutting, skid trails and roads openings, are stronger in the understory than in the canopy, explaining the reported differences. Despite the detectable effects of RIL on the composition of fruit-feeding butterflies assemblages the overall diversity was not affected, this pattern is very similar for many other taxa indicating that a noticeable part of the diversity of many taxa could be preserved in areas under RIL management. Therefore, in view of the problems of creating protected areas in the Amazon, RIL is a good alternative to preserve fruit-feeding butterflies and surely many other taxa, and it might be a desirable economic alternative for the region.

**Keywords:** Canopy, Ecological indicators, Forest degradation, Nymphalidae, Tropical, Understory.

## INTRODUCTION

The Amazon region represents 60% of all tropical forest areas in the world (Lovejoy 1999). A total of 6,451 km<sup>2</sup> was cleared, and additional 13,301 km<sup>2</sup> suffered logging activities of different intensities from August 2009 to August 2010 (INPE 2010; Sist 2000).

The major causes of forest degradation in the Amazon are the understory fires and timber extraction (INPE 2010). Timber extraction can be done, without clear cutting, in two basically different ways: 1) conventional logging, where most individuals of the species of high economic value are removed, without previous planning, and 2) Reduced-Impact logging where only few individuals are removed per hectare using techniques to reduce the impact of timber extraction in the remaining vegetation (Sist 2000; Laurance et al. 2005).

Most of the logging activities in the tropics are carried out by untrained and unsupervised crews without previous planning and it implies in several impacts in the remaining vegetation and high levels of injuries to workers (Putz 2008). Traditional selective logging affects several different groups of organisms (Johns 1985; Azevedo-Ramos et al. 2006; DeVries et al. 1997; Devy and Davidar 2001; Dumbrell and Hill 2005) and changes the structure of the remaining forest (Gerwing 2002). This also causes changes in physical environment, including soil compaction, and light incidence in the understory (Rab 1994; Whitman et al. 1997), leading to an increase in erosion (Megahan and Kidd 1972). Additionally, the process can affect streams by increasing temperature and causing silting (Holtby 1988). Other detected effects of conventional selective logging are the increased chances of forest fires due to the increased amounts of coarse woody debris and dryness caused by the greatly reduced canopy cover (Gerwing 2002). These factors can change the forest structure (Johns et al. 1996; Aström et al. 2005), the recruitment rates of

forest trees, the seedling survival (Whitman et al. 1997) and gene flow among tree populations (Murawski et al. 1994).

The Reduced Impact Logging is an alternative to conventional timber harvest that aim to reduce the risks to workers and the environmental impacts in the stand vegetation and can be defined as intensively planned and carefully controlled timber harvesting conducted by trained workers in ways that minimize the deleterious impacts of logging (Putz and Pinard 1993). In Brazil these practice involves a series of recommendations of how to planning the timber extraction, to execute it avoiding unnecessary damage to non-extracted trees and monitoring the forest after timber harvest (Sabogal et al. 2000). Those recommendations leads to less skid trails opened, the extraction of a controlled number of individuals and wood volume (up to 40m<sup>3</sup>/ha), a recovery time (20~30 years) between each harvest and many other activities aiming to reduce the environmental damage caused by logging activities (Sabogal et al. 2000).

Despite all benefits of RIL in Amazon same studies have demonstrated that this activity can affect some groups of animals (Castro-Arellano et al. 2007; Dias et al. 2010; Felton et al. 2008). However those studies often target vertebrates species with few exceptions(e.g. Azevedo-Ramos et al. 2006) and little attention is given to insect communities. Considering that insects comprising 77% of knew animal species on earth (Grimaldi and Engel 2005) it is important to know how RIL affect this group.

Among insects, butterflies can be considered one of the best groups to study RIL effects. Butterflies combine a series of characteristics such as relatively large size, high conspicuousness, ease of sampling and a relatively well-known taxonomy (Brown 1991; Brown 1992; DeVries et al. 1997; Veddeler et al. 2005). This combination of factors in such a well-known group of insects suggests an great potential for their use as ecological

models for conservation studies of species and habitats (Brown 1991; New 1991; Steffan-Dewenter and Tschardt 1997; Brown and Freitas 2000; Schulze et al. 2001; Barlow et al. 2007a; Ghazoul 2002). Adult butterflies are normally divided into two major guilds: nectar-feeding and fruit-feeding (DeVries 1987). Fruit-feeding butterflies gain most of their nutritional requirements from rotting fruits, plant sap and decaying material, and they are represented mainly by Nymphalidae subfamilies Satyrinae, Biblidinae, Charaxinae and the tribe Coeini (Nymphalinae) (Wahlberg et al. 2009), comprising 50-75% of all neotropical Nymphalidae (Brown 2005). Species in this guild can be easily sampled with traps baited with rotting fruits, which allow simultaneous sampling in several areas with similar effort. Additionally, local richness and diversity in this group are correlated with total butterfly and bird diversity (Brown and Freitas 2000; Schulze et al. 2001; Horner-Devine et al. 2003), and they are good predictors of the community responses of several arthropod groups, vertebrates, trees and lianas (Gardner et al. 2007; Barlow et al. 2007b).

Several studies have shown that logging activities can affect the richness, diversity, composition, and vertical stratification of the fruit-feeding butterflies, but there is still no consensus about these effects (Koh 2007; Dumbrell and Hill 2005). Additionally, most of the published studies took place in tropical Asia, West Amazonia and Central America (DeVries et al. 1997; Devy and Davidar 2001; Lewis 2001; Dumbrell and Hill 2005), and only one of them was conducted in an area under an experimental RIL regime (Lewis 2001). The present paper is the first one conducted in an area under a commercial regime of RIL, to test the effects of RIL on butterflies, and the first to study effects of logging *sensu lato* in fruit-feeding butterflies in the Brazilian Amazon.

We aimed to test whether fruit-feeding butterfly assemblages differ among areas with and without RIL regimes by answering two main questions:

1 - Are there differences in the community parameters (diversity, abundance and species composition) of fruit-feeding butterfly assemblages between the RIL and the unlogged areas?

2 - Does the RIL regime affect the vertical stratification of fruit-feeding butterflies?

## **MATERIAL AND METHODS**

### **STUDY SITE**

The study site is located in the Amazon River Basin, Itacoatiara Municipality, Amazon State, Brazil, and is property of the “Precious Woods Amazon” (centred in 2°53'39" S e 58°42'58" W) (Fig. 1a). The altitude is ca. 18m above sea level, and the climate is hot, rainy and humid, without dry season, with mean temperature of 26°C and average annual rainfall of about 2 250 mm (MME 1983). In the present study, we compared the fruit-feeding butterfly assemblage of an area of primary forest with a 3-year-old RIL (8 100 ha) area (hereafter called unlogged forest and RIL forest respectively). The two areas are ca. 25 km apart, and are within a continuum of forest of ca. 6 million km<sup>2</sup>. The main differences between the forest structure in both areas is that the canopy cover (measured 0.4m above the ground) is greater in the unlogged forest, probably due to an increase of understory plants in the RIL forest, and the trees had a wider basal area and a taller height in unlogged forest. Another noticeable difference is the number of seedlings and saplings, which are significantly bigger in the logged forest (D.B.R. & L.C.Garcia, unpublished data).

### **MANAGEMENT SYSTEM**

The company owns several areas of wood extraction based on the Celos Management System described by De Graaf and Poels (1990) and has an unlogged forest of 7,500 hectares with no extraction. The low-impact standard operation is based on an inventory that selects trees with more than 50 cm DBH (Diameter at Breast Height) from among 70 valuable species. A system of roads and skill trails is implemented, and trees are cut using directional felling practices. Around 15-20 m<sup>3</sup> of roundwood were extracted per hectare (with a maximum of six trees extracted per hectare) during the first rotation cycle, which lasted 30 years. The cut trees are then locally processed providing employment opportunities and other services to the local community, and the products are sold to the US, Europe and Asia.

This study was conducted in an upland forest, which is commonly more open than other Amazon vegetations, with greater spacing among trees and not subject to flooding. There are many rare plant species and no clear dominance of any single species (Rizzini et al. 1988).

### **BUTTERFLY SAMPLING**

The sampling protocol was adapted from Ribeiro et al. (2008, 2010). Fifty traps were placed in each area in two heights: 25 in the understory (1.5 m above the ground) and 25 in the canopy (ca. 20 m above the ground inside the tree crowns). The canopy traps were installed using a catapult to get a line over a limb then hauled up to the appropriate height. Traps were installed in groups of ten in alternating heights to avoid the interference of canopy traps in the understory traps (see Fig. 1b for a detailed description of the sampling layout). Based on previous studies (Pinheiro and Ortiz 1992; Hill et al. 2001; Hamer et al. 2003), all traps were disposed at a distance of 100 m from

each other to reduce the interference among traps. Additionally, D.B.R. et al. (unpublished data) showed that fruit-feeding butterfly assemblages are significantly affected by the vegetation structure in the nearest 100-200m radius around each trap. The groups of 10 traps were disposed 900 m apart from each other. The traps were disposed in a 10 km “U” transect, ignoring topography, and comprising a representative range of variation in forest structure within each habitat (Fig. 1b). The butterflies were sampled monthly from July to November 2007 during the dry season, to maximize butterfly sampling {Ebert, 1969 #2463; Checa, 2009 #2381; K.S. Brown personal communication} traps remained open for 14 days, and were visited at 48 h intervals (adapted from Ribeiro et al. 2008, 2010) totaling 4 800 trap days. During each visit the bait was replaced, and all captured individuals were collected.

#### **DATA ANALYSIS**

To verify whether RIL management reduce/increase the number of species in the butterfly assemblage we calculate indices of diversity, Shannon ( $H'$ ), Simpson ( $1 - D$ ) and Fisher's Alpha ( $\alpha$ ), for each management system and height: unlogged understory (UU), unlogged canopy (UC), RIL understory (RU), and RIL canopy (RU).

Rarefaction curves were produced to eliminate the influence of sample size when comparing richness. These curves calculate the expected species richness with the use of random sub-samples of individuals (Gotelli and Graves 1996), making it possible to compare the richness among different sized samples.

We used Fisher's Alpha as the diversity index (Fisher et al. 1943) because it is a robust, trustworthy index, little affected by the sample size and broadly used in biodiversity studies (Magurran 2004). The diversity index (Fisher's Alpha) was compared with the

bootstrap procedure, with confidence intervals of the indices calculated and compared using the software PAST® (Hammer et al. 2001). The critical values of  $\alpha$  (Fisher's Alpha) were corrected with the FDR procedure (False Discovery Rate), in order to minimize the incidence of type I errors (i.e., to reject the null hypothesis when it is true). This kind of correction (FDR) is more powerful than FWER (Family Wise Error Rate) procedures (e.g. Bonferroni, Hochberg), and, therefore, it is more appropriate for multiple comparisons (Benjamini and Hochberg 1995).

The richness estimates (Chao2 and Jackknife 1) were calculated with the software Estimates 7.5 (Colwell 2005) to evaluate the representation of each sample according to the total community. We choose these estimators because they provides the least biased estimates of species richness for small numbers of samples, and allow detectability to vary across species (Burnham and Overton 1978; Colwell and Coddington 1994).

To compare whether was feasible to detect differences between butterfly assemblages using high taxonomic levels we calculate the differences in butterfly abundance and subfamilies proportion in each combination of management and height (UU, UC, RU, RC). These differences were tested with analyses of variance (ANOVA). For comparative purposes with other studies we followed (Freitas and Brown Jr. 2004) division of subfamilies modified after (Wahlberg et al. 2009) (Biblidinae, Charaxinae, Satyrinae: tribes Morphini, Brassolini and Satyrini, and the Nymphalinae: tribe Coeini). Two additional analyses were performed to verify the difference among butterfly assemblage composition, Cluster analysis and Principal Coordinates Analyses. A cluster analysis using Bray-Curtis distance was used to verify if traps were grouped by management system and/or heights (UU, UC, RU, RC). To verify the influence of the composition of fruit-feeding butterflies in the distribution of the samples in the ordination space, we performed

Principal Coordinates Analyses (PCO). In this analysis, we used the Morisita-Horn similarity index as it measures the beta diversity independent of the alpha (Jost 2007). The PCO was performed with understory and canopy samples separately, to test the effect of RIL in each height. Anosim analyses were conducted to compare assemblage composition between RIL and Unlogged areas in each trapping height. We used a transformed ( $\log_{10} x+1$ ) matrix to avoid the over-influence of abundance in the results. PCO, Anosim and cluster analyses were carried with Fitopac 2.0 (Shepherd 2009). Additionally, we perform an Mann – Withney test between the abundance of species with more than 14 individuals and noticeable differences between RIL and Unlogged areas.

Additive partitioning of diversity was also done to test how diversity is distributed vertically (understory and canopy) and horizontally (among sampling points). The analyses were performed with Partition@ 3.0 Software (Veech & Crist 2009). Additive richness and Shannon index were used as diversity measures; using the trap average diversity as  $\alpha$  diversity, the  $\beta$  diversity was measured in tree levels:  $\beta_1$  - among traps in the same group and height,  $\beta_2$  - among groups in the same height,  $\beta_3$  -among height in the same treatment. We used individual-based procedure to calculate the  $\alpha$  and  $\beta_1$ ; for the other measurements we used a sample-based procedure. We weighted the partitioning by abundance and used the pooled data of all sampling months aggregated by trap, group and height resulting in hierarchy of 100, 20 and 4 units. The randomization process was repeated 1,000 times to obtain null distributions of the beta diversity estimates at each hierarchical level (Crist et al., 2003).

## **RESULTS**

We collected 1 091 individuals of 68 species belonging to all fruit-feeding Nymphalidae clades (Biblidinae, Charaxinae, Nymphalinae: Coeini, Satyrinae: Morphini, Brassolini and Satyrini), with 22 species collected only in the canopy, 21 only in the understory, and 25 in both strata (Appendix ). The richness and diversity ( $H'$ , 1-D, Fisher's  $\alpha$ ) were significantly different between layers but not between management systems (Table 1), with the canopy richer than the understory (Fig. 2). The richness estimators showed that we sampled about 67- 77% of the total richness, which can be considered a good representation of the actual assemblage.

The abundance of fruit-feeding butterflies was significantly different between layers ( $F = 15.59$ ;  $p = 0.00015$ ) and management systems ( $F = 52.74$ ;  $p < 0.0001$ ) and there was no interaction between factors ( $F = 0.500$ ;  $p = 0.48$ ). The proportion of subfamilies was significantly different between heights ( $F = 45.75$ ;  $p < 0.0001$ ) and marginally significantly between management systems ( $F = 9.49$ ;  $p = 0.056$ ).

The samples were grouped by height in cluster analysis (UPGMA/Bray-Curtis) but not by management system (Fig. 3). In the Principal Coordinates Analyses (PCO) we found segregation by management system in the understory samples ( $R = 0.241$ ;  $p < 0.0001$ ) (Fig 4b) but not in the canopy samples ( $R = 0.042$ ;  $p = 0.08$ ) (Fig. 4a). *Catonephele acontius* ( $U=235.5$ ;  $p = 0.03$ ) and *Hamadryas arinome* ( $U = 237.5$ ;  $p = 0.01$ ) had significant differences in the canopy abundance between RIL and Unlogged areas. The main species leading to the pattern found in understory samples were *Catonephele acontius*, *Hamadryas arinome*, *Memphis vicinia* and *Tigridia acesa* that increased their abundance in the RIL while *Catoblepia xanthus* and *Morpho helenor* that were less abundant in the RIL area (Appendix). Despite the increase in abundance significant differences between the

understory abundances in RIL and unlogged areas were found just in *C. acontius* (  $U = 57.5$ ;  $p < 0.001$ ) and *M. vicinia* ( $U = 209.5$ ;  $p = 0.004$ ).

The additive partitioning of the butterfly diversity indicated that the additive richness and diversity (Shannon  $H'$ ) in each trap ( $\alpha$ ) and among traps in the same group and layer ( $\beta_1$ ) are not higher than that expected by chance (Table 2). The richness among groups in the same layer ( $\beta_2$ ) was not different from that expected by chance, but the Shannon diversity was higher than that expected by chance (Table 2). The diversity (Richness and Shannon Index) between heights in the same management system was significantly higher than that expected by chance ( $\beta_3$ ) (Table 2).

## **DISCUSSION**

### **METHODOLOGICAL IMPLICATIONS**

Fruit-feeding butterflies have often been used in ecological studies (Horner-Devine et al. 2003; Veddeler et al. 2005; Ribeiro and Freitas 2010; Barlow et al. 2007b; Shahabuddin and Ponte 2005) and our results could be useful to avoid some methodological caveats.

As found by (DeVries et al. 1997; DeVries and Walla 2001) in Ecuador, the effects of RIL in fruit-feeding butterfly assemblages in the present study are much greater in the understory than the canopy (Fig 4a,b). This suggests that RIL has a relatively low impact in the canopy structure; on the other hand, the vegetation structure in the understory changes very much, probably because of the trails opened for timber removal. If the objective is to monitor logging effects in tropical forests, we suggest that sampling only the understory is enough to detect the ecological impacts that affect the forest structure.

Besides that, using the proportion of subfamilies instead of species could be a reasonable solution to overcome limitations in butterfly identification in very rich communities in Neotropical habitats. However, the above procedure can mask some small changes that are detectable when species composition is used. Accordingly, in the present study we found marginally significant differences between managements when using subfamily composition ( $F = 9.49$ ;  $p = 0.056$ ), despite the noticeable difference between species composition (Fig. 4b). The subfamily level has been investigated in other studies with relative success; (DeVries et al. 1997) detected great beta diversity in subfamilies among habitats, and (Schulze et al. 2001) found differences between forest strata. Therefore, we will recommend the use of subfamily level analyses only if species identification is an impediment.

The canopy assemblage comprised about 31% of the observed richness in our samples (Table 1), being richer (Fig. 1) and more diverse than the understory (Table 1). In the Amazon forest, exclusive canopy species comprised 17% (Barlow et al. 2007b) to 31% (DeVries et al. 1999) of the fruit-feeding butterfly assemblage, showing that sampling this stratum is essential for butterfly inventories in any forest with high canopies. The additive partitioning of butterfly diversity showed that the increment in richness and diversity ( $\beta_3$ ) when canopy traps are included (Table 2) is higher than the expected by the increment in sampling effort, corroborating our previous statement, and also the findings of DeVries et al. (1997, 1999).

The additive partitioning of butterfly diversity demonstrates that the increments in richness in “among traps” in the same group and layer ( $\beta_1$ ) is a consequence of the increase in sampling effort. The butterfly density in the present study (ca. 0.2 butterfly/ trap/day) was much smaller than observed by other authors in the Amazon Forest (ca. 0.8 butterfly/

trap/day - (DeVries and Walla 2001; Barlow et al. 2007b) for this reason we recommend the use of sampling units combining at least 20 traps for each layer and habitat in forests with similar butterfly densities such as the Central Amazon. The present study is the first to decouple canopy and understory traps by placing them 100m apart from each other. We strongly suggest that future studies use this protocol to maintain the independence among sampling points and to avoid the interference of one trap to another, which is especially important in studies comparing different forest layers.

### **BIOLOGICAL IMPLICATIONS**

The present study demonstrates that the canopy assemblage is significantly richer and has fewer individuals than the understory, a pattern similar to that found by Schulze et al. (2001) and Dumbrell & Hill (2005) in Malaysia. Barlow et al. (2007b), however, found a lower abundance in the canopy, and no detectable differences in richness, working in Pará (Brazilian Amazon), and DeVries et al. (1999) and DeVries & Walla (2001) found no differences in both richness and abundance in Ecuadorian Amazon. These divergent responses could be attributed to the interference of the understory traps with the canopy traps, as the above studies installed both traps in the same point. We also note that disturbance levels and recovery periods are variable in the above studies. Anyway, the high diversity in the canopy appears to be a common pattern in tropical forests, but we still have no evidence about the reasons that explain such pattern.

Several studies showed that forest disturbance disrupt the vertical stratification of butterfly assemblages in forests (DeVries 1988; Schulze et al. 2001; Fermon et al. 2005). In the present study, we noticed this process in *M. vicinia* only, this specie was more common

in the canopy of unlogged area and was evenly distributed in both strata of the RIL area (Appendix), showing that this change in vertical stratification can be specie dependent.

Thus, detectable effects of RIL were observed only in understory assemblages, which differed between treatments (Fig. 4a), while canopy assemblages maintained the same structure (Fig 4b). Canopy assemblages are probably more tolerant to high levels of light and temperature and low humidity than understory butterflies, whose assemblages are structured under the forest shade. However, even if RIL does not change significantly the canopy structure, it has a noticeable effect in the forest understory by opening trails for timber removal (D.B.R. & L.C.Garcia, unpublished data), and benefiting some sun-loving species, displacing several typical understory butterfly species. The changes in vegetation structure could also increase the growth of pioneer plant species and decrease the populations of some shadowy plants (Silva et al. 1995), consequently changing the butterfly assemblages that depend on these resources. Other biological aspects such as microhabitat and forest specialization could also determine the final species pool that will persist after the logging (Koh 2007), but these data are still not available for most Neotropical butterfly species. In the present study differences in understory assemblages between RIL and unlogged areas were found mainly due to the increase in Biblidinae and Charaxinae and the decrease of Brassolini and Morphini in the RIL area (Appendix ). Our results were similar to the results found by (Hamer et al. 2003) in Borneo, showing that logging activities can affect in the same way related tribes and subfamilies of butterflies in tropical forests even in places as far as Borneo and Brazil, leading to a noticeable change in the butterflies' assemblage.

In the present study, we found no differences in both richness and diversity when comparing RIL and unlogged areas (Fig. 2). Showing that the differences found between

butterflies assemblages in understory were caused by species replacement and differences in abundance and not by species extinction. Two species had a significant abundance increase in RIL area *C. acontius* and *M. vicinia*. The lack of information about the biology of those species is an impediment for an extensive discussion about possible process leading to this pattern, however it is very likely that an increase in host-plant availability caused by RIL could be the main factor driving the differences in *C. acontius*.

The median term (2 – 8 years after logging) effect of RIL in assemblages of ground foraging ants, birds, small mammals, bats and fishes were similar to our results, showing that RIL promotes changes in abundance of some species and species composition without, however, changing overall diversity (Castro-Arellano et al. 2007; Presley et al. 2008; Lambert et al. 2005; Kalif et al. 2001; Wunderle et al. 2006). Changes in diversity were usually associated with other silvicultural treatments (e.g. enrichment strips) that were often absent in RIL areas or higher volumes of timber extraction (more than 80m<sup>3</sup>/ha)(Mason 1996; Davies 2000). The RIL regime proposed to Brazilian Amazon (Sabogal et al. 2000) do not impose intensive silvicultural practices or high volumes of timber extraction, therefore this could be considered an alternative to preserve fruit-feeding butterflies and many other taxa in the Brazilian Amazon and is an economically viable option for local populations.

## **ACKNOWLEDGEMENTS**

We thank F. S. Santos, R. B. Andrade, O. Lewis and J. Barlow for the critical review of the manuscript. We also thank L. C. Garcia by the help in field work and for providing the vegetation structure data. D.B.R. thanks a fellowship from FAPESP (grant #07/50896-0) and The Lepidoptera Research Foundation for financial support. A.V.L.F.

was supported by CNPq (300282/2008-7), FAPESP (00/01484-1 and 04/05269-9) and US National Science Foundation (DEB-0527441). The authors thank the “Precious Woods Amazon” by permitting field work in the forest areas and by the logistic support during all field work.

## REFERENCES

- Aström M, Dynesius M, Hylander K, Nilsson C (2005) Effects of slash harvest on bryophytes and vascular plants in Southern Boreal Forest clear-cuts. *Journal of Applied Ecology* 42:1194-1202
- Azevedo-Ramos C, Carvalho Jr O, do Amaral BD (2006) Short-term effects of reduced-impact logging on eastern Amazon fauna. *Forest Ecology and Management* 232:26-35
- Barlow J, Gardner TA, Araujo IS, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MIM, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Nunes-Gutjahr AL, Overal WL, Parry L, Peters L, Ribeiro-Junior MA, Motta CdS, Silva MNFd, Peres CA (2007a) Quantifying the biodiversity value of tropical primary, secondary and plantation forests. *Proceedings of the National Academy of Science of the United States of America* 104:18555-18560
- Barlow J, Overal WL, Araujo IS, Gardner TA, Peres CA (2007b) The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *Journal of Applied Ecology* 44:1001-1012
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* 57:289-300
- Brown KS (1991) Conservation of the Neotropical environments: insects as indicators. In: Collins NM, Thomas JA (eds) *The Conservation of Insects and their Habitats*. Academic Press, San Diego, pp 350-404
- Brown KS (1992) Borboletas da Serra do Japi: diversidade, habitats, recursos alimentares e variação temporal. In: Morellato LPC (ed) *História Natural da Serra do Japi: Ecologia e Preservação de uma Área Florestal no Sudeste do Brasil*. Editora Unicamp, Campinas, pp 142-186
- Brown KS (2005) Geologic, evolutionary, and ecological bases of the diversification of neotropical butterflies: Implications for conservation. In: Dick CW, Moritz G (eds) *Tropical Rainforest: Past, Present, and Future*. The University of Chicago Press, Chicago, pp 166-201
- Brown KS, Freitas AVL (2000) Atlantic forest butterflies: Indicators for Landscape Conservation. *Biotropica* 32 (4b):934-956
- Burnham KP, Overton PS (1978) Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65:927-936

- Castro-Arellano I, Presley SJ, Saldanha LN, Willig MR, Wunderle-Jr JM (2007) Effects of reduced impact logging on bat biodiversity in terra firme forest of lowland Amazonia. *Biological Conservation* 138:269 - 285
- Checa MF, Barragan A, Rodriguez J, Christman M (2009) Temporal abundance patterns of butterfly communities (Lepidoptera: Nymphalidae) in the Ecuadorian Amazonia and their relationship with climate. *Annales de la Société entomologique de France* 45:470-486
- Colwell RK (2005) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide. <http://purloinc.org/estimates>
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345:101-118
- Davies AJ (2000) Does Reduced-Impact Logging Help Preserve Biodiversity in Tropical Rainforests? A Case Study from Borneo using Dung Beetles (Coleoptera: Scarabaeoidea) as Indicators. *Environmental Entomology* 29:467-475
- de Graaf NR, Poels RLH (1990) The Celos Management System: a polycyclic method for sustained timber production in South American rain forest. In: Anderson AB (ed) *Alternatives to deforestation: steps towards sustainable use of the Amazon rain forest*. Columbia University Press, New York, pp 116-127
- DeVries PJ (1987) *The butterflies of Costa Rica and their natural history*. Princeton University Press, Princeton, N.J.
- DeVries PJ (1988) Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera* 26:98-108
- DeVries PJ, Murray D, Lande R (1997) Species diversity in vertical, horizontal and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62:343-364
- DeVries PJ, Walla TR (2001) Species diversity and community structure in neotropical fruit-feeding butterflies *Biological Journal of the Linnean Society* 74:1-15
- DeVries PJ, Walla TR, Greeney HF (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 68:333-353
- Devy MS, Davidar P (2001) Response of wet forest butterflies to selective logging in Kalakad-Mundanthurai Tiger Reserve: Implications for conservation. *Current Science* 80:400-405
- Dias MS, Magnusson WE, Zuanon J (2010) Effects of Reduced-Impact Logging on Fish Assemblages in Central Amazonia. *Conservation Biology* 24:278-286
- Dumbrell AJ, Hill JK (2005) Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: Implications for sampling. *Biological Conservation* 125:123-131
- Ebert H (1969) On the frequency of butterflies in eastern Brazil, with a list of the butterfly fauna of Poços de Caldas, Minas Gerais. *The Journal of the Lepidopterists' Society* 23:1-35
- Felton A, Wood J, Felton AM, Hennessey B, Lindenmayer DB (2008) Bird community responses to reduced-impact logging in a certified forestry concession in lowland Bolivia. *Biological Conservation* 141:545 - 555

- Fermon H, Waltert M, Vane-Wright RI, Mühlenberg M (2005) Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodiversity and Conservation* 14:333-350
- Fisher RA, Steven-Corbet A, Williams CB (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *The Journal of Animal Ecology* 12 (1):42-58
- Freitas AVL, Brown Jr. KS (2004) Phylogeny of the Nymphalidae (Lepidoptera) *Systematic Biology* 53:363-383
- Gardner TA, Barlow J, Araujo IS, Avila-Pires TCS, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hemández MIM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santas R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Gunior MA, Silva MNFd, Motta CdS, Peres C (2007) The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters* 11:139-150
- Gerwing JJ (2002) Degradation of forests through logging and fire in the eastern Brazilian Amazon. *Forest Ecology and Management* 157:131-150
- Ghazoul J (2002) Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. *Biodiversity and Conservation* 11:521-541
- Gotelli NJ, Graves GR (1996) *Null models in ecology*. Smithsonian Institution Press, Washington DC
- Grimaldi D, Engel MS (2005) *Evolution of the insects*. Cambridge University Press, New York
- Hamer KC, Hill JK, Benedick S, Mustaffa N, Sherratt TN, Maryati M, Chey VK (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology* 40:150-162
- Hammer O, Harper DAT, Ryan PD (2001) Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4
- Hill JK, Hamer KC, Tangah J, Dawood M (2001) Ecology of tropical butterflies in rainforest gaps. *Oecologia* 128:294-302
- Holtby LB (1988) Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the Coho salmon (*Oncorhynchus kisutch*) *Canadian Journal of Fisheries and Aquatic Sciences* 45:502-515
- Horner-Devine MC, Daily GC, Ehrlich PR, Boggs CL (2003) Countryside biogeography of tropical butterflies. *Conservation Biology* 17:168-177
- INPE (2010) Mapeamento da degradação florestal na Amazônia brasileira
- Johns AD (1985) Selective logging and wildlife conservation in tropical rain-forest: problems and recommendations. *Biological Conservation* 31:355-375
- Johns JS, Barreto P, Uhl. C (1996) Logging damage during planned and unplanned logging operations in the eastern Amazon. *Forest Ecology and Management* 89:59-77
- Kalif KAB, Azevedo-Ramos C, Moutinho P, Malcher SAO (2001) The Effect of Logging on the Ground-Foraging Ant Community in Eastern Amazonia. *Studies on Neotropical Fauna and Environment* 36:215-219
- Koh LP (2007) Impacts of land use change on South-east Asian forest butterflies: a review. *Journal of Applied Ecology* 44:703-713
- Lambert TD, Malcolm JR, Zimmerman BL (2005) Effects of mahogany (*Swietenia macrophylla*) logging on small mammal communities, habitat structure, and seed

- predation in the southeastern Amazon Basin. *Forest Ecology and Management* 206:381-398
- Laurance WF, Bergen S, Cochrane MA, Fearnside PM, Delamônica P, d'Angelo S, Barber C, Fernandes T (2005) The future of the Amazon. In: E. Bermingham, Dick CW, Moritz G (eds) *Tropical Rainforest: Past, Present, and Future*. The University of Chicago Press, Chicago, pp 583-609
- Lewis OT (2001) Effect of experimental selective logging on tropical butterflies. *Conservation Biology* 15:389-400
- Lovejoy TE (1999) Preface. *Biological Conservation* 91:100
- Magurran AE (2004) *Measuring Biological Diversity*. 2 edn. Blackwell Science, Oxford
- Mason D (1996) Responses of Venezuelan Understorey Birds to Selective Logging, Enrichment Strips, and Vine Cutting. *Biotropica* 28:296-309
- Megahan WF, Kidd WJ (1972) Effects of logging and logging roads on erosion and sediment deposition from steep terrain. *Journal of Forestry* 70:136-141
- Murawski DA, Gunatilleke IAUN, Bawa KS (1994) The Effects of Selective Logging on Inbreeding in *Shorea megistophylla* (Dipterocarpaceae) from Sri Lanka. *Conservation Biology* 8:997-1002
- New TR (1991) *Butterfly Conservation*. Oxford University Press, Melbourne
- Pinheiro CEG, Ortiz JVC (1992) Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography* 19:505-511
- Presley SJ, Willig MR, Wunderle Jr. JM, Saldanha LN (2008) Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. *Journal of Applied Ecology* 45:14-25
- Putz FE, Pinard MA (1993) Reduced-Impact Logging as a Carbon-Offset Method. *Conservation Biology* 7:755-757
- Rab MA (1994) Changes in physical properties of a soil associated with logging of *Eucalyptus regnans* forest in southeastern Australia. *Forest Ecology and Management* 70:215-229
- Ribeiro DB, Freitas AVL (2010) Differences in thermal responses in a fragmented landscape: Temperature affects the sampling of diurnal, but not nocturnal fruit-feeding Lepidoptera. *Journal of Research on the Lepidoptera* 42:1-4
- Ribeiro DB, Prado PI, Brown KS, Freitas AVL (2008) Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. *Diversity and Distributions* 14:961-968
- Ribeiro DB, Prado PI, Jr. KSB, Freitas AVL (2010) Temporal Diversity Patterns and Phenology in Fruit-Feeding Butterflies in the Atlantic Forest. *Biotropica* 42:710-716
- Rizzini CT, Coimbra Filho AF, A. H (1988) *Ecosistemas brasileiros*. Index Editora, Rio de Janeiro
- Sabogal C, Silva JNM, Zweede J, Pereira R, Barreto P, Guerreiro CA (2000) Diretrizes técnicas para a exploração de impacto reduzido em operações florestais de terra firme na Amazonia brasileira. Documentos 64. EMBRAPA, Belém, Brazil
- Schulze CH, Linsenmaier KE, Fiedler K (2001) Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology* 153:133-152
- Shahabuddin G, Ponte CA (2005) Frugivorous butterfly species in tropical forest fragments: correlates of vulnerability to extinction. *Biodiversity and Conservation* 14:1137-1152

- Sist P (2000) Reduced-impact logging in the tropics. Objectives, principles and impacts. *International forestry review* 2:3-10
- Steffan-Dewenter I, Tscharntke T (1997) Early succession of butterfly and plant communities on set-aside fields. *Oecologia* 109:294-302
- Veddeler D, Schulze CH, Steffan-Dewenter I, Buchori D, Tscharntke T (2005) The contribution of tropical secondary forest fragments to the conservation of fruit-feeding butterflies: effects of isolation and age. *Biodiversity and Conservation* 14:3577-3592
- Wahlberg N, Leneveu J, Kodandaramaiah U, Peña C, Nylin S, Freitas AVL, Brower AVZ (2009) Nymphalid butterflies diversify following near demise at the cretaceous/tertiary boundary. *Proceedings of the Royal Society B* 276:4295-4302
- Whitman AA, Brokaw NVL, Hagan JM (1997) Forest damage caused by selection logging of mahogany (*Swietenia macrophylla*) in northern Belize. *Forest Ecology and Management* 92:87-96
- Wunderle JM, Henriques LMP, Willig MR (2006) Short term responses of birds to forest gaps and closed canopy: An assessment of reduced-impact logging in a lowland Amazon forest. *Biotropica* 38:235-255

**Table 1** - Diversity, richness and abundance of the fruit-feeding butterflies assemblage in Central Amazon, Brazil. Different letters in front of Diversity measures indicate the significantly differences ( $p < 0.01$ ) in bootstrap (10000 runs) test.

Management		Richness	Abundance	Diversity			Richness Estimators				
				(H')	(1-D)	$\alpha$	Chao 1	SD	Jack 2	SD	
RIL											
	Undestory	40	440	2.71	0.886	10.69	a	45.6	4.8	53.6	2.7
	Canopy	41	204	3.35	0.956	15.45	b	46.9	5.6	57.4	3.7
	Total	62	644	3.28	0.943	16.91		79.1	11.5	84.6	2.4
Unlogged											
	Undestory	34	291	2.58	0.888	9.98	a	58.0	16.4	59.7	3.7
	Canopy	38	156	3.31	0.954	16	b	45.9	6.3	52.5	2.2
	Total	54	447	3.31	0.943	15.07		71.5	12.1	78.4	2.2
Total		68	1091	3.38	0.943	16.06		89.0	14.7	93.7	1.0

**Table 2** - Spatial partitioning of species diversity of the assemblage of fruit-feeding Nymphalidae in Central Amazon, Brazil. Results in bold type indicate that the observed diversity is significantly different from that expected in a random distribution., n.s. = non significant. Hyphens (-) indicate that the difference between diversity was not tested in that level.

Diversity		Observed	(%)	Expected	(%)	$p$
<b>S<sup>a</sup></b>						
$\alpha$	Within trap	7.92	11.6	10.4	14.9	n.s
$\beta_1$	Among traps	11.75	17.3	16.01	23.0	n.s
$\beta_2$	Among groups	18.63	27.4	18.34	26.4	n.s
$\beta_3$	Between layers	<b>20.42</b>	30.0	<b>11.4</b>	16.4	<b>&lt;0.001</b>
$\beta_4$	Between managements	9.28	13.6	13.45	19.3	-
$\gamma$	Total	68		69.6		
<b>H<sup>b</sup></b>						
$\alpha$	Within trap	6.2	50.7	8.58	59.2	n.s
$\beta_1$	Among traps	2.02	16.5	2.18	15.0	n.s
$\beta_2$	Among groups	<b>1.42</b>	11.6	<b>1.41</b>	9.7	<b>0.009</b>
$\beta_3$	Between layers	<b>1.51</b>	12.3	<b>1.12</b>	7.7	<b>&lt;0.001</b>
$\beta_4$	Between managements	1.09	8.9	1.21	8.3	-
$\gamma$	Total	12.24		14.5		

$a$  = Additive species richness,

$b$  = Shannon diversity Index

## FIGURE LEGENDS

**Figure 1** - A - Localization of the study area, Itacoatiara Municipality, Amazon State, Brazil ( $2^{\circ}53'39''$  S e  $58^{\circ}42'58''$  W); the two parallel black lines represent the positions of the sampling transects (as follows). B - Layout of the sampling design. The lines of small circles represent the ten sampling unities of 10 traps each in both areas (RIL and unlogged; see text for further details). Solid circles represent understory traps; open circles represent canopy traps

**Figure 2-** Rarefaction analyses of the fruit-feeding butterflies' assemblage in Central Amazon, Brazil. RU-Samples in Understory of RIL management areas, RC-Samples in Canopy of RIL management areas, UU-Samples in Understory of Unlogged areas, UC-Samples in Canopy of Unlogged areas.

**Figure 3** - Cluster analyses of the fruit-feeding butterflies assemblage in Central Amazon, Brazil. The cluster method used was UPGMA and the distance measure was Bray-Curtis, Cofenetic correlation = 0.8137. RU-Samples in Understory of RIL management areas, RC-Samples in Canopy of RIL management areas, UU-Samples in Understory of Unlogged areas, UC- Samples in Canopy of Unlogged areas.

**Figure 4-** Principal Components Analysis of fruit-feeding butterflies in Central Amazon, Brazil. We used Morisita-Horn as similarity measure. The filled dots represent samples of Unlogged areas and the empty dots represent samples in areas under RIL management. A- Canopy samples. B - Understory samples. The R and p showed in the plots concern to Anosim analyses performed with Morisita-Horn distance.

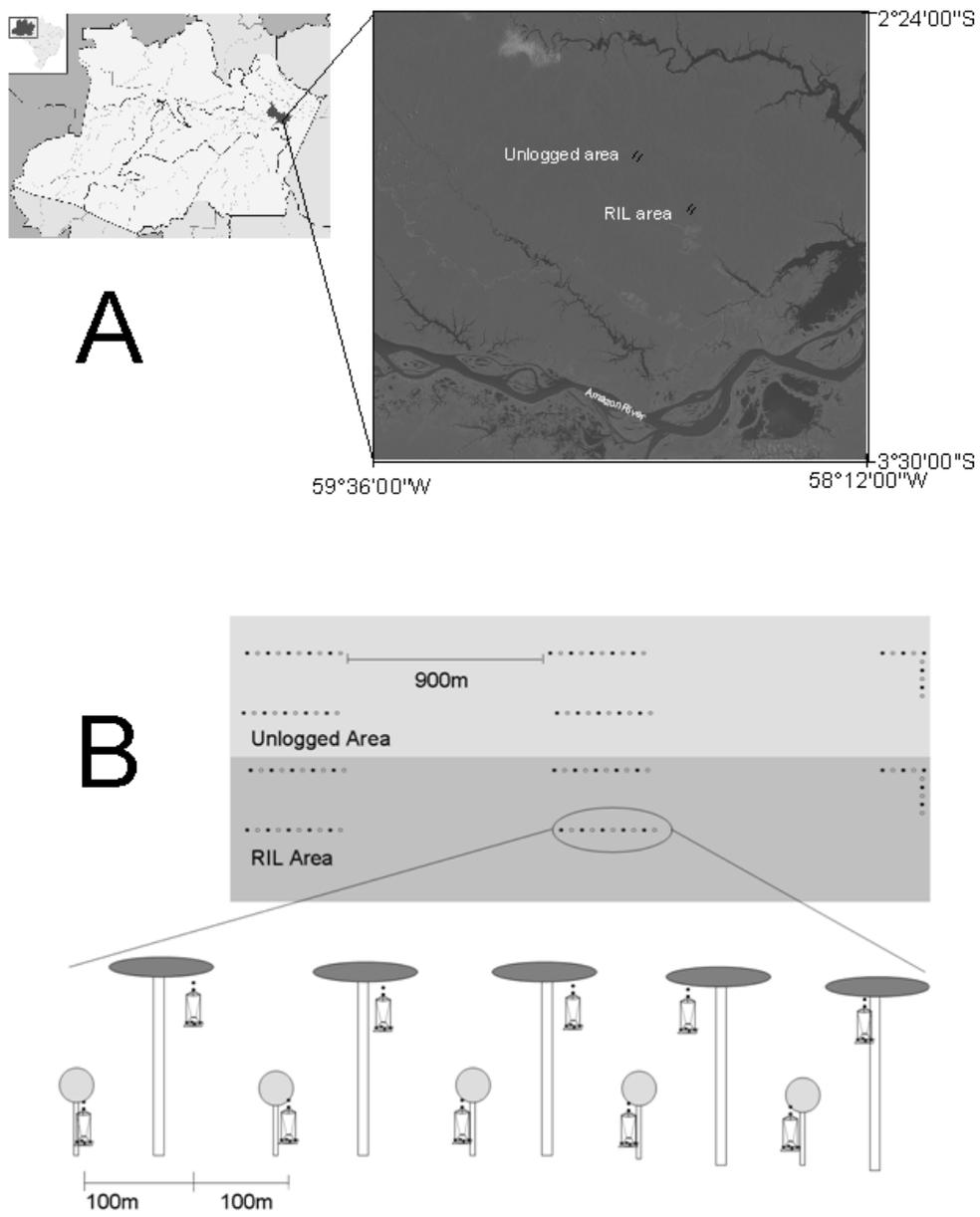
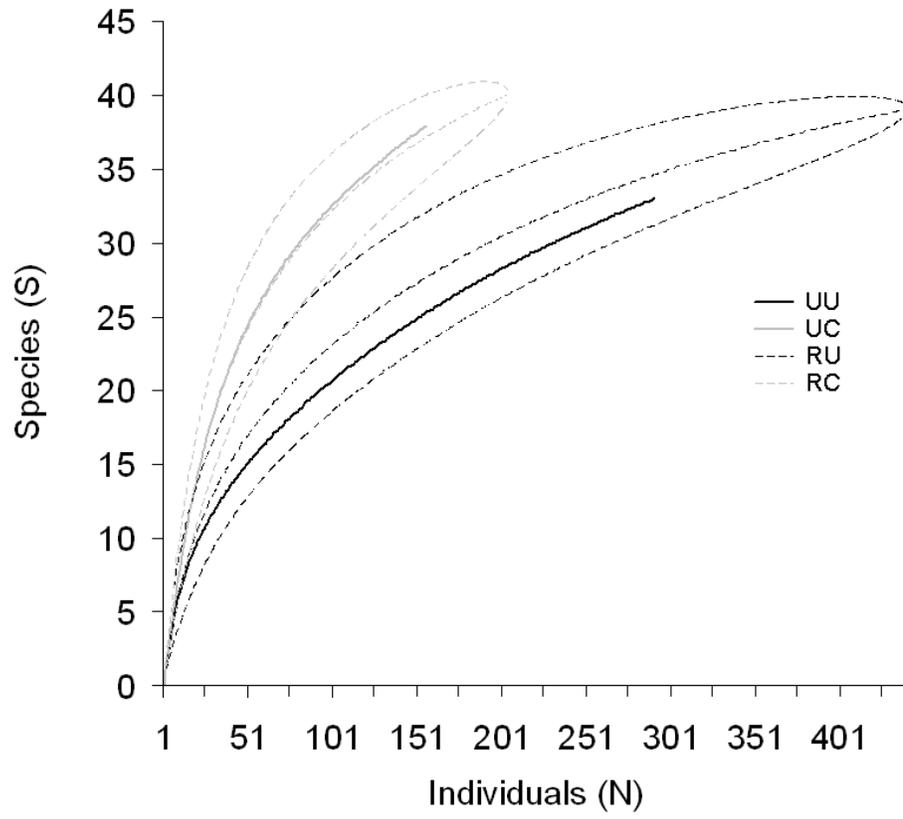
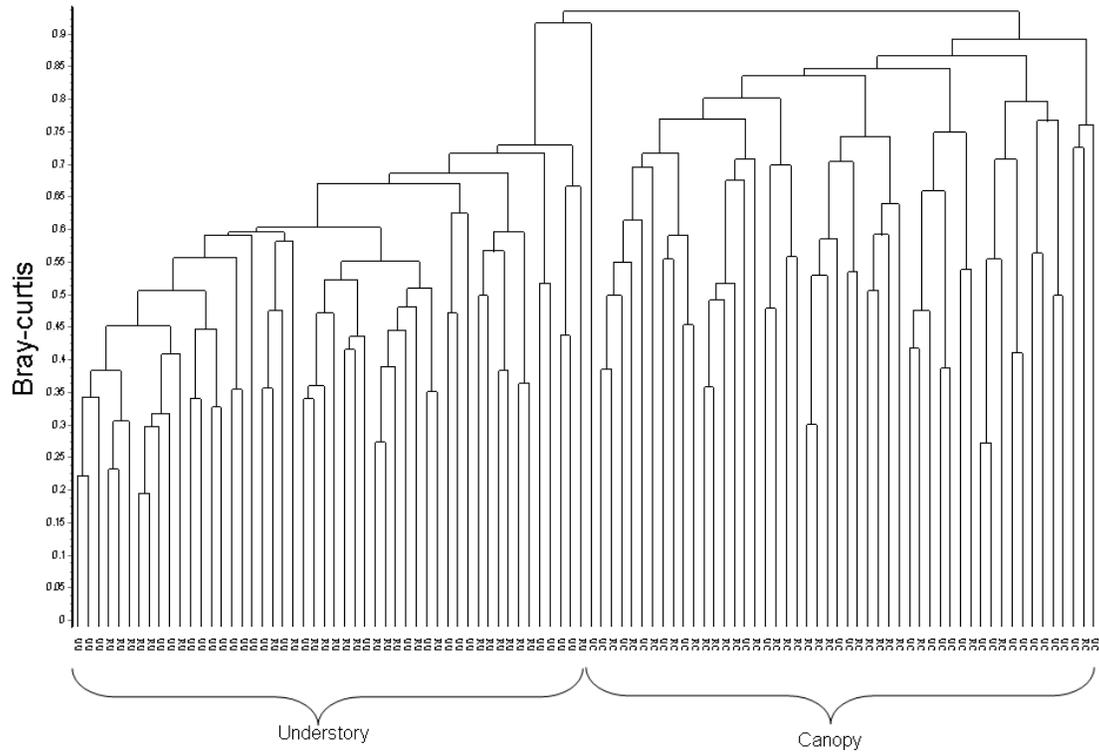


Figure 2

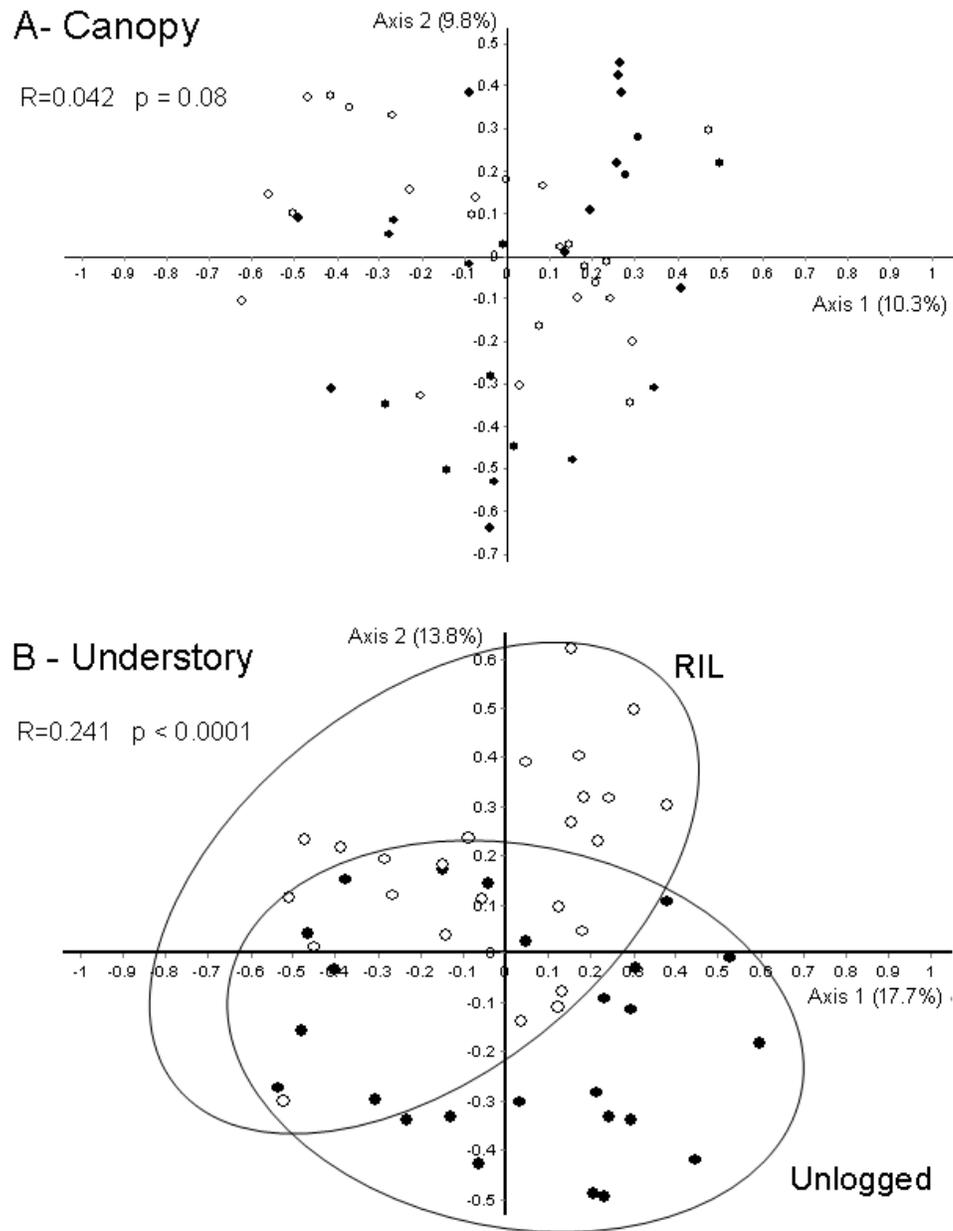


Figure



3

Figure 4



**Appendix** - Occurrence of the fruit-feeding butterflies' species in Itacoatiara - AM, Central Amazon, Brazil.

Specie	Unlogged		RIL*		Total
	Understory	Canopy	Understory	Canopy	
<b>BIBLIDINAE</b>					
<i>Callicore excelsior</i> (Hewitson, [1858])	0	2	0	5	7
<i>Callicore pygas</i> (Godart, [1824])	0	4	0	3	7
<i>Catonephele acontius</i> (L., 1771)	24	2	114	10	150
<i>Catonephele numilia</i> (Cramer, 1771)	0	5	1	2	8
<i>Ectima iona</i> Doubleday, [1848]	0	0	1	0	1
<i>Eunica bechina bechina</i> (Hewitson, 1852)	0	0	0	1	1
<i>Eunica orphise</i> (Cramer, 1775)	0	1	0	2	3
<i>Hamadryas arinome</i> (Lucas, 1853)	1	0	14	8	23
<i>Myscelia capenas</i> (Hewitson, [1857])	0	0	1	0	1
<i>Nessaea obrinus</i> (L., 1758)	56	1	56	1	114
<i>Temenis laothoe</i> (Cramer, 1777)	0	9	0	7	16
<b>Total</b>	<b>81</b>	<b>24</b>	<b>187</b>	<b>39</b>	<b>331</b>
<b>CHARAXINAE</b>					
<i>Agrias amydon</i> Hewitson, [1854]	1	0	0	1	2
<i>Agrias claudina</i> (Godart, [1824])	2	10	4	16	32
<i>Agrias narcissus</i> Staundinger, [1885]	1	3	2	1	7
<i>Archaeoprepona amphimachus</i> (Fabricius, 1775)	1	0	1	0	2
<i>Archaeoprepona demophon</i> (L., 1758)	23	2	22	2	49
<i>Archaeoprepona demophoon</i> (Hübner, [1814])	1	4	3	7	15
<i>Archaeoprepona licomedes</i> (Cramer, 1777)	0	0	1	0	1
<i>Archaeoprepona meander</i> (Cramer, 1775)	3	1	1	0	5
<i>Memphis acidalia</i> (Hübner, [1819])	1	3	2	2	8
<i>Memphis basilia</i> (Stoll, 1780)	0	0	0	2	2
<i>Memphis glauce</i> (Felder & Felder, 1862)	0	5	0	9	14
<i>Memphis laertes</i> (Cramer, 1775)	1	2	1	2	6
<i>Memphis leonida</i> (Stoll, 1782)	0	0	0	1	1
<i>Memphis moruus</i> (Fabricius, 1775)	0	1	4	3	8
<i>Memphis oenomais</i> (Boisduval, 1870)	0	3	0	3	6
<i>Memphis phantes</i> (Hopffer, 1874)	1	10	23	16	50
<i>Memphis philumena</i> (Doubleday, [1849])	0	5	0	6	11
<i>Memphis polycarmes</i> (Fabricius, 1775)	0	0	4	8	12
<i>Polygrapha xenocrates</i> (Westwood, 1850)	0	5	0	5	10
<i>Prepona dexamenus</i> Hopffer, 1874	1	5	0	1	7
<i>Prepona eugenes</i> Bates, 1865	0	1	0	0	1
<i>Prepona laertes</i> (Hübner [1811])	1	10	1	7	19
<i>Prepona pheridamas</i> (Cramer, 1777)	10	0	14	0	24
<i>Prepona philipponi</i> Le Moul, 1932	0	2	5	3	10
<i>Prepona pseudomphale</i> Le Moul, 1932	0	2	0	6	8
<i>Prepona rothschildi</i> Moul, 1932	0	1	0	0	1
<i>Siderone galanthis</i> (Cramer, 1775)	0	0	0	1	1
<i>Zaretis itys</i> (Cramer, 1777)	4	4	6	8	34
<i>Zaretis isidora</i> (Cramer, 1779)	0	4	0	8	12
<b>Total</b>	<b>51</b>	<b>83</b>	<b>94</b>	<b>118</b>	<b>346</b>
<b>NYMPHALINAE:COEINI</b>					
<i>Baeotus aeilus</i> (Stoll, 1780)	0	15	2	12	29

Specie	Unlogged		RIL*		Total
<i>Baeotus deucalion</i> (Felder & Felder, 1860)	0	1	0	1	2
<i>Baeotus japetus</i> (Staudinger, [1885])	1	0	0	0	1
<i>Colobura dirce</i> (L., 1758)	0	0	4	0	4
<i>Historis acheronta</i> (Fabricius, 1775)	2	12	0	7	21
<i>Historis odius</i> (Fabricius, 1775)	0	0	0	1	1
<i>Tigridia acesa</i> (L., 1758)	21	1	31	0	53
<b>Total</b>	<b>24</b>	<b>29</b>	<b>37</b>	<b>21</b>	<b>111</b>
SATYRINAE:SATYRINI					
<i>Cepheptychia cephus</i> (Fabricius, 1775)	0	0	1	0	1
<i>Chloreptychia herseis</i> (Godart, [1824])	0	0	4	0	4
<i>Cissia myncea</i> (Cramer, 1780)	0	1	0	0	1
<i>Magneptychia ca. analis</i> (Godman, 1905)	0	3	0	4	7
<i>Magneptychia libie</i> (L., 1767)	0	0	0	1	1
<i>Megeptychia antonoe</i> (Cramer, 1775)	0	6	0	1	7
<i>Pareptychia lydia</i> (Cramer, 1777)	1	0	0	0	1
<i>Taygetis ca. cleopatra</i> Felder & Felder, 1867	1	0	3	0	4
<i>Taygetis echo</i> (Cramer, 1775)	2	0	3	0	5
<i>Taygetis laches</i> (Fabricius, 1793)	2	0	5	0	7
<i>Taygetis sosis</i> Hopffer, 1874	4	0	2	0	6
<i>Taygetis</i> sp1	3	0	0	0	3
<i>Taygetis</i> sp2	1	0	2	0	3
<b>Total</b>	<b>14</b>	<b>10</b>	<b>20</b>	<b>6</b>	<b>50</b>
SATYRINAE:BRASSOLINI					
<i>Bia actorion</i> (L., 1763)	51	1	49	0	101
<i>Catoblepia berecynthia</i> (Cramer, 1777)	12	0	17	0	29
<i>Catoblepia xanthus</i> (L., 1758)	42	1	25	2	70
<i>Opsiphanes cassiae</i> (L., 1758)	0	0	1	0	1
<i>Opsiphanes invirae</i> (Hübner, [1808])	3	8	3	18	32
<i>Opsiphanes quiteria</i> (Stoll, 1780)	1	0	2	0	3
<i>Selenophanes cassiope</i> (Cramer, 1775)	1	0	2	0	3
<b>Total</b>	<b>110</b>	<b>10</b>	<b>99</b>	<b>20</b>	<b>239</b>
SATYRINAE:MORPHIINI					
<i>Morpho helenor</i> (Cramer, 1776)	11	0	3	0	14
<b>Total Abundance</b>	<b>291</b>	<b>156</b>	<b>440</b>	<b>204</b>	<b>1091</b>

\* = Reduced Impact Logging

## **Stratigraphic and temporal variability in the detectability of fruit-feeding butterflies and moths in tropical forest**

**Danilo Bandini Ribeiro<sup>1,2\*</sup>, Matthew R. Williams<sup>3</sup>, Alexandre Specht<sup>4</sup>, André V. L. Freitas<sup>1</sup>**

<sup>1</sup> Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, P.O. Box 6109, 13083-970 Campinas, São Paulo, Brazil.

<sup>2</sup> Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas

<sup>3</sup> Department of Environment and Conservation, Science Division, Locked Bag 104, Bentley Delivery Centre, Western Australia 6983, Australia.

<sup>4</sup> Centro de Ciências Agrárias e Biológicas, Instituto de Biotecnologia, Universidade de Caxias do Sul, Caxias do Sul, Rio Grande do Sul, Brasil PO Box 1352, 95070-560.

\*correspondence author: [biodbr@yahoo.com.br](mailto:biodbr@yahoo.com.br)

Running headline: Detectability of fruit-feeding butterflies and moths

## ABSTRACT

1. One source of variation in sampling protocols is detectability: failure to detect a species at a site does not necessarily imply that it is absent. This is an important issue for taxa that are widely used as environmental indicators, such as butterflies.
2. In tropical forests, the detectability of many species is very low and they may be overlooked, it is therefore important to measure it, to avoid false inferences.
3. To address this question, we examined how detectability of fruit feeding butterflies and moths varied between strata (understory vs. canopy), temporally across sampling periods during the year, and in relation to observed abundance. We used the results to estimate the sampling effort needed to detect a representative fraction of the butterfly and moth assemblage.
4. Detectability was positively and significantly correlated with observed abundance.
5. In the Amazon, most species significantly more detectable in one specific strata (canopy or understory).
6. Detectability showed large temporal variation in Atlantic Forest, with Biblidinae, Charaxinae and Satyrini all showing distinct peaks during July-August, November and March. In contrast, Brassolini and Coeini showed peak detectability in January and March respectively.
7. The stratigraphic and temporal variation in detectability lead us to conclude that sampling designs must strategically apply sampling effort to the correct seasons and strata to improve the accuracy of results.

8. The minimal sampling effort for detecting 25% of the species present in these tropical forests is 130 trap-days in Atlantic Forest and 510 days in Central Amazon.

**Keywords:** Amazon, Atlantic Forest, Catocalinae, Lepidoptera, Noctuidae, Nymphalidae, Sampling design.

## INTRODUCTION

A crucial task for conserving and managing biodiversity is estimating the number and abundance of species present in a given area (Colwell & Coddington 1994; Lawton *et al.* 1998; Waltert *et al.* 2011). One important source of variation in sampling protocols is detectability - few animals will always be detected when present, and failure to detect a species does not necessarily mean that it is absent (MacKenzie *et al.* 2002). False absences occur when a species is actually present but is overlooked, and these lead to incomplete species lists and underestimates of the geographic distribution of the species (Pellet 2008). This is an important issue for taxa that are widely used as environmental indicators, such as butterflies, and for which biased inferences can cascade down to other taxonomic groups of interest (Thomas 2005; Barlow *et al.* 2007a). Assessing the adequacy of sampling regimes and the adequacy of species lists therefore is important to avoid bias and ensure correct inference (Dorazio *et al.* 2006; Kery & Plattner 2007; Kery *et al.* 2009; Longcore *et al.* 2010).

Tropical regions harbor 90% of the butterfly diversity in the world, however, tropical species are very poorly studied when compared with their temperate counterparts (Bonebrake *et al.* 2010). In addition to the financial and logistical constraints of working in tropical biomes, the high diversity also presents challenges: the numbers of butterfly species in these habitats are so high that daily lists can exceed 500 recorded species (K.S. Brown and A.V.L. Freitas, personal communication). In these diverse spots, the detectability of many species could be very low, and these could be easily overlooked. For this reason it is important to know the detectability of these species in tropical areas,

both to avoid false inferences and to quantify the (un)certainty in estimates of species richness and diversity.

Detectability can also vary between observers (Schlicht, Swengel & Swengel 2009) and it is further affected by the appearance and behavior of butterflies (Dennis *et al.* 2006) as well as by weather conditions (Zheng *et al.* 2007). Therefore, the assumptions of perfect detection or even equal detection across species are far from being true when using the standard methods of assessing diversity, such as transect counts (Kery & Plattner 2007). In tropical regions the use of transect counts is even more problematic due to the high diversity of butterflies (Holloway 1998; Walpole & Sheldon 1999; Caldas & Robbins 2003).

An alternative way to sample butterflies in tropical areas is to focus on fruit-feeding Nymphalidae (Hamer *et al.* 2003; Hamer *et al.* 2005; Veddeler *et al.* 2005; Ribeiro *et al.* 2008; Ribeiro *et al.* 2010; Waltert *et al.* 2011). The adults in this clade gain virtually all of their nutritional requirements by feeding on rotting fruits or plant sap, and are represented mainly by species in the subfamilies Biblidinae, Charaxinae, Satyrinae (including Satyrini, Brassolini and Morphini), and the tribe Coeini (Nymphalinae) (Wahlberg *et al.* 2009). The richness of fruit-feeding butterflies represents 50% to 75% of the total richness of the Neotropical Nymphalidae (Brown 2005) and is strongly correlated with the total butterfly richness in a given area (Brown & Freitas 2000; Horner-Devine *et al.* 2003).

Sampling fruit-feeding butterflies also offers practical advantages, as they can be easily captured in traps baited with rotting fruits and simultaneous sampling with standardized effort at different sites is feasible. The use of baited traps also avoids problems such as

different detection rates between observers (Kery & Plattner 2007; Schlicht, Swengel & Swengel 2009) and biased detection of the most active and conspicuous species (Dennis *et al.* 2006; Zheng *et al.* 2007). These traps also enable capture of moths, which have been rarely studied. However, an unresolved question is how detectability using this sampling method varies across species and habitats, and how much sampling effort is necessary to adequately assess the fauna in a given area. To address this question, we examined how detectability of fruit feeding butterflies and moths 1) varied between strata (understory vs. canopy); 2) varied temporally across sampling periods during the year; 3) varied in relation to observed abundance; and 4) affects estimates of the sampling effort needed to detect a representative fraction of the butterfly and moth assemblage.

## **MATERIALS AND METHODS**

### **Lepidoptera sampling**

We sampled butterflies and moths in two regions (Atlantic and Amazon forests, Brazil) using baited traps and standard methodology (Ribeiro *et al.* 2008; Ribeiro *et al.* 2010). Each trap was baited with a fermented mixture of banana and sugar-cane juice, and sampled at 48 h intervals. At each visit, every captured individual was identified and released, and the bait replaced. The few individuals that could not be readily identified in the field were retained for later identification.

### *Atlantic Forest*

Field work was carried out in a landscape fragmented by clearing for agriculture, in the São Luiz do Paraitinga municipality, São Paulo State, south-eastern Brazil (centred in 23°20'S, 45°20'W), near the 'Serra do Mar' mountain range. We sampled 10 replicate fragments with similar structural characteristics (size, shape and normalized difference in vegetation index) from two landscapes in adjacent river basins of similar area. In each fragment five traps 30 m apart were deployed along a linear transect, with each trap suspended from low branches such that the platform hung between 1 m and 1.5 m above the ground (Ribeiro *et al.* 2008; Ribeiro *et al.* 2010). Traps remained open for eight days each month, yielding 4800 total trap days. The butterflies were sampled monthly from June 2004 to May 2005.

### *Amazon Forest*

The study area was located in the Amazon River Basin, Itacoatiara Municipality, Amazon State, Brazil, and is property of the "Precious Woods Amazon" (centred in 2°53'39" S, 58°42'58" W). Two sites were sampled: an area of primary forest and a 3-year-old area of regenerating forest under Reduced-Impact Logging management (Putz *et al.* 2008). The sites were ca. 25 km apart, and embedded within a continuum of forest of ca. 6 million km<sup>2</sup>.

Fifty traps were placed in each site, within two strata: 25 in understory (1.5 m above the ground) and 25 in canopy (ca. 20 m above ground and inside tree crowns). Traps were installed along transects, comprising ten traps at alternating heights to avoid any

interference of canopy traps with the understory traps. Each transect of 10 traps was disposed 900 m apart from any other. The transects were arranged in a 10 km long “U” shape, ignoring topography, and sampling a representative range of variation in forest structure within each habitat. Traps were sampled monthly from August to November 2007, and remained open for 12 days (Ribeiro *et al.* 2008; Ribeiro *et al.* 2010) totaling 4,800 trap-days.

### **Data analysis**

We estimated the detectability of each species for which the number of captures was 10 or greater. The analytical approach and notation follows that of MacKenzie *et al.* (2002): the observed data (i.e.,  $N$ , the total number of surveyed sites;  $T$ , the number of distinct sampling occasions;  $n_t$ , the number of sites where the species was detected at time  $t$ ; and  $n$ , the total number of sites at which the species was detected at least once) was used to estimate two parameters ( $\Psi_i$ , the probability that a species is present at site  $i$ ; and  $p_i$ , the probability that a species will be detected at site  $i$ , given that it is present). The software MARK (White & Burnham 1999) was used to calculate the detectability of each species for two alternative models: in the first, detectability was time invariant ( $p_i$ ); in the second, detectability varied between months ( $p_{it}$ ). In both models  $\Psi$  and  $p$  varied across species. We used Akaike’s information criterion, adjusted for small sample size (AICc), to select the best model for each species (Burnham & Anderson 2002).

Spearman rank correlation was used test to the relationship between estimated detectability and observed abundance for four abundance categories: “rare” species, with 10 to 20 observed individuals; “common” species, with 21 to 50 individuals; “abundant”

species, with 51 to 150 individuals; and “very abundant” species, with more than 150 individuals.

## RESULTS

The numbers of observed species with abundances of 10 or more were: Atlantic Forest butterflies (45 species), Amazon Forest butterflies (25) and Amazon Forest moths (7). In the Amazon, 11 species were significantly more detectable in the canopy than in the understory, whereas 11 were more detectable in the understory, and for three species detectability was similar in both strata (Fig. 1a, b). Similarly, of the Amazon Forest moths, four were significantly more detectable in canopy, two in understory and one had similar detectability in both strata (Fig. 1c).

The time varying model was the best fit for all Atlantic Forest butterflies (Appendix 1). Detectability showed large variation between months, with Biblidinae, Charaxinae and Satyrini all showing three distinct peaks – during July-August, November and March (Fig. 2a). In contrast, Brassolini and Coeini showed peak detectability in January and March, respectively (Fig. 2b).

Similarly, half of the Amazon Forest understory butterflies and all of the Amazon Forest Moths were best fit by a time varying model (Appendix 2). The remaining species (Amazon Forest canopy butterflies, and the other half of the Amazon Forest understory butterflies) were best fit by the time invariant model (Appendix 2).

The cumulative detectability (i.e. the number of species recorded with increasing sample effort) of butterflies in the Atlantic forest was greater than in both strata of Amazon forest (Fig. 3). For the most common species in the Amazon Forest, understory species were

detected more rapidly than those in the canopy, but beyond approximately 200 trap surveys was almost equal for both common and rare species.

Detectability was positively and significantly correlated with abundance in all levels tested (Fig. 4): “rare” species (d.f. = 42;  $p < 0.001$ ;  $r = 0.70$ ), “common” species (d.f.= 22,  $p = 0.004$ ;  $r = 0.56$ ), “abundant” species (d.f. = 13;  $p = 0.005$ ,  $r = 0.68$ ) and “very abundant” species (d.f. = 13  $p < 0.001$ ,  $r = 0.77$ ).

## **DISCUSSION**

Determining habitat preference (canopy or understory) is very important for assessing the likely impacts of fragmentation and disturbance on individual species (Koh 2007) and almost all Amazon butterflies and moths sampled in the present study were more readily trapped in one specific stratum. Although several species were trapped in both, there was a tendency for species to be generally restricted to (and be captured more frequently) in only one. Similar patterns were found in previous studies (DeVries, Walla & Greeney 1999; Barlow *et al.* 2007b), showing that the stratification of fruit feeding butterflies is a common pattern in undisturbed tropical forest. Indeed, in the present study, even the most common canopy species were rarely sampled in the understory. Thus, using a sampling protocol that does not locate traps in both strata will increase the imperfect detection of many butterflies and could lead to incorrect inferences about the richness and diversity in a given area, as has been found in studies elsewhere (DeVries 1988; Schulze, Linsenmaier & Fiedler 2001; Fermon *et al.* 2005). Locating traps in different strata is indispensable in studies on tall forests like the Amazon.

Butterfly subfamilies showed two main patterns of detectability in Atlantic forest, with one or three peaks in detectability during the year. The period with highest average detectability for all subfamilies was from January to April, and is probably the best season for sampling fruit feeding butterflies in Atlantic forest (Ebert 1969; Brown 1992). This is a dominant pattern for fruit feeding butterflies (Ribeiro *et al.* 2010), and may also hold for butterflies in general in the southern portion of the Atlantic Forest. The differences in detectability between months in the Amazon forest showed that even in an experimental designed to sample butterflies during periods that enhance capture probability, there are still important differences in butterfly detectability across months. The great variation in butterfly assemblages among seasons is a well known characteristic of fruit feeding Nymphalidae (DeVries & Walla 2001; Barlow *et al.* 2007b), but this study showed that this variation also occurs at smaller temporal scales. The remarkable exceptions to this pattern were found in the canopy butterflies in Amazon forest, all of which were better explained by the time invariant model, i.e., detectability was temporally less variable than in understory. This “seasonal invariance” in canopy butterflies assemblages may be due to the microclimatic differences between canopy and understory – the forest canopy is an exposed habitat with great infra-daily variations in microclimatic conditions and the fauna in this stratum should be more adapted to these variations. Those adaptations to infra-daily variations probably enable canopy species to withstand a greater range of microclimatic conditions and stay active during days when understory species are not able to fly, leading to different patterns in detectability between strata. Similarly, the detectability of moths may be better explained by the time

invariant model because they are less sensitive to changes in temperature than butterflies (Ribeiro & Freitas 2010) due to their nocturnal behavior (Daily & Ehrlich 1996).

The maximum detectability (i.e. the higher value found in the present study) for a given species ranged from 0.02 to 0.80 per trap/survey (i.e one trap opened for 48h and inspected at the end of the period; Appendices). Similar ranges were found for transect surveys in temperate regions (Dorazio *et al.* 2006; Gross *et al.* 2007; Zheng *et al.* 2007; Pellet 2008; Williams 2009; Williams, Lamont & Henstridge 2009; Longcore *et al.* 2010), however, they were rarely as low as 0.02, because most of the transects were conducted during the season that enhanced detection probability, and many of them were focal studies addressed to one or few species. The modeling of detectability has several underlying assumptions that impose some caveats on our results. First, detectability is estimated using the assumption that the species is actually present at the site, and so available to be captured. This cannot be known for many species, which may have strongly seasonal appearance (notably Brassolini and Nymphalinae in this study) or be highly vagile and only temporary visitors to some sites. These factors will bias detectability downwards. Nonetheless, the values presented for each species (Appendices) provide a method of determining minimum sample effort required to detect each with a specified level of certainty (i.e. to obtain a level of certainty of detecting a particular species of 95%, the number of repeat samples required is ~

$$\frac{\log(1-0.95)}{\log(1-p)}).$$

Detectability increased with abundance, presumably as the more individuals available for capture the greater the likelihood of recording that species one or more times. However, this is not the only factor affecting detectability, as we could see inspecting the data

dispersion around the trend line (Fig. 4). Morphological and behavioral features affect butterfly detection in transect counts, as well as local weather conditions, temperature, season and the variability in observer ability (Dennis *et al.* 2006; Dennis, Shreeve & Van Dyck 2006; Zheng *et al.* 2007; Pellet 2008; Schlicht, Swengel & Swengel 2009). Except for the last factor, all of these can affect detection probability of butterflies in baited traps. Another crucial factor in fruit-feeding butterflies is the relative attractiveness to the bait for each species, and this needs further investigation. However, this study is the first to estimate the detection probability of butterflies in tropical areas and provides an initial point to improve sampling protocols in this diverse region, with a view to reduce the present lack of detailed information about tropical butterflies.

According to (Pearman & Weber 2007) the general pattern of butterfly distribution is correlated with the 25% most common species. Assuming the same pattern for fruit-feeding Nymphalidae, a minimum “adequate” sampling regime should detect 25% of the actual number of species to minimally describe regional diversity patterns. The estimated number of species in the Atlantic and Amazon forests are 86 and 103 species, respectively (D.B.R., unpublished data), so an adequate number of traps should detect at least 22 and 26 of the most common species. The minimum sampling effort to achieve this is 65 trap surveys (130 trap-days) in Atlantic forest, and 255 trap surveys (510 trap-days) in Amazon forest (Fig. 3), with half of the traps placed in the canopy if the study area is tall forest. Additionally, such sampling should use temporal replication over a short period to improve the interpretability of the data collected (Kéry *et al.* 2009).

## ACKNOWLEDGEMENTS

We thank the Department of Environment and Conservation, Western Australia for support during the manuscript preparation. D.B.R. thanks FAPESP for a fellowship (grants #07/50896-0, #03/11697-0) and The Lepidoptera Research Foundation for financial support. A.V.L.F. was supported by CNPq (300282/2008-7), FAPESP (00/01484-1 and 04/05269-9) and the US National Science Foundation (DEB-0527441).

## LITERATURE CITED

- Barlow, J., Gardner, T.A., Araujo, I.S., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, L., Ribeiro-Junior, M.A., Motta, C.d.S., Silva, M.N.F.d. & Peres, C.A. (2007a) Quantifying the biodiversity value of tropical primary, secondary and plantation forests. *Proceedings of the National Academy of Science of the United States of America*, **104**, 18555-18560.
- Barlow, J., Overal, W.L., Araujo, I.S., Gardner, T.A. & Peres, C.A. (2007b) The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *Journal of Applied Ecology*, **44**, 1001-1012.
- Bonebrake, T.C., Ponisio, L.C., Boggs, C.L. & Ehrlich, P.R. (2010) More than just indicators: A review of tropical butterfly ecology and conservation. *Biological Conservation*, **143**, 1831-1841.
- Brown, K.S. (1992) Borboletas da Serra do Japi: diversidade, habitats, recursos alimentares e variação temporal. *História Natural da Serra do Japi: Ecologia e Preservação de uma Área Florestal no Sudeste do Brasil* (ed. L.P.C. Morellato), pp. 142-186. Editora Unicamp, Campinas.
- Brown, K.S. (2005) Geologic, evolutionary, and ecological bases of the diversification of neotropical butterflies: Implications for conservation. *Tropical Rainforest: Past, Present, and Future* (eds C.W. Dick & G. Moritz), pp. 166-201. The University of Chicago Press, Chicago.
- Brown, K.S. & Freitas, A.V.L. (2000) Atlantic forest butterflies: Indicators for Landscape Conservation. *Biotropica*, **32**, 934-956.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer, New York.
- Caldas, A. & Robbins, R.K. (2003) Modified Pollard transects for assessing tropical butterfly abundance and diversity. *Biological Conservation*, **110**, 211-219.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B*, **345**, 101-118.

- Daily, G.C. & Ehrlich, P.R. (1996) Nocturnality and species survival. *Proceedings of the National Academy of Science of the United States of America*, **93**, 11709-11712.
- Dennis, R.L.H., Shreeve, T.G., Isaac, N.J.B., Roy, D.B., Hardy, P.B., Fox, R. & Asher, J. (2006) The effects of visual apparency on bias in butterfly recording and monitoring. *Biological Conservation*, **128**, 486-492.
- Dennis, R.L.H., Shreeve, T.G. & Van Dyck, H. (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity and Conservation*, **15**, 1943-1946.
- DeVries, P.J. (1988) Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera*, **26**, 98-108.
- DeVries, P.J. & Walla, T.R. (2001) Species diversity and community structure in neotropical fruit-feeding butterflies *Biological Journal of the Linnean Society*, **74**, 1-15.
- DeVries, P.J., Walla, T.R. & Greeney, H.F. (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, **68**, 333-353.
- Dorazio, R.M., Royle, J.A., Soderstrom, B. & Glimskar, A. (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, **87**, 842-854.
- Ebert, H. (1969) On the frequency of butterflies in eastern Brazil, with a list of the butterfly fauna of Poços de Caldas, Minas Gerais. *The Journal of the Lepidopterists' Society*, **23**, 1-35.
- Fermon, H., Waltert, M., Vane-Wright, R.I. & Mühlenberg, M. (2005) Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodiversity and Conservation*, **14**, 333-350.
- Gross, K., Kalendra, E.J., Hudgens, B.R. & Haddad, N.M. (2007) Robustness and uncertainty in estimates of butterfly abundance from transect counts. *Population Ecology*, **49**, 191-200.
- Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M. & Chey, V.K. (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, **40**, 150-162.
- Hamer, K.C., Hill, J.K., Mustaffa, N., Benedick, S., Sherratt, T.N., Chey, V.K. & Maryati, M. (2005) Temporal variation in abundance and diversity of butterflies in Bornean rain forests: opposite impacts of logging recorded in different seasons. *Journal of Tropical Ecology*, **21**, 417-425.
- Holloway, J.D. (1998) Geological signal and dispersal noise in two contrasting insect groups in the Indo-Australian tropics: R-mode analysis of pattern in Lepidoptera and cicadas. *Biological and Geological Evolution of SE Asia* (eds R. Hall & J.D. Holloway), pp. 291-314. Backhuys, Leiden.
- Horner-Devine, M.C., Daily, G.C., Ehrlich, P.R. & Boggs, C.L. (2003) Countryside biogeography of tropical butterflies. *Conservation Biology*, **17**, 168-177.
- Kery, M. & Plattner, M. (2007) Species richness estimation and determinants of species detectability in butterfly monitoring programmes. *Ecological Entomology*, **32**, 53-61.

- Kéry, M., Royle, J.A., Plattner, M. & Dorazio, R.M. (2009) Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, **90**, 1279-1290.
- Kéry, M., Soldaat, L., van Strien, A., Zuiderwijk, A., Dorazio, R.M. & Royle, J.A. (2009) Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, **46**, 1163-1172.
- Koh, L.P. (2007) Impacts of land use change on South-east Asian forest butterflies: a review. *Journal of Applied Ecology*, **44**, 703-713.
- Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. & Watt, A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, **391**, 72-76.
- Longcore, T., Lam, C.S., Kobernus, P., Polk, E. & Wilson, J.P. (2010) Extracting useful data from imperfect monitoring schemes: endangered butterflies at San Bruno Mountain, San Mateo County, California (1982-2000) and implications for habitat management. *Journal of Insect Conservation*, **14**, 335-346.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy when detection probabilities are less than one. *Ecology*, **83**, 2248-2255.
- Pearman, P.B. & Weber, W. (2007) Common species determine richness patterns in biodiversity indicator taxa. *Biological Conservation*, **138**, 109-119.
- Pellet, J. (2008) Seasonal variation in detectability of butterflies surveyed with Pollard walks *Journal of Insect Behaviour*, **12**, 155-162.
- Putz, F.E., Sist, P., Fredericksen, T. & Dykstra, D. (2008) Reduced-impact logging: Challenges and opportunities. *Forest Ecology and Management*, **256**, 1427-1433.
- Ribeiro, D.B. & Freitas, A.V.L. (2010) Differences in thermal responses in a fragmented landscape: Temperature affects the sampling of diurnal, but not nocturnal fruit-feeding Lepidoptera. *Journal of Research on the Lepidoptera*, **42**, 1-4.
- Ribeiro, D.B., Prado, P.I., Brown, K.S. & Freitas, A.V.L. (2008) Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. *Diversity and Distributions*, **14**, 961-968.
- Ribeiro, D.B., Prado, P.I., Jr., K.S.B. & Freitas, A.V.L. (2010) Temporal Diversity Patterns and Phenology in Fruit-Feeding Butterflies in the Atlantic Forest. *Biotropica*, **42**, 710-716.
- Schlicht, D., Swengel, A. & Swengel, S. (2009) Meta-analysis of survey data to assess trends of prairie butterflies in Minnesota, USA during 1979-2005. *Journal of Insect Conservation*, **13**, 429-447.
- Schulze, C.H., Linsenmaier, K.E. & Fiedler, K. (2001) Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology*, **153**, 133-152.
- Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 339-357.
- Veddeler, D., Schulze, C.H., Steffan-Dewenter, I., Buchori, D. & Tschardtke, T. (2005) The contribution of tropical secondary forest fragments to the conservation of

- fruit-feeding butterflies: effects of isolation and age. *Biodiversity and Conservation*, **14**, 3577-3592.
- Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V.L. & Brower, A.V.Z. (2009) Nymphalid butterflies diversify following near demise at the cretaceous/tertiary boundary. *Proceedings of the Royal Society B*, **276**, 4295-4302.
- Walpole, M.J. & Sheldon, I.R. (1999) Sampling butterflies in tropical rainforest: an evaluation of a transect walk method. *Biological Conservation*, **87**, 85-91.
- Waltert, M., Bobo, K.S., Kaupa, S., Montoya, M.L., Nsanyi, M.S. & Fermon, H. (2011) Assessing conservation values: biodiversity and endemism in tropical land use systems. *PLoS ONE*, **6**, e16238.
- White, G.C. & Burnham, K.P. (1999) Program mark: survival estimation from populations of marked animals. *Bird Study*, **46 Supplement**, 120-139.
- Williams, M.R. (2009) Butterflies and day-flying moths in a fragmented urban landscape, south-west Western Australia: patterns of species richness. *Pacific Conservation Biology*, **15**, 32-46.
- Williams, M.R., Lamont, B.B. & Henstridge, J.D. (2009) Species-area functions revisited. *Journal of Biogeography*, **36**, 1994-2004.
- Zheng, C., Ovaskainen, O., Saastamoinen, M. & Hanski, I. (2007) Age-dependent survival analyzed with Bayesian models of mark-recapture data. *Ecology Letters*, **88**, 1970-1976.

## Figure captions

Figure 1 - Estimated detectability (per trap per 48 h sample period,  $p$ , +/- S.E.) of fruit-feeding lepidopterans in baited traps in canopy (open bars) and understory (closed bars) in: (a) Amazon Forest butterflies (Charaxinae), Brazil; (b) Amazon Forest butterflies (Satyrinae:Brassolini, Biblinae, Nymphalinae:Coeni), Brazil; and (c) Amazon Forest moths (Catocalinae), Brazil.

Figure 2 - Temporal variation in the detectability (per trap per 48 h sample period,  $p$ , +/- S.E.) of fruit feeding butterflies in Atlantic forest, Brazil: (a) Biblidinae, Charaxinae, and Satyrinae: Satyrini; and (b) Satyrinae: Brassolini, Nymphalinae: Coeni.

Figure 3 - Percentage of fruit-feeding butterflies species detected according to sampling effort (number of traps, sampled after 48 h) needed to detect species with 95% confidence, for three locations: Atlantic Forest, Amazon Forest canopy and understory. The percentage of butterflies is related to the total number of species estimated by each location using the Chao 2 estimator: Atlantic Forest(86), Amazon Forest canopy (67) and understory(60).

Figure 4 - Relationships between detectability and observed abundance, in four categories: (a) “rare” species, with 10 to 20 observed individuals; (b) “common” species, with 21 to 50 individuals; (c) “abundant” species, with 51 to 150 individuals; and (d) “very abundant” species, with more than 150 individuals.

Figure 1a

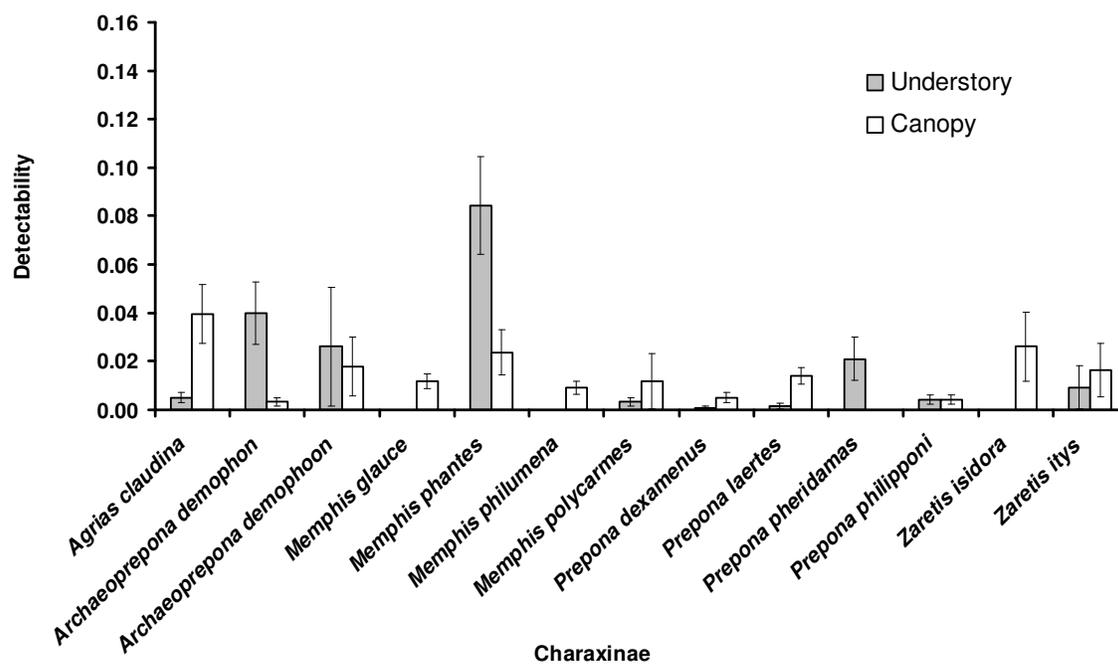


Figure 1b

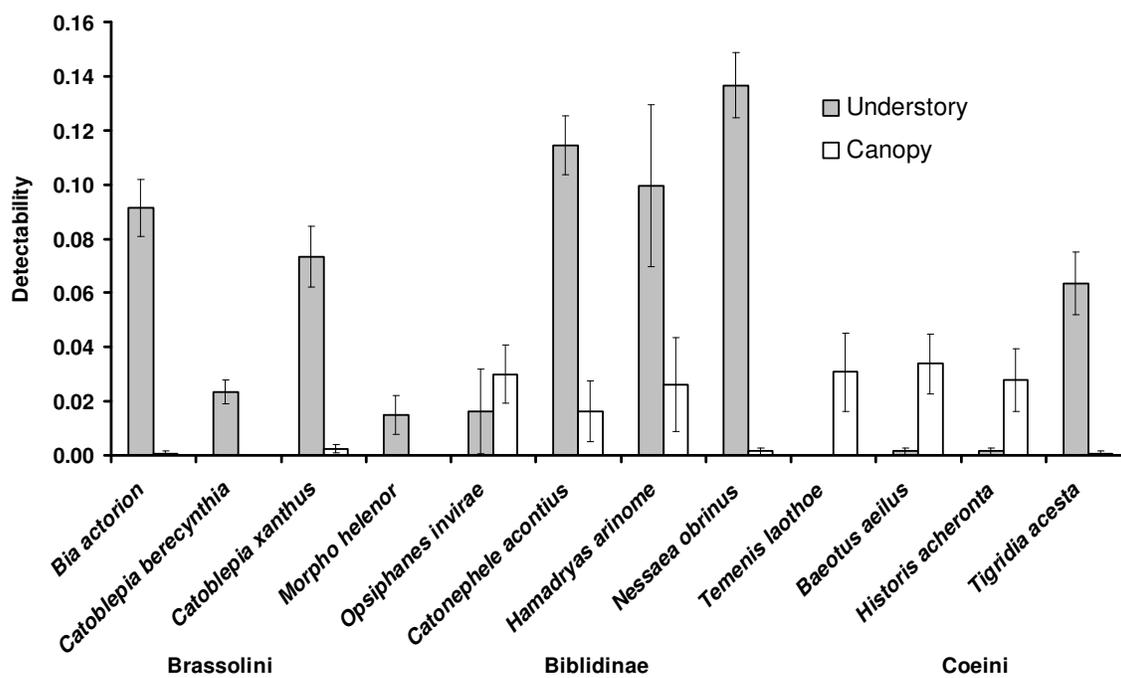


Figure 1c-

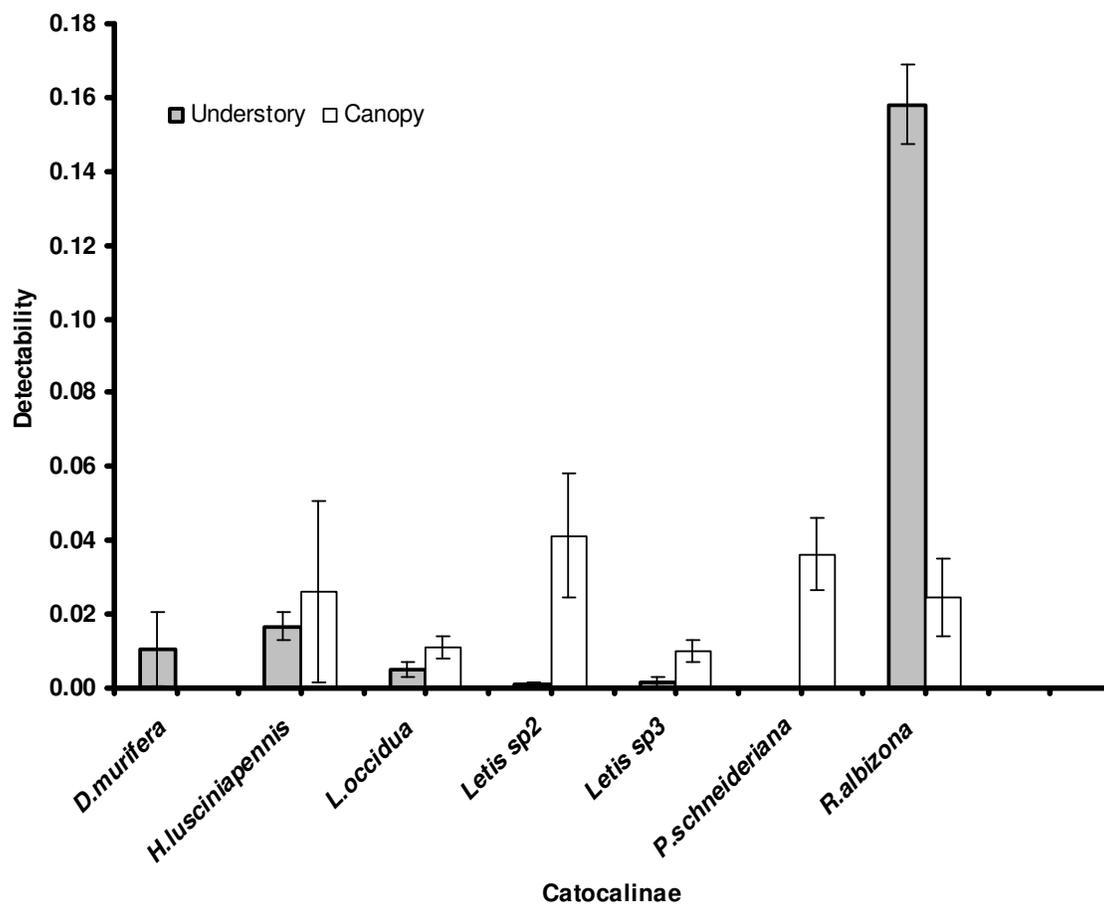


Figure 2-

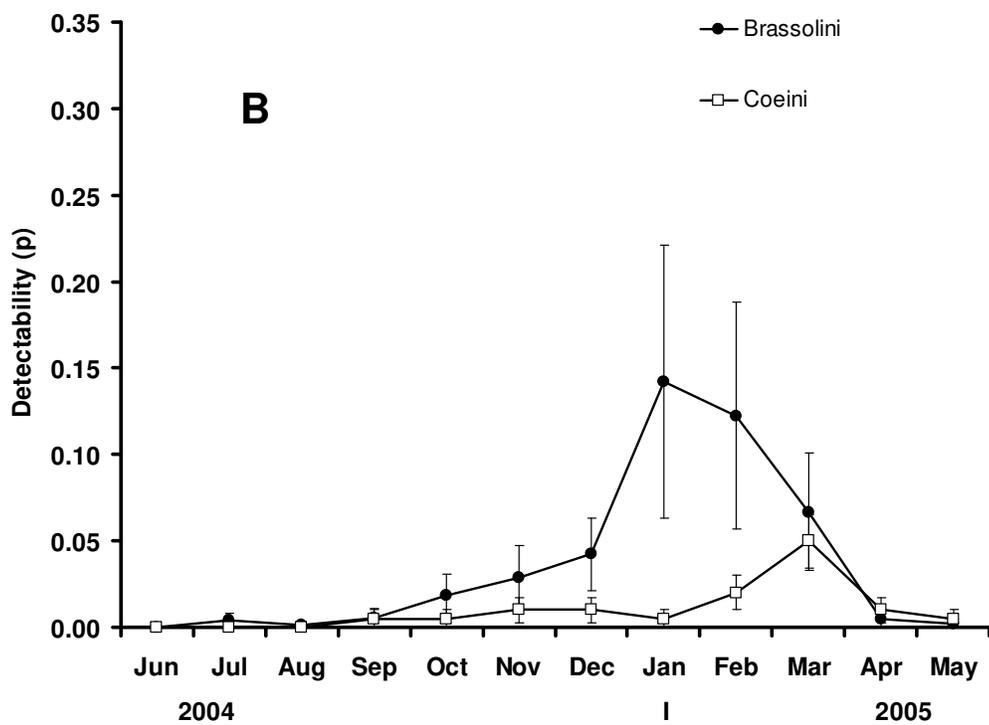
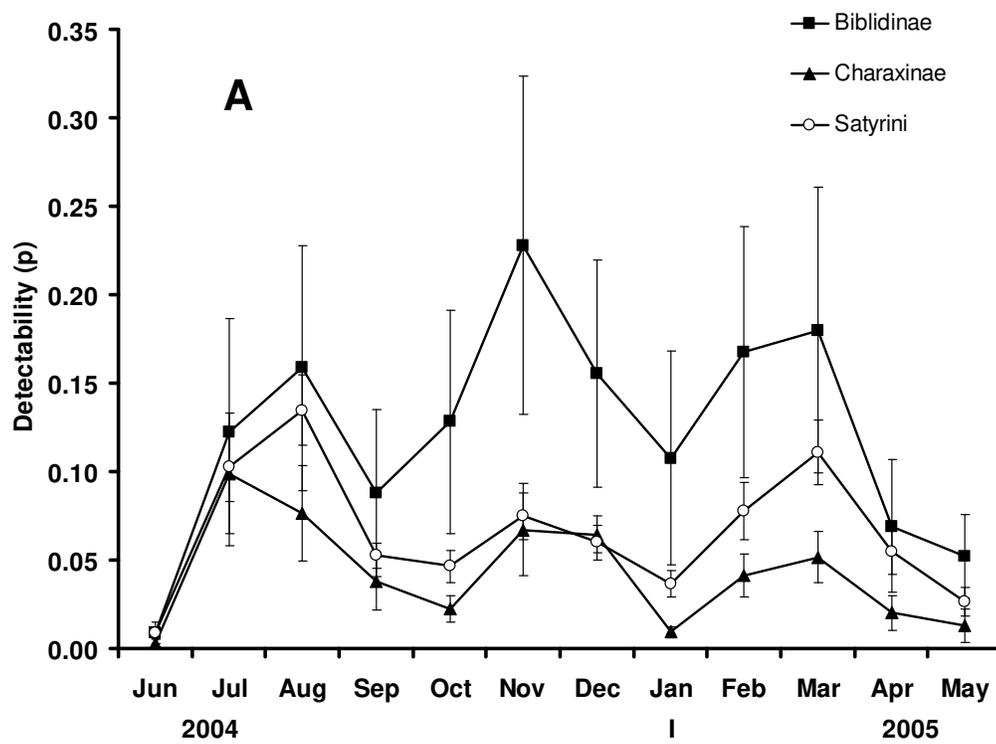


Figure 3-

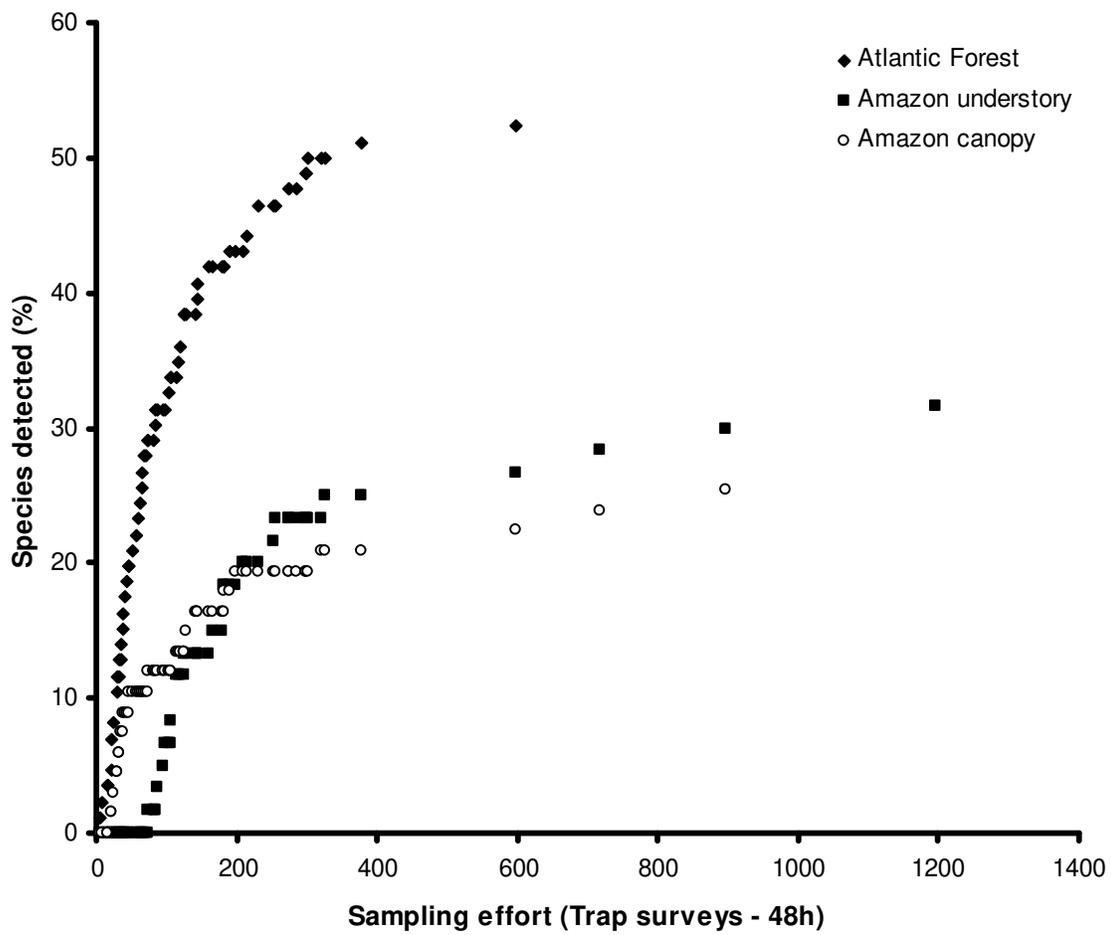
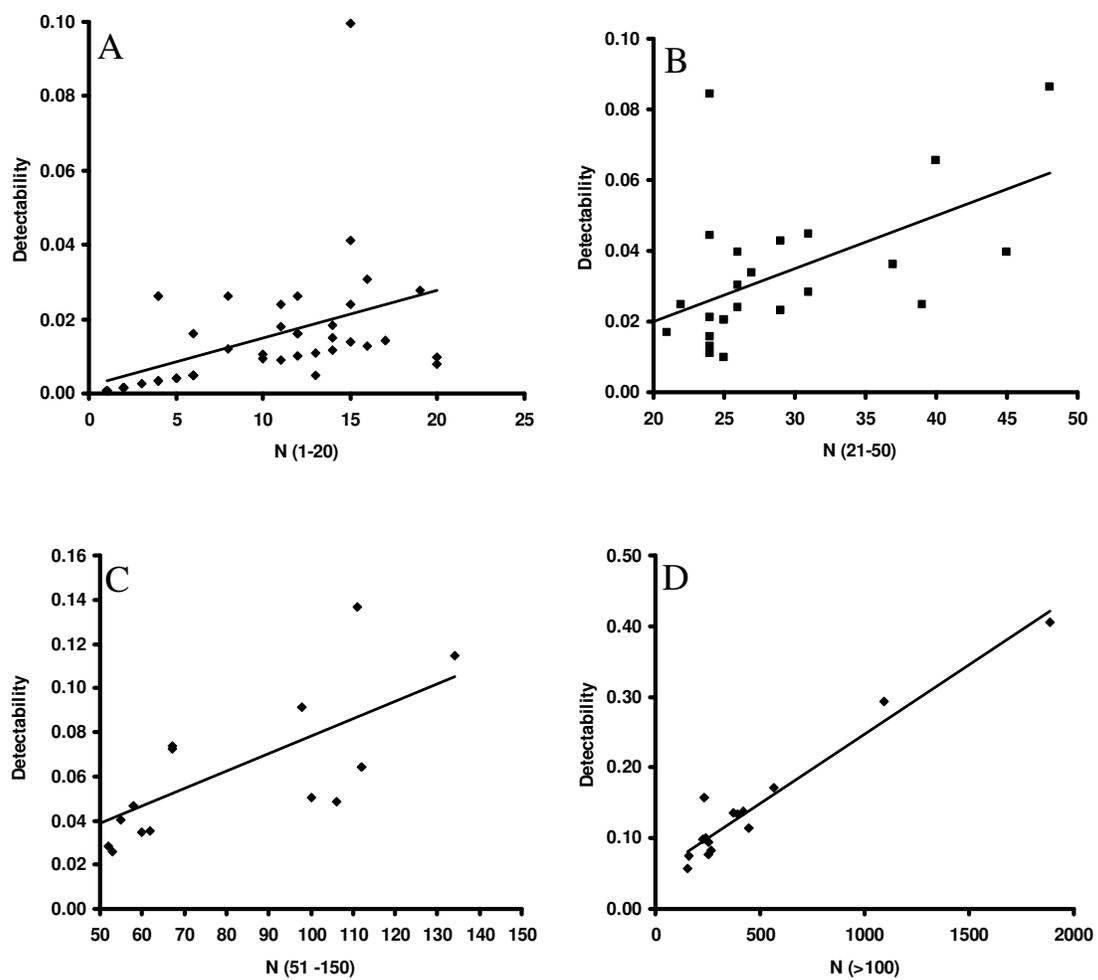


Figure 4-



Appendix 1- Detectability of fruit-feeding butterflies on a fragmented landscape in Atlantic Forest. naïve = proportion of sites observed to be occupied by the species.  $\Psi$  = estimated true occupancy given detectability and trapping effort. Hyphens (-) indicate that the parameter was not estimable.

Clade	Species	Parameter	Month												naïve	$\psi$
			Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May		
Charaxinae	<i>Archaeoprepona chalciope</i> (Hübner, [1823])	Estimate	-	-	0.02	0.061	0.051	0.01	0.091	0.01	0.01	-	-	-	0.32	0.49
		S.E.	-	-	0.015	0.028	0.025	0.01	0.036	0.01	0.01	-	-	-		0.13
	<i>Hypna clytemnestra</i> (Cramer, 1777)	Estimate	0.015	0.044	0.007	-	0.007	0.022	0.059	0.015	0.037	0.088	0.059	0.066	0.56	0.68
		S.E.	0.01	0.018	0.007	-	0.007	0.013	0.021	0.01	0.017	0.026	0.021	0.022		0.1
	<i>Memphis appias</i> (Hübner, [1825])	Estimate	-	0.257	0.201	0.112	0.039	0.112	0.112	0.022	0.045	0.028	0.006	-	0.88	0.9
		S.E.	-	0.033	0.03	0.024	0.015	0.024	0.024	0.011	0.015	0.012	0.006	-		0.05
	<i>Memphis moruus</i> (Fabricius, 1775)	Estimate	-	0.02	0.02	0.007	0.007	0.013	0.046	-	0.02	0.026	-	-	0.64	0.76
		S.E.	-	0.013	0.013	0.007	0.007	0.01	0.023	-	0.013	0.015	-	-		0.26
	<i>Memphis otrere</i> (Hübner, [1825])	Estimate	-	0.15	0.077	-	0.015	0.196	0.052	-	0.108	0.077	0.021	-	0.92	0.97
		S.E.	-	0.026	0.019	-	0.009	0.029	0.016	-	0.023	0.019	0.01	-		0.04
	<i>Fountainea ryphea</i> (Crammer, 1775)	Estimate	0.006	0.135	0.142	0.068	0.037	0.086	0.062	0.012	0.037	0.105	0.055	0.025	0.78	0.81
		S.E.	0.006	0.027	0.028	0.02	0.015	0.022	0.019	0.009	0.015	0.024	0.018	0.012		0.06
	<i>Zaretis strigosus</i> Gmelin 1790	Estimate	-	0.087	0.068	0.019	-	0.031	0.031	0.006	0.031	0.037	-	-	0.58	0.8
		S.E.	-	0.025	0.022	0.011	-	0.014	0.014	0.006	0.014	0.016	-	-		0.13
	<b>Average</b>	<b>Estimate</b>	<b>0.003</b>	<b>0.099</b>	<b>0.077</b>	<b>0.038</b>	<b>0.022</b>	<b>0.067</b>	<b>0.065</b>	<b>0.009</b>	<b>0.041</b>	<b>0.052</b>	<b>0.02</b>	<b>0.013</b>		
		<b>S.E.</b>	<b>0.002</b>	<b>0.034</b>	<b>0.027</b>	<b>0.016</b>	<b>0.007</b>	<b>0.026</b>	<b>0.01</b>	<b>0.003</b>	<b>0.012</b>	<b>0.015</b>	<b>0.01</b>	<b>0.009</b>		
	<i>Ectima thecla</i> (Fabricius, 1796)	Estimate	-	0.031	0.023	-	0.031	0.054	0.054	0.015	0.046	0.031	0.008	0.008	0.46	0.65
		S.E.	-	0.016	0.014	-	0.016	0.022	0.022	0.011	0.02	0.016	0.008	0.008		0.13
<i>Epiphile huebneri</i> Hewitson, 1861	Estimate	-	0.018	0.024	-	-	0.024	0.018	0.012	0.006	0.006	0.006	0.006	0.32	0.84	
	S.E.	-	0.013	0.016	-	-	0.016	0.013	0.01	0.006	0.006	0.006	0.006		0.36	
<i>Epiphile oreia</i> (Hübner, [1823])	Estimate	-	0.024	0.016	0.016	0.016	0.063	0.016	-	0.032	-	-	0.008	0.34	0.63	
	S.E.	-	0.015	0.012	0.012	0.012	0.028	0.012	-	0.018	-	-	0.008		0.19	
<i>Hamadryas epinome</i> (C. Felder & R. Felder, 1867)	Estimate	0.05	0.515	0.49	0.39	0.5	0.795	0.5	0.45	0.43	0.46	0.12	0.155	1	-	
	S.E.	0.015	0.035	0.035	0.034	0.035	0.029	0.035	0.035	0.035	0.035	0.023	0.026		-	
<i>Hamadryas februa</i> (Hübner, [1823])	Estimate	0.005	0.13	0.299	0.147	0.234	0.37	0.239	0.076	0.234	0.201	0.071	0.054	0.92	0.92	
	S.E.	0.005	0.025	0.034	0.026	0.031	0.036	0.031	0.02	0.031	0.03	0.019	0.017		0.04	



Clade	Species	Parameter												naïve	$\psi$	
			Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr			May
		S.E.	-	0.036	0.043	0.02	0.02	0.036	-	-	0.029	0.02	-	-	0.09	
	<i>Forsterinaria necys</i> (Godart, [1824])	Estimate	0.013	0.238	0.179	0.066	0.046	0.106	0.079	0.007	0.04	0.053	0.046	0.026	0.74	0.76
		S.E.	0.009	0.035	0.031	0.02	0.017	0.025	0.022	0.007	0.016	0.018	0.017	0.013	0.06	
	<i>Forsterinaria quantius</i> (Godart, [1824])	Estimate	0.022	0.333	0.272	0.061	0.061	0.111	0.078	0.05	0.15	0.266	0.15	0.056	0.9	0.9
		S.E.	0.011	0.035	0.033	0.018	0.018	0.023	0.02	0.016	0.027	0.033	0.027	0.017	0.04	
	<i>Godartiana muscosa</i> (Butler, 1870)	Estimate	0.056	0.286	0.133	0.082	0.031	0.051	0.097	0.076	0.127	0.28	0.25	0.178	0.98	0.98
		S.E.	0.016	0.032	0.024	0.02	0.012	0.016	0.021	0.019	0.024	0.032	0.031	0.027	0.02	
	<i>Hermeuptychia hermes</i> (Fabricius, 1775)	Estimate	0.045	0.182	0.266	0.058	0.097	0.13	0.039	-	0.032	0.084	0.058	0.006	0.76	0.77
		S.E.	0.017	0.031	0.036	0.019	0.024	0.027	0.016	-	0.014	0.022	0.019	0.006	0.06	
	<i>Moneuptychia soter</i> (Butler, 1877)	Estimate	0.012	0.134	0.268	0.055	0.097	0.189	0.152	0.097	0.274	0.225	0.073	0.049	0.82	0.82
		S.E.	0.009	0.027	0.035	0.018	0.023	0.031	0.028	0.023	0.035	0.033	0.02	0.017	0.05	
	<i>Paryphthimoides phronius</i> (Godart, [1824])	Estimate	-	0.157	0.207	0.066	0.191	0.224	0.091	0	0.05	0.091	0.083	0.017	0.6	0.6
		S.E.	-	0.033	0.037	0.023	0.036	0.038	0.026	-	0.02	0.026	0.025	0.012	0.07	
	<i>Paryphthimoides poltys</i> (Prittwitz, 1865)	Estimate	-	0.037	0.037	0.075	0.019	0.131	0.056	0.037	0.037	0.112	-	-	0.24	0.27
		S.E.	-	0.026	0.026	0.037	0.019	0.048	0.032	0.026	0.026	0.045	-	-	0.07	
	<i>Pharneuptychia sp.</i>	Estimate	-	0.059	0.131	0.024	0.036	0.024	0.024	0.012	0	0.024	-	0.012	0.32	0.42
		S.E.	-	0.028	0.043	0.017	0.021	0.017	0.017	0.012	-	0.017	-	0.012	0.1	
	<i>Pseudodebis euptychidia</i> (Butler, 1868)	Estimate	-	0.049	0.074	0.148	0.049	0.123	0.099	0.099	0.148	0.123	0.074	0.049	0.2	0.2
		S.E.	-	0.034	0.041	0.056	0.034	0.052	0.047	0.047	0.056	0.052	0.041	0.034	0.06	
	<i>Splendeuptychia doxes</i> (Godart, [1824])	Estimate	0.017	0.165	0.182	0.033	0.05	0.077	0.028	0.044	0.143	0.254	0.121	0.022	0.9	0.91
		S.E.	0.009	0.028	0.029	0.013	0.016	0.02	0.012	0.015	0.026	0.032	0.024	0.011	0.04	
	<i>Taygetis acuta</i> Weymer, 1910	Estimate	-	-	0.018	0.018	-	0.018	0.092	0.111	0.037	0.148	0.074	-	0.24	0.27
		S.E.	-	-	0.018	0.018	-	0.018	0.041	0.045	0.026	0.051	0.037	-	0.07	
	<i>Taygetis laches</i> (Fabricius, 1793)	Estimate	-	0.02	-	0.039	0.01	0.01	-	0.01	-	0.039	-	0.03	0.24	0.51
		S.E.	-	0.016	-	0.025	0.011	0.011	-	0.011	-	0.025	-	0.021	0.22	
	<i>Taygetis tripunctata</i> Weymer, 1907	Estimate	-	-	0.044	0.044	0.044	0.067	0.067	0.022	0.044	0.089	0.089	0.022	0.2	0.22
		S.E.	-	-	0.031	0.031	0.031	0.038	0.038	0.022	0.031	0.044	0.044	0.022	0.07	
	<i>Taygetis ypthima</i> Hübner, [1821]	Estimate	-	0.04	0.02	0.013	0.02	0.121	0.128	0.027	0.013	0.034	0.013	-	0.62	0.74
		S.E.	-	0.017	0.012	0.01	0.012	0.029	0.03	0.014	0.01	0.015	0.01	-	0.09	
	<i>Ypthimoides borasta</i> (Schaus, 1902)	Estimate	-	0.088	0.22	0.11	0.022	-	0.132	0.066	0.11	0.022	-	0.022	0.22	0.23
		S.E.	-	0.042	0.063	0.047	0.022	-	0.051	0.037	0.047	0.022	-	0.022	0.06	

Clade	Species	Parameter												naïve	$\psi$	
			Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr			May
Nymphalinae: Coeini	<i>Euptychoides castrensis</i> (Schaus, 1902)	Estimate	-	0.114	0.282	0.061	0.101	0.087	0.067	0.04	0.222	0.215	0.007	-	0.74	0.74
		S.E.	-	0.026	0.037	0.02	0.025	0.023	0.021	0.016	0.034	0.034	0.007	-		0.06
	<i>Paryphthimoides grimon</i> (Godart, [1824])	Estimate	-	0.04	0.081	0.06	0.01	-	-	-	0.01	0.03	0.02	-	0.32	0.5
		S.E.	-	0.022	0.033	0.028	0.01	-	-	-	0.01	0.019	0.015	-		0.13
	<i>Yphthimoides ochracea</i> (Butler, 1867)	Estimate	0.01	0.132	0.152	0.02	0.051	0.03	0.051	0.051	0.132	0.132	0.061	0.051	0.48	0.49
		S.E.	0.01	0.034	0.037	0.014	0.022	0.017	0.022	0.022	0.034	0.034	0.024	0.022		0.07
	<b>Average</b>	<b>Estimate</b>	<b>0.009</b>	<b>0.103</b>	<b>0.135</b>	<b>0.052</b>	<b>0.046</b>	<b>0.075</b>	<b>0.06</b>	<b>0.036</b>	<b>0.077</b>	<b>0.111</b>	<b>0.055</b>	<b>0.026</b>		
		<b>S.E.</b>	<b>0.003</b>	<b>0.02</b>	<b>0.02</b>	<b>0.007</b>	<b>0.009</b>	<b>0.013</b>	<b>0.01</b>	<b>0.007</b>	<b>0.016</b>	<b>0.018</b>	<b>0.013</b>	<b>0.008</b>		
	<i>Colobura dirce</i> (L., 1758)	Estimate	-	-	-	0.005	0.005	0.01	0.01	0.005	0.02	0.05	0.01	0.005	0.4	-
		S.E.	-	-	-	0.005	0.005	0.007	0.007	0.005	0.01	0.015	0.007	0.005		-

Appendix 2- Detectability of fruit-feeding butterflies and moths in Amazon Forest. .  
 naïve = proportion of sites observed to be occupied by the species.  $\Psi$  = estimated true  
 occupancy given detectability and trapping effort. Hyphens (-) indicate that the parameter  
 was not estimable.

Clade	Specie	Stratum		August	September	October	November			
								overall	naïve	$\Psi$
Catocalinae	<i>Dysglyptogona murifera</i> Dognin, 1914	Understory	Estimate	-	-	0.024	0.014	0.005	0.16	0.7
			S.E.	-	-	0.024	0.015	0.005		0.64
	<i>Hemeroblemma lusciniapennis</i> (Guenée,1852)	Canopy	Estimate	0.026	0.026	0.026	0.026	0.026	0.06	0.13
			S.E.	0.033	0.033	0.033	0.033	0.019		0.11
		Understory	Estimate	0.017	0.013	0.03	0.007	0.015	0.36	-
			S.E.	0.007	0.007	0.01	0.005	0.004		
	<i>Letis occidua</i> (Linnaeus,1758)	Canopy	Estimate	-	-	0.023	0.017	0.01	0.24	-
			S.E.	-	-	0.009	0.007	0.004		
		Understory	Estimate	-	-	0.013	0.003	0.004	0.12	-
			S.E.	-	-	0.007	0.003	0.002		
	<i>Letis</i> sp2 Druce, 1890	Canopy	Estimate	0.072	0.012	0.084	-	0.032	0.18	0.28
			S.E.	0.036	0.013	0.04	-	0.017		0.11
	Understory	Estimate	-	-	-	0.003	0	0.02	-	
		S.E.	-	-	-	0.003	0			
<i>Letis</i> sp3 (scops DHJ 02)	Canopy	Estimate	-	0.003	0.023	0.013	0.009	0.22	-	
		S.E.	-	0.003	0.009	0.007	0.004			
	Understory	Estimate	-	-	0.003	0.003	0.001	0.04	-	
		S.E.	-	-	0.003	0.003	0.001			
<i>Pararcte schneideriana</i> (Stoll,1782)	Canopy	Estimate	0.06	0.072	0.016	-	0.033	0.5	0.83	
		S.E.	0.02	0.022	0.009	-	0.013		0.18	
<i>Ramphia albizona</i> (Latreille, 1817)	Canopy	Estimate	0.009	0.038	0.028	0.024	0.018	0.32	0.71	
		S.E.	0.007	0.019	0.015	0.013	0.009		0.26	
	Understory	Estimate	0.104	0.107	0.319	0.104	0.158	0.98	0.99	
		S.E.	0.018	0.018	0.028	0.018	0.032		0.02	
<i>Agrias claudina</i> (Godart, [1824])	Canopy	Estimate	-	-	-	-	0.04	0.34	0.55	
		S.E.	-	-	-	-	0.012		0.15	
	Understory	Estimate	-	-	0.013	0.007	0.005	0.12	-	
		S.E.	-	-	0.007	0.005	0.002			
<i>Archaeoprepona demophon</i> (L., 1758)	Canopy	Estimate	-	-	-	-	0.003	0.08	-	
		S.E.	-	-	-	-	0.002			
	Understory	Estimate	-	0.021	0.07	0.07	0.04	0.3	0.47	
		S.E.	-	0.013	0.028	0.028	0.013		0.14	

Charaxinae

<i>Archaeoprepona demophoon</i> (Hübner, [1814])	Canopy	Estimate	-	-	-	-	0.018	0.18	0.51
		S.E.	-	-	-	-	0.012		0.31
	Understory	Estimate	-	-	0.028	0.083	0.026	0.06	0.12
		S.E.	-	-	0.035	0.079	0.025		0.1
<i>Memphis glauce</i> (Felder & Felder, 1862)	Canopy	Estimate	-	-	-	-	0.012	0.28	-
		S.E.	-	-	-	-	0.003		
<i>Memphis philumena</i> (Doubleday, [1849])	Canopy	Estimate	-	-	-	-	0.009	0.2	-
		S.E.	-	-	-	-	0.003		
<i>Memphis polycarmes</i> (Fabricius, 1775)	Canopy	Estimate	-	-	-	-	0.012	0.14	0.56
		S.E.	-	-	-	-	0.011		0.51
	Understory	Estimate	-	-	-	-	0.003	0.08	-
		S.E.	-	-	-	-	0.002		
<i>Memphis phantes</i> (Hopffer, 1874)	Canopy	Estimate	-	-	-	-	0.024	0.4	0.91
		S.E.	-	-	-	-	0.009		0.31
	Understory	Estimate	0.029	0.074	0.103	0.132	0.084	0.2	0.23
		S.E.	0.021	0.033	0.039	0.045	0.02		0.07
<i>Prepona dexamenus</i> Hopffer, 1874	Canopy	Estimate	-	-	-	-	0.005	0.12	-
		S.E.	-	-	-	-	0.002		
	Understory	Estimate	-	-	-	-	0.001	0.02	-
		S.E.	-	-	-	-	0.001		
<i>Prepona laertes</i> (Hübner [1811])	Canopy	Estimate	-	-	-	-	0.014	0.3	-
		S.E.	-	-	-	-	0.003		
	Understory	Estimate	-	-	-	-	0.002	0.04	-
		S.E.	-	-	-	-	0.001		
<i>Prepona pheridamas</i> (Cramer, 1777)	Understory	Estimate	-	-	-	-	0.021	0.38	0.94
		S.E.	-	-	-	-	0.009		0.35
<i>Prepona philipponi</i> Le Moul, 1932	Canopy	Estimate	-	-	-	-	0.004	0.1	-
		S.E.	-	-	-	-	0.002		
	Understory	Estimate	-	-	-	-	0.004	0.1	-
		S.E.	-	-	-	-	0.002		
<i>Zaretis isidora</i> (Cramer, 1779)	Canopy	Estimate	-	-	-	-	0.026	0.18	0.38
		S.E.	-	-	-	-	0.014		0.19
<i>Zaretis itys</i> (Cramer, 1777)	Canopy	Estimate	-	-	-	-	0.016	0.2	0.61
		S.E.	-	-	-	-	0.011		0.38
	Understory	Estimate	-	-	-	-	0.009	0.18	0.89
		S.E.	-	-	-	-	0.009		0.83
<i>Bia actorion</i> (L., 1763)	Canopy	Estimate	-	-	-	-	0.001	0.02	-
		S.E.	-	-	-	-	0.001		
	Understory	Estimate	0.046	0.081	0.127	0.112	0.091	0.78	0.87
		S.E.	0.013	0.018	0.022	0.021	0.01		0.07

Biblidinae	<i>Catoblepia berecynthia</i> (Cramer, 1777)	Understory	Estimate	0.02	0.047	0.017	0.01	0.023	0.44	-
			S.E.	0.008	0.012	0.007	0.006	0.004		
	<i>Catoblepia xanthus</i> (L., 1758)	Canopy	Estimate	0.042	0.093	0.084	0.02	0.003	0.06	-
			S.E.	0.014	0.022	0.075	0.019	0.001		
		Understory	Estimate	-	-	-	-	0.073	0.6	0.71
			S.E.	-	-	-	-	0.011		0.09
	<i>Morpho helenor</i> (Cramer, 1776)	Understory	Estimate	-	-	-	-	0.015	0.22	0.71
			S.E.	-	-	-	-	0.007		0.32
	<i>Opsiphanes invirae</i> (Hübner, [1808])	Canopy	Estimate	-	-	-	-	0.03	0.36	0.69
			S.E.	-	-	-	-	0.011		0.21
		Understory	Estimate	-	-	-	-	0.016	0.1	0.3
			S.E.	-	-	-	-	0.016		0.26
<i>Catonephele acontius</i> (L., 1771)	Canopy	Estimate	-	-	-	-	0.016	0.2	0.61	
		S.E.	-	-	-	-	0.011		0.38	
	Understory	Estimate	0.085	0.1	0.15	0.123	0.114	0.82	0.87	
		S.E.	0.018	0.019	0.023	0.021	0.011		0.06	
<i>Hamadryas arinome</i> (Lucas, 1853)	Canopy	Estimate	-	-	-	-	0.026	0.12	0.26	
		S.E.	-	-	-	-	0.017		0.16	
	Understory	Estimate	0.062	0.216	0.062	0.062	0.1	0.1	0.11	
		S.E.	0.043	0.078	0.043	0.043	0.03		0.05	
<i>Nessaea obrinus</i> (L., 1758)	Canopy	Estimate	-	-	-	-	0.002	0.04	-	
		S.E.	-	-	-	-	0.001			
	Understory	Estimate	-	-	-	-	0.137	0.64	0.67	
		S.E.	-	-	-	-	0.012		0.07	
<i>Temenis laothoe</i> (Cramer, 1777)	Canopy	Estimate	-	-	-	-	0.031	0.2	0.38	
		S.E.	-	-	-	-	0.014		0.16	
<i>Baeotus aeilus</i> (Stoll, 1780)	Canopy	Estimate	-	-	-	-	0.034	0.36	0.64	
		S.E.	-	-	-	-	0.011		0.18	
	Understory	Estimate	-	-	-	-	0.002	0.04	-	
		S.E.	-	-	-	-	0.001			
<i>Historis acheronta</i> (Fabricius, 1775)	Canopy	Estimate	-	-	-	-	0.028	0.28	0.57	
		S.E.	-	-	-	-	0.012		0.21	
	Understory	Estimate	-	0.007	-	-	0.002	0.04	-	
		S.E.	-	0.005	-	-	0.001			
<i>Tigridia acesta</i> (L., 1758)	Canopy	Estimate	-	-	-	-	0.001	0.02	-	
		S.E.	-	-	-	-	0.001			
	Understory	Estimate	-	-	-	-	0.064	0.52	0.66	
		S.E.	-	-	-	-	0.011		0.1	

## CONCLUSÕES GERAIS

O corte seletivo de madeira com impacto reduzido (RIL) efetivamente altera a estrutura da vegetação na Floresta Amazônica. As principais diferenças foram registradas na altura e largura média das árvores, ambas menores nas áreas exploradas. Além disso, a vegetação do subosque é mais densa com mais plantas de menor porte e uma menor abertura de dossel, quando medida a 100 cm de altura. Todavia, esta mudança não é grande o suficiente para alterar a densidade de árvores, juvenis e herbáceas e os valores de abertura do dossel, apesar de diferentes, são bastante próximos, mostrando que o RIL preserva algumas características da estrutura da vegetação da floresta.

Os resultados obtidos para as borboletas frugívoras mostram parcialmente este padrão. A fauna do subosque foi mais afetada pela exploração do que a fauna de dossel, provavelmente porque o dossel foi menos alterado após a retirada de madeira, e as alterações maiores ocorreram no subosque como consequência da abertura de trilhas para retiradas das toras.

Em relação a amostragem de borboletas frugívoras alguns cuidados devem ser tomados para aumentar as chances de que as espécies presentes na área sejam detectadas. Em florestas altas deve-se utilizar armadilhas no dossel, pois mesmo espécies comuns no dossel raramente são detectadas no subosque. A detectabilidade dos diferentes clados varia muito entre os meses, portanto, as amostragens devem sempre incluir os meses com maior chance de detecção das espécies e quando estes forem desconhecidos, deve-se amostrar durante um ano todo. Além disso, o esforço mínimo de coleta nunca deve ser inferior a 130 armadilhas/dia para a mata atlântica e 510 armadilhas/dia para a Amazônia central.

Em resumo, apesar dos efeitos registrados nas borboletas frugívoras como consequência da RIL, essas diferenças não são suficientes para alterar a diversidade de espécies podendo ser uma alternativa para preservar uma parcela significativa da fauna em áreas com este tipo de exploração. Tendo em vista as dificuldades para a criação de áreas protegidas na Amazônia, o RIL é uma alternativa para a preservação de borboletas frugívoras e certamente de muitos outros grupos biológicos, e poderia ser uma alternativa econômica e relativamente sustentável para a região.