



VICTOR HUGO FONSECA OLIVEIRA

**USOS MÚLTIPLOS DA PAISAGEM
AMAZÔNICA E A COMUNIDADE DE
ESCARABEÍNEOS**

LAVRAS – MG

2011

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DE ESCARABEÍNEOS**

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do curso de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestre.

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*A Deus,
E à minha família,*

DEDICO

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*“Se o Cristianismo oferecesse o tipo de universo que esperaríamos encontrar,
eu acharia que ele havia sido inventado pelo homem.”*

Clive Staples Lewis

RESUMO

A Floresta Amazônica é a maior e uma das mais importantes florestas do mundo. Seus limites estendem-se por nove países, e sua maior parte está localizada no Brasil. Nos últimos anos as taxas de perda florestal, degradação e fragmentação da Amazônia aumentaram consideravelmente, gerando paisagens altamente heterogêneas. Portanto, torna-se cada vez mais importante o estudo destas paisagens para a melhor compreensão do valor de conservação que elas possuem. Neste sentido, esta dissertação teve o objetivo de verificar as diferenças entre áreas de floresta primária, floresta secundária, pastagem e agricultura, numa região amazônica, utilizando os besouros da subfamília Scarabaeinae como indicadores biológicos. Além disso, foi verificado o efeito de espécies ocasionais na medida do valor de conservação desses ambientes. As amostragens foram realizadas na microrregião de Santarém, no estado do Pará. Foram dispostos transectos ao longo dos usos da terra predominantes em 18 microbacias pré-estabelecidas. Os besouros foram capturados através de armadilhas do tipo *pitfall* iscados com fezes (80% porco, 20% humana). Foi observado que os valores de riqueza, abundância e equitabilidade das comunidades de besouros rola-bosta diminuíram com a intensificação do uso da terra. Em relação à estrutura, as comunidades foram claramente separadas entre ‘florestais’ e ‘não-florestais’. Houve diferenças significativas entre floresta primária e secundária, o que não ocorreu entre pastagem e agricultura. Floresta secundária apresentou alto valor de conservação, mas mostrou-se bastante influenciada pelo entorno. Pastagem e agricultura apresentaram baixos valores para a conservação devido à partilha mínima de espécies destes ambientes com a floresta primária. A remoção de espécies ocasionais provocou um decréscimo acentuado no valor de conservação dos ambientes modificados. Os resultados encontrados mostram que os escaravelhos são fortemente influenciados pela presença ou ausência de cobertura florestal, mais do que pelo uso da terra em si. Apesar da grande importância da floresta secundária, este trabalho ressalta a singularidade dos ambientes primários. Mais do que isso, indicam que é necessário ter cautela antes de tomar decisões baseadas na diversidade das florestas secundárias. Por fim, propõe-se aos conservacionistas que considerem a influência das espécies ocasionais em seus resultados.

Palavras-chave: Valor de conservação. Floresta secundária. Bioindicação. Florestas Tropicais. Rola-bosta.

ABSTRACT

The Amazon Rainforest is the biggest and one of the most important forests of the world. Its boundaries extend across nine countries, and its biggest area is located in Brazil. In the last years, the deforestation, degradation and fragmentation rates of the Amazon increased considerably, generating highly heterogeneous landscapes. Therefore, it is important to study these landscapes for a better understanding of their conservation value. This work aimed at investigating the differences among primary forest, secondary forest, pasture and agriculture land-use types, in Amazon region, using Scarabaeinae subfamily beetles as biological indicators. Furthermore, we observed the effect of occasional species in the conservation value measure of these land-uses. This study was carried out in Santarém micro-region, in the state of Pará, Brazil. Transects were distributed along the predominant land-uses, within 18 predetermined micro-watersheds. Dung beetles were collected through pitfall traps baited with dung (20% human dung, 80% pig dung). The richness, abundance and evenness values of the dung beetles communities decreased with land-use intensification. Communities were clearly separated in ‘forested’ and ‘non-forested’ land-uses, regarding to structure. There were significant differences between primary and secondary forest, unlike pasture and agriculture. The secondary forest presented high conservation value, but was strongly influenced by landscape context. Pasture and agriculture showed low conservation values, due to the minimal sharing of species among these land-use types and the primary forest. The removal of occasional species decreased the conservation value of anthropogenic land-uses. Our findings show the dung beetles are strongly influenced by the presence/absence of forest cover, rather than by the land-use type itself. Despite the importance of secondary forest, this work highlights the primary forest uniqueness. More, we show that we need to have caution before making decisions based in secondary forest diversity. Finally, it is proposed to conservationists consider the influence of occasional species in their results.

Keywords: Conservation value. Secondary forest. Bioindication. Tropical Forest. Dung beetle

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CAPÍTULO I Referencial Teórico

1 REFERENCIAL TEÓRICO

1.1 Amazônia

A Floresta Amazônica é a maior e uma das mais importantes florestas do mundo em termos de biodiversidade (MALHI et al., 2008; STONE *et al.*, 2009), abrigando o maior número de espécies endêmicas por unidade de área e uma altíssima diversidade de vertebrados (INTERNATIONAL UNION FOR CONSERVATION OF NATURE – IUCN *et al.*, 2008). Seus limites estendem-se por nove países: Bolívia, Brasil, Colômbia, Equador, Guiana, Guiana Francesa, Peru, Suriname e Venezuela. A maior parte da Floresta Amazônica está localizada no Brasil, ocupando cerca de 40% do território brasileiro (FERRI, 1980).

Atualmente, a legislação brasileira estabelece que os proprietários de terras na região amazônica mantenham pelo menos 80% de sua área como reserva legal. Apesar desta restrição, as taxas de perda florestal, degradação e fragmentação têm aumentado consideravelmente (INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS – INPE, 2006). Nos últimos anos, a Amazônia experimentou grande crescimento da atividade pecuária e do cultivo de soja. Houve também uma expansão sem precedentes de novas rodovias, estradas e outras infraestruturas de transporte (LAURANCE, 2005). Além disso, as atividades ilegais se tornaram uma ameaça constante à conservação deste bioma, devido a não aplicação das leis que regulam o desmatamento (LAURANCE, 2001). Hoje o desmatamento é com certeza uma das maiores preocupações para os conservacionistas, sobretudo quando envolve a conversão de florestas em sistemas agrícolas.

Cerca de 13 milhões de hectares/ano de floresta são desmatados no mundo inteiro, e apenas um terço das florestas primárias originais permanece intacto. Dos dois terços restantes, 90% estão distribuídos em uma ampla variedade de usos da terra, e somente 10% estão presentes na forma de plantações e sistemas agroflorestais (FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS – FAO, 2006). Portanto, torna-se cada vez mais importante o estudo das paisagens florestais de usos múltiplos para a melhor compreensão do valor de conservação destas áreas (GARDNER, 2010). Em algumas regiões, as florestas exploradas, degradadas, agroflorestas, plantações e florestas secundárias podem ser os últimos refúgios para espécies incapazes de sobreviver em matrizes agrícolas abertas. Sua manutenção, portanto, pode garantir a persistência de espécies florestais em paisagens modificadas (CHAZDON, 2008; CHAZDON et al., 2009; GARDNER et al., 2009; GARDNER, 2010).

Vários estudos têm mostrado que a manutenção da cobertura florestal e da complexidade estrutural em ambientes modificados pode ajudar a manter comunidades semelhantes às encontradas em áreas intactas (QUINTERO; ROSLIN, 2005; VULINEC; LAMBERT; MELLOW, 2006; NICHOLS et al., 2007).

1.2 Os besouros da subfamília Scarabaeinae

Os besouros escaravelheiros (Coleoptera: Scarabaeidae: Scarabaeinae) adultos utilizam-se basicamente do líquido rico em microorganismos, presente em fezes, carcaças e frutos em decomposição, para a sua alimentação (HALFFTER; MATTHEWS, 1966; HALFFTER; EDMONDS, 1982). O hábito de confeccionar, rolar e enterrar porções esféricas de massas fecais (HALFFTER; MATTHEWS, 1966), característico de várias espécies desta

subfamília, tornou este grupo conhecido popularmente como “rola-bostas”. As comunidades de besouros rola-bostas apresentam grande riqueza na região Neotropical (HANSKI; CAMBERFORT, 1991), sendo que na América do Sul existem registros de mais de 1250 espécies. No Brasil, mais de 600 espécies já foram registradas (VAZ-DE-MELLO, 2000).

1.3 Funções ecológicas

A capacidade de os processos naturais e seus componentes em prover benefícios e serviços que satisfaçam às necessidades do homem é definida como função ecossistêmica (DE GROOT, 1992). As funções podem ser divididas em quatro principais grupos: de regulação, habitat, produção e informação (*para mais detalhes ver DE GROOT et al., 2000*); e sua importância pode ser dividida em três tipos: ecológica, sociocultural e econômica (Figura 1).

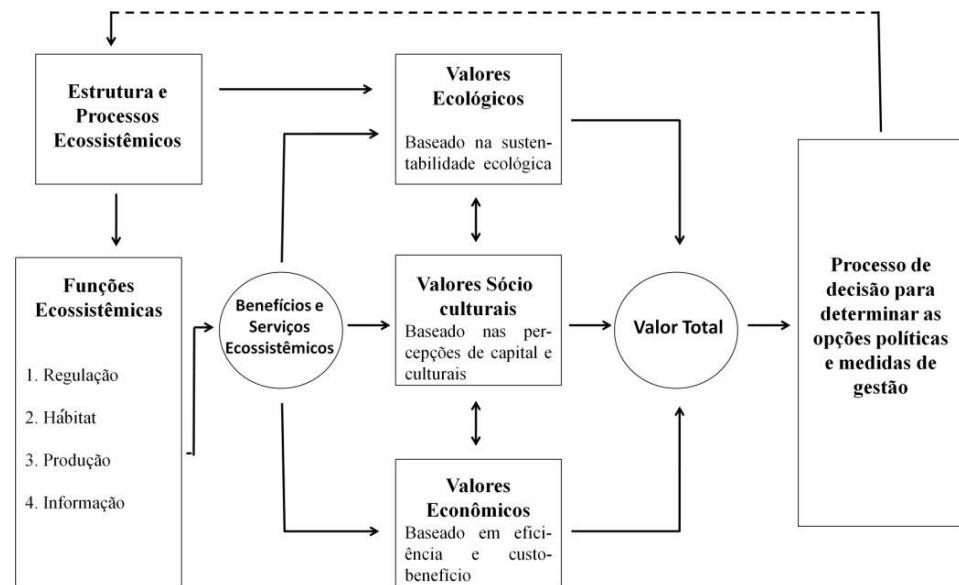


Figura 1 Quadro para a avaliação integrada e valorização das funções do ecossistema, bens e serviços

Devido principalmente à ligação intrínseca com recursos efêmeros, especialmente fezes, e com o solo, os besouros escarabeíneos afetam várias funções ecossistêmicas, entre elas: ciclagem de nutrientes, bioturbação, crescimento de plantas, dispersão secundária de sementes e controle de parasitas (NICHOLS et al., 2008).

Braga (2009), por exemplo, verificou que para cada 70 gramas de fezes removidas pelos rola-bostas mais de três vezes esse peso de solo é revolvido. Através da construção de galerias para a nidificação e alimentação, os escarabeíneos promovem a incorporação de matéria orgânica, aumentam a aeração, infiltração (BANG et al., 2005) e retenção de água no solo (KIRK, 1992; MITTAL, 1993), processos fortemente relacionados à manutenção da ‘saúde’ e produtividade dos solos (DE GROOT; WILSON; BOUMANS, 2002) e ao desenvolvimento da vegetação.

Os rola-bostas podem também remover accidentalmente uma parte de massas fecais com sementes e levá-las para o fundo de suas galerias. Muitas espécies de planta têm suas sementes eliminadas nas fezes de mamíferos, mesmo após a passagem pelo trato digestivo destes e a germinação facilitada pela escarificação realizada no intestino desses animais (SCHIFFMAN, 1997). Dentro das galerias os besouros realizam a ‘limpeza’ do recurso, eliminando tudo aquilo que não é interessante para sua reprodução e alimentação (ex. sementes) (HALFFTER; EDMONDS, 1982; HANSKI; CAMBERFORT, 1991). A dispersão secundária de sementes feita pelos escarabeíneos pode afetar a probabilidade de sobrevivência de sementes e plântulas por vários motivos: (1) as sementes enterradas correm menor risco de predação do que sementes na superfície (FEER, 1999; ANDRESEN, 2001), (2) as sementes são depositadas em ambientes mais úmidos, o que pode favorecer a germinação ou o ataque de patógenos (PRICE; JENKINS, 1986; CHAMBERS; MACMAHON, 1994), (3) a profundidade de enterro pode impedir ou facilitar a germinação de plântulas

(ANDRESEN, 2001) e (4) através da dispersão horizontal, os efeitos da competição por recursos entre sementes e entre plântulas pode ser diminuído (HOWE, 1989).

A eficiência na utilização de fezes em sua alimentação (HALFFTER; MATTHEWS, 1966; HALFFTER; EDMONDS, 1982) faz dos besouros rola-bostas grandes competidores de organismos que também se utilizam deste recurso. As populações de moscas que se desenvolvem em fezes, por exemplo, sofrem uma redução significativa na sua população em áreas com maior diversidade de escaravelhos (RIDSDILL-SMITH, 1993). Isso porque, além da competição por recurso, pode ocorrer predação de moscas por ácaros foréticos dos rola-bostas e a danificação de ovos das moscas pelos besouros durante o manuseio das fezes (NICHOLS et al., 2008). Moscas que se desenvolvem em fezes podem causar diversos prejuízos aos seus hospedeiros, seja pela perda sanguínea ou pelo estresse (BISHOP et al., 2005) e, ainda, atuar como agentes de dispersão de ovos de parasitas intestinais, fungos e bactérias (LOUZADA, 2008). Os besouros da subfamília Scarabaeinae têm se mostrado controladores biológicos efetivos destes organismos (NICHOLS et al., 2008).

Apesar de serem importantes na manutenção do funcionamento do ecossistema, estas funções não são igualmente desempenhadas pelas espécies de rola-bostas. Besouros maiores podem remover desproporcionalmente mais fezes do que besouros de menor porte, revolver maiores quantidades de terra e construir maiores galerias (SLADE et al., 2007; NICHOLS et al., 2008). Ao mesmo tempo, estes besouros são os primeiros a serem afetados pela fragmentação (KLEIN, 1989; LARSEN; WILLIAMS; KREMEN, 2005), conversão de florestas em agricultura (GARDNER et al., 2008; SHAHABUDDIN et al., 2010) e perda florestal (SCHEFFLER, 2005).

1.4 Escarabeíneos como indicadores de modificação do hábitat

A composição e/ou a estrutura das comunidades de escarabeíneos são fortemente afetadas pelo tipo de vegetação (HALFFTER; ARELLANO, 2002; VIEIRA; LOUZADA; SPECTOR, 2008). Alterações como o corte seletivo (DAVIS, 2000; GARDNER et al., 2008), conversão de florestas em áreas de produção (NUMMELIN; HANSKI, 1989; HALFFTER; FAVILLA; HALFFTER, 1992; NICHOLS et al., 2008) e fragmentação florestal (KLEIN, 1989; ESTRADA; ANZURES; COATES-ESTRADA, 1999) são capazes de alterar drasticamente os padrões de riqueza e abundância dos besouros rola-bostas, tanto em escala local como regional (NICHOLS et al., 2008).

Entretanto, numa recente meta-análise que reuniu 33 estudos para sintetizar o conhecimento atual sobre as respostas dos escarabeíneos às mudanças no uso da terra em florestas tropicais modificadas pelo homem, Nichols et al. (2007) mostraram que áreas modificadas que conservam um elevado grau de cobertura florestal (ex. corte seletivo, agroflorestas, florestas secundárias) possuem comunidades de besouros rola-bostas semelhantes às encontradas em florestas tropicais intactas (PINEDA et al., 2005). Em contraste, áreas com pouca ou nenhuma cobertura florestal apresentam comunidades pobres em espécies, com altos níveis de *turnover*, distribuições de abundância dramaticamente alteradas e besouros de tamanho corpóreo reduzido (NAVARRETE; HALFFTER, 2008).

Esta sensibilidade às alterações ambientais, associada ao fato de (1) representarem um grupo diverso, abundante e bem definido em termos taxonômicos e funcionais, (2) serem constituídos por espécies que apresentam características variadas e (3) serem de amostragem fácil e barata (NICHOLS et al., 2007; GARDNER et al. 2008a) faz dos rola-bostas organismos extremamente úteis como indicadores biológicos.

REFERÊNCIAS

- ANDRESEN, E. Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. **Journal of Tropical Ecology**, v. 17, p. 61-78, Jan. 2001.
- BANG, H. S. et al. Effects of paracoprid dung beetles (Coleoptera : Scarabaeidae) on the growth of pasture herbage and on the underlying soil. **Applied Soil Ecology**, v. 29, n. 2, p. 165-171, Jun. 2005.
- BRAGA, R. F. **Efeitos da alteração do uso do solo na Amazônia Brasileira sobre serviços ecológicos proporcionados pelos Scarabaeinae (Coleoptera, Scarabaeidae)**. 2009. 50p. Dissertação (Mestrado em Entomologia) - Universidade Federal de Lavras, Lavras, MG.
- BISHOP, A. L. et al. Interactions between dung beetles (Coleoptera: Scarabaeidae) and the arbovirus vector *Culicoides brevitarsis* Kieffer (Diptera: Ceratopogonidae). **Australian Journal of Entomology**, v. 44, n. 2, p. 89-96, Mai. 2005.
- CHAMBERS, J. C.; MACMAHON, J. A. A Day in the Life of a Seed - Movements and Fates of Seeds and Their Implications for Natural and Managed Systems. **Annual Review of Ecology and Systematics**, v. 25, n. 1, p. 263-292. 1994.
- CHAZDON, R. L. Beyond deforestation: restoring forests and ecosystem services on degraded lands. **Science**, v. 320, n. 5882, p. 1458-1460, Jun. 2008.
- CHAZDON, R. L. et al. The potential for species conservation in tropical secondary forests. **Conservation Biology**, v. 23, n. 6, p. 1406-1417, Dez. 2009.
- DAVIS, A. J. Does reduced-impact logging help preserve biodiversity in tropical rainforests? A case study from Borneo using dung beetles (Coleoptera :

Scarabaeoidea) as indicators. **Environmental Entomology**, v. 29, n. 3, p. 467-475, Jun. 2000.

DE GROOT, R.S. **Functions of Nature: evaluation of nature in environmental planning, management and decision-making**. Groningen: Wolters Noordhoff BV, 1992. 333 p.

DE GROOT, R.S. et al. Ecological functions and socio economic values of critical natural capital as a measure for ecological integrity and environmental health. In: CRABBE, P. et al. (Ed). **Implementing Ecological Integrity: Restoring Regional and Global Environmental and Human Health**. 1. ed. London: Kluwer Academic Publishers, 2000. p. 191–214.

DE GROOT, R. S.; WILSON, M. A.; BOUMANS, R. M. J. A typology for the classification, description and valuation of ecosystem functions, goods and services. **Ecological Economics**, v. 41, n. 3, p. 393-408, Jun. 2002.

ESTRADA, A.; ANZURES, A.; COATES-ESTRADA, R. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. **American Journal of Primatology**, v. 48, n. 4, p. 253-262, Jun. 1999.

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS. **Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management**, Rome: Food and Agriculture Organization of the United Nations.

FEER, F. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. **Journal of Tropical Ecology**, v. 15, n. 2, p. 129-142, Mar. 1999.

FERRI, M. G. **Vegetação brasileira**. São Paulo: USP, 1980. 157 p.

GARDNER, T. A. et al. The cost-effectiveness of biodiversity surveys in tropical forests. **Ecology Letters**, v. 11, n. 2, p. 139-150, Feb. 2008a.

GARDNER, T. A. et al. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. **Journal of Applied Ecology**, v. 45, n. 3, p. 883-893, Jun. 2008b.

GARDNER, T. A. et al. Prospects for tropical forest biodiversity in a human-modified world. **Ecology Letters**, v. 12, n. 6, p. 561-582, Jun. 2009.

GARDNER, T. A. **Monitoring forest biodiversity:** improving conservation through ecologically-responsible management. London: Earthscan, 2010. 388p.

HALFFTER, G.; ARELLANO, L. Response of dung beetle diversity to human-induced changes in a tropical landscape. **Biotropica**, v. 34, n. 1, p. 144-154, Mar. 2002.

HALFFTER, G.; EDMONDS, W. D. **The nesting behavior of dung beetles (Scarabaeinae): An ecological and evolutive approach.** México DF: Instituto de Ecología, 1982. 242p.

HALFFTER, G.; FAVILLA, M. E.; HALFFTER, V. Comparative studies on the structure of scarab guild in tropical rain forest. **Folia Entomológica Mexicana**, v. 84, n. 2, p. 131-156. 1992.

HALFFTER, G.; MATTHEWS, E. G. The natural history of dung beetles of the subfamily Scarabaeinae. **Folia Entomológica Mexicana**, v. 12-14, p. 1-312. 1966.

HANSKI, I.; CAMBERFORT, Y. **Dung beetle ecology.** Princeton: Princeton University Press, 1991. 481p.

HOWE, H. F. Scatter-Dispersal and Clump-Dispersal and Seedling Demography - Hypothesis and Implications. **Oecologia**, v. 79, n. 3, p. 417-426, Mai. 1989.

INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS. **Monitoramento da Floresta Amazônica brasileira por satélite**. Disponível em: <<http://www.obt.inpe.br/prodes/>> Acesso em: 28 abr. 2011.

INTERNATIONAL UNION FOR CONSERVATION OF NATURE et al. **An Analysis of Mammals on the 2008 IUCN Red List**. Disponível em: <<http://www.iucnredlist.org/initiatives/mammals>> Acesso em: 28 abr. 2011.

KIRK, A. A. Dung beetles (Coleoptera: Scarabaeidae) active in patchy forest and pasture habitats in Santa Cruz Province, Bolívia, during spring. **Folia Entomológica Mexicana**, v. 84, p. 45-54, 1992.

KLEIN, B. C. Effects of Forest Fragmentation on Dung and Carrion Beetle Communities in Central Amazonia. **Ecology**, v. 70, n. 6, p. 1715-1725, Dec. 1989.

LARSEN, T. H.; WILLIAMS, N. M.; KREMEN, C. Extinction order and altered community structure rapidly disrupt ecosystem functioning. **Ecology Letters**, v. 8, n. 5, p. 538-547, Mai. 2005.

LAURANCE, W. F. When bigger is better: the need for Amazonian mega-reserves. **Trends in Ecology and Evolution**, v. 20, n. 12, p. 645-648, Dez. 2005.

LAURANCE, W. F. et al. The future of the Brazilian Amazon. **Science**, v. 291, n. 5506, p. 438-439, Feb. 2001.

LOUZADA, J. N. C. Scarabaeidae (Coleoptera-Scarabaeidae) detritívoros em ecossistemas tropicais: diversidade e serviços ambientais. In: MOREIRA, F. M. S.; SIQUEIRA, J. O.; BRUSSAARD, L. (Ed.). **Biodiversidade dos solos em ecossistemas brasileiros**. Lavras: UFLA, 2008. cap. 3, p. 299-322.

MALHI, Y. et al. Climate change, deforestation, and the fate of the Amazon. **Science**, v. 319, n. 5860, p. 169-172, Jan. 2008.

MITTAL, I. C. Natural manuring and soil conditioning by dung beetles. **Tropical Ecology**, v. 34, n. 2, p. 150-159, 1993.

NAVARRETE, D.; HALFFTER, G. Dung beetle (Coleoptera : Scarabaeidae : Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. **Biodiversity and Conservation**, v. 17, n. 12, p. 2869-2898, Nov. 2008.

NICHOLS, E. et al. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. **Biological Conservation**, v. 137, n. 1, p. 1-19, Jun. 2007.

NICHOLS, E. et al. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. **Biological Conservation**, v. 141, n. 6, p. 1461-1474, Jun. 2008.

NUMMELIN, M.; HANSKI, I. Dung Beetles of the Kibale Forest, Uganda - Comparison between Virgin and Managed Forests. **Journal of Tropical Ecology**, v. 5, n. 3, p. 349-352, Ago. 1989.

PINEDA, E. et al. Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. **Conservation Biology**, v. 19, n. 2, p. 400-410, Abr. 2005.

PRICE, M. V.; JENKINS, S. H. Rodents as seed consumers and dispersers. In: MURRAY, D. R. (Ed.). **Seed dispersal**. Sydney: Academic Press, 1986. p. 191-235.

QUINTERO, I.; ROSLIN, T. Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. **Ecology**, v. 86, n. 12, p. 3303-3311, Dez. 2005.

RIDSDILL-SMITH, T.J. Asymmetric competition in cattle dung between two species of Onthophagus dung beetle and the bush fly, *Musca vetustissima*. **Ecological Entomology**, v. 18, n. 3, p. 241-246, Mar. 1993.

SCHEFFLER, P. Y. Dung beetle (Coleoptera : Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. **Journal of Tropical Ecology**, v. 21, n. 1, p. 9-19, Jan. 2005.

SCHIFFMAN, P. M. Animal-mediated dispersal and disturbance: driving forces behind alien plant naturalization. In: LUKEN, J.O.; THIERET, J.W. (Eds.) **Assessment and Management of Plant Invasions**, New York: Springer-Verlag, 1997, p. 87-94.

SHAHABUDDIN, P. H. et al. Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. **Journal of Tropical Ecology**, v. 26, n. 1, p. 53-65, Jan. 2010.

SLADE, E. M. et al. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. **Journal of Animal Ecology**, v. 76, n. 6, p. 1094-1104, Nov. 2007.

STONE, A. I. et al. Non-volant mammalian diversity in fragments in extreme eastern Amazonia. **Biodiversity and Conservation**, v. 18, n. 6, p. 1685-1694, Jun. 2009.

VAZ-DE-MELLO, F. Z. Estado atual de conhecimento dos Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) do Brasil. **Monografias Tercer Milênio**, v. 1, p. 183-195. 2000.

VIEIRA, I.; LOUZADA, J. N. C.; SPECTOR, S. Effects of Degradation and Replacement of Southern Brazilian Coastal Sandy Vegetation on the Dung Beetles (Coleoptera: Scarabaeidae). **Biotropica**, v. 40, n. 6, p. 719-727, Nov. 2008.

VULINEC, K.; LAMBERT, J. E.; MELLOW, D. J. Primate and dung beetle communities in secondary growth rain forests: implications for conservation of seed dispersal systems. **International Journal of Primatology**, v. 27, n. 3, p. 855-879, Jun. 2006.

CAPÍTULO II Multiple use of the Amazon Landscape and the dung beetle communities

1 INTRODUCTION

The Amazon forest is the largest rainforest in the world, and has high multi-scale importance, both economically and ecologically (MALHI et al., 2008). However, due to increased human pressure, mainly resulting from deforestation driven by agro-silvo-pastoral expansion, and unsustainable forestry, the provision of a wide range of ecosystem services (including climate regulation, water purification and biodiversity conservation) is under increasing threat (MALHI et al., 2008).

The survival of many tropical forest biota depends on the success of their management and conservation in human-dominated landscapes. However, according to Peres et al. (2010) there is a clear mismatch in the location of the areas where the majority of conversion and degradation of forests in the Amazon countries occur, and the spatial allocation effort in ecological and conservation research.

Despite the unprecedented expansion of agriculture in the past two decades, studies on the impact of forest conversion to pastures and crops are scarce in many areas with high deforestation rates, such as in the Mato Grosso, Rondônia and Pará states in Brazil. Brazilian people are responsible for more than 75% of the deforestation occurring in the Amazon (PERES et al., 2010), and most of this take place in Pará state, which in the last decade accumulated 622 km² of deforested area (HAYASHI et al., 2010). In June 2010, 97% of the forest degradation in the Brazilian Amazon occurred in Pará, especially along the BR163 federal highway (HAYASHI et al., 2010). The range of human disturbances including fires, selective logging, as well as the conversion of forests into large farms and monocultures (exotic or otherwise), have resulted in an increasingly complex human-dominated landscape (SKOLE; TUCKER, 1993; ASNER et al., 2005).

Nowdays conservationists have a broad consensus about the need of going from a focus that is manly exclusive to protected areas to a new view that consider landscapes as whole unit (PALMER et al., 2004; SAYER; MAGINNINS, 2005). The future of more sustainable approaches of forest management (including considerations for the biodiversity conservation) depends upon recognizing context-dependent management approaches that are effective in different situations in the real world.

It is clear that modified forests which have been managed for other kinds of human-use represent an important and valuable resource for biodiversity conservation. Besides providing habitat in their own right, human-modified areas can potentially help to connect the remains of primary forest, as well as provide reserve buffer zones. In fact, in many parts of the world, managed forest areas, degraded or recovered (some of the recovering using even exotic species) are all that remains to ensure the future of regional biodiversity, and should not be neglected (DAILY, 2001; LINDENMAYER; FRANKLIN, 2002; BAWA et al., 2004; GARDNER et al., 2009).

Despite its importance, the conservation value of modified forests remains poorly understood (REID; HUQ, 2005; GARDNER et al., 2007), due to limitations of studies concerned with the effect of habitat change on tropical forest species, that includes: 1) the lack of undisturbed baseline as comparative control, 2) non-independence among samples due to limitations in the spatial extent of the study, 3) poor sample representation through low capture or trapping success, and 4) inappropriate analyses (GARDNER et al., 2007). Moreover, the conservation value - rather than biodiversity value - is not easily predicted, as it is strongly dependent of a broader landscape context (NORRIS, 2008), in this particular case, the amount of native forest areas remaining (GARDNER et al., 2009). Thus, although the modified forests have been proposed as important habitats that can help conserve biodiversity in highly human-modified landscapes (HERRERA-MONTES; BROKAW, 2010), it is important to bear in mind that a gradient of

'structural integrity' also exists within this systems (GARDNER, 2010). Different levels of logging intensity in managed native forests, differently aged secondary forests, and a wide variety of agroforestry and exotic tree plantation may have also different values for biodiversity conservation. Furthermore, the effects of the occasional species presence in these land-uses on the measures of conservation value are not well known (BARLOW et al., 2010a). The occasional species (e.g. singletons and doubletons) may be unable to exist as viable populations in isolation, and may inflate the estimates of conservation value of disturbed and secondary habitats.

Despite their enormous importance for the interpretation of biodiversity responses to disturbance (DUMBRELL et al., 2008)and for conservation planning (FERRIER et al., 2007), data on meso-scale patterns of diversity (e.g. tens to hundreds kilometers) is almost nonexistent for most tropical forest regions, and the Amazon is no exception. Research on biodiversity patterns should be implemented at scales at which management strategies are most often implemented, and where their impacts most clearly manifest. To address this knowledge gap the current work employs entire landscapes (micro watersheds) as sampling units, thus allowing assessment of landscape characteristics in determining local patterns of diversity. Furthermore, our study area was composed by a forest matrix area, geographically distant of natural Brazilian Savannas. This may allow us a better understanding of the forest contribution to the disturbed areas diversity. The amount of native forest in landscapes adjacent to disturbed areas, for example, may be more important than land use *per se* in determining species richness of plants and vertebrates (GARDNER et al., 2009).

In general, species responses to forest conversion from human activity is highly varied, though largely negative(GARDNER, 2010). Given this variability field data will be mostly ineffective, unless care is taken to elaborate a careful experimental design with a selection of appropriate indicator groups for sampling work. Dung Beetles (Coleoptera,

Scarabaeidae) are known as a diverse taxonomic group, with approximately 4,500 species (HALFFTER; EDMONDS, 1982), and at least 618 species in Brazil (VAZ-DE-MELLO, 2000). These beetles play various key ecological roles, including: the incorporation of organic matter decomposition in the soil (HORGAN, 2001; BANG et al., 2005; NICHOLS et al., 2008), increase of soil permeability and aeration (BANG et al., 2005; NICHOLS et al., 2008), control of parasite and fly vectors (MILLER, 1961; FINCHER, 1975), control of leaf-cutting ants (*Atta* sp.) (SILVEIRA et al., 2006), secondary seed dispersion and pollination (NICHOLS et al., 2008). The importance of dung beetles to terrestrial ecosystems, summed to their high performance and cost-effectiveness for monitoring purposes and bioindication (NICHOLS; GARDNER, 2011) adequately justifies the selection of these organisms to this work.

The objective of this work was to identify the most important factors involved in the dung beetle diversity variation, and to test the following hypotheses:

- (1) There is a consistent loss of dung beetle community structure (species richness, abundance and evenness) along a disturbance gradient from primary forest, through secondary forest, pasture and agriculture.
- (2) The conservation value of the non-forested land uses (defined as the proportion of primary forest species that they harbour) is very low for dung beetles, and will be reduced further by the removal of occasional species from samples.
- (3) The conservation value of the secondary forest is higher than the non-forest landscapes uses, but highly dependent of the landscape context.
- (4) The primary forest biota dominates the dung beetle assemblages in non-forested land-uses diversity, due to the absence of representative natural open systems on the landscape context and the recent colonization history of the study area.

2 METHODS

2.1 Study site

This study was carried out in Santarém micro region (Figure 2), localized in the middle region of the Lower Amazon, in the state of Pará, north Brazil ($02^{\circ}25'S$, $54^{\circ}42'W$). The climate is classified as Af (Köppen classification), receiving 2,096mm of rainfall/yr with a annual mean temperature of $26^{\circ}C$ (BASTOS, 1972).

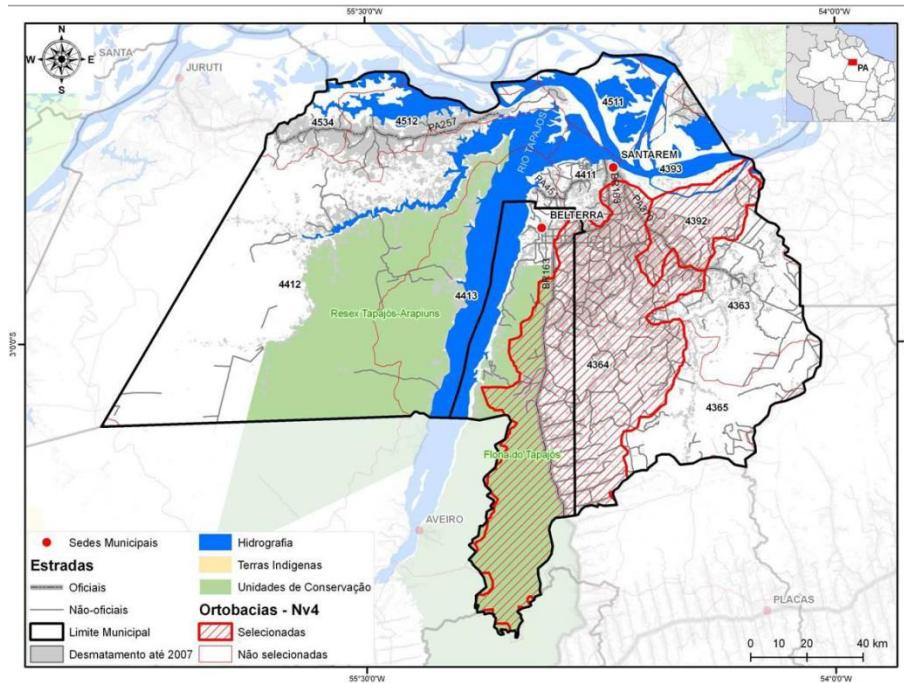


Figure 2 Santarém micro region area with the main landscape elements. The selected micro watersheds are localized inside the area marked in red.

Santarém is an important regional market centre and its economy is mainly based on agriculture and cattle raising. The agricultural development in the region occurred in two main stages: the first stage began disorderly and concentrated in the north, approx. 50 years ago, and resulted in a highly degraded and heterogeneous landscape. Nowadays, just a few primary forest

fragments remains, although there are many areas of secondary forest of different ages. The second stage began further south, along the BR163 federal highway, supported by the *Instituto Nacional de Colonização e Reforma Agrária* (INCRA) during the 1970s. This occupation led to a classic fishbone pattern of deforestation, characterised by standard sized farm-lots of 100 ha. Today, the total land area of cattle ranches is greater than the mechanised agriculture area in this region, although less important economically.

Dung beetle sampling was conducted in 18 micro watersheds (Figure 3) previously established according to past deforestation levels, soil type, and present-day land-use (Figure 4).

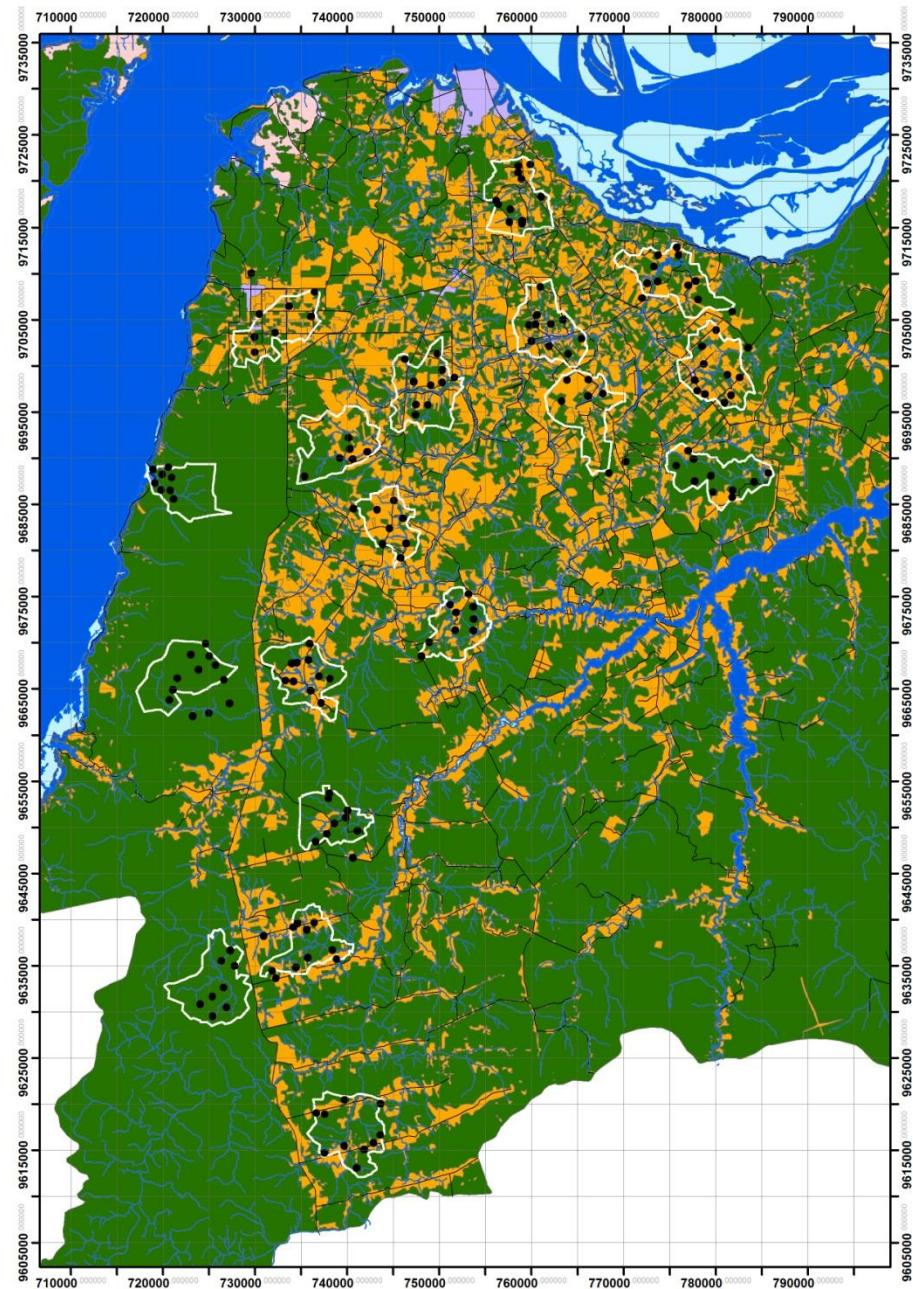


Figure 3 Micro watersheds studied in Santarem micro region. Green area is forest (secondary and primary) while the yellow area comprises all non-forested land-uses (pasture, agriculture). Water courses are represented by blue areas and the roads by the black lines. Studied micro watersheds are delimited by white lines. Black dots represent the localization of transects sampled (total of 154 transects).

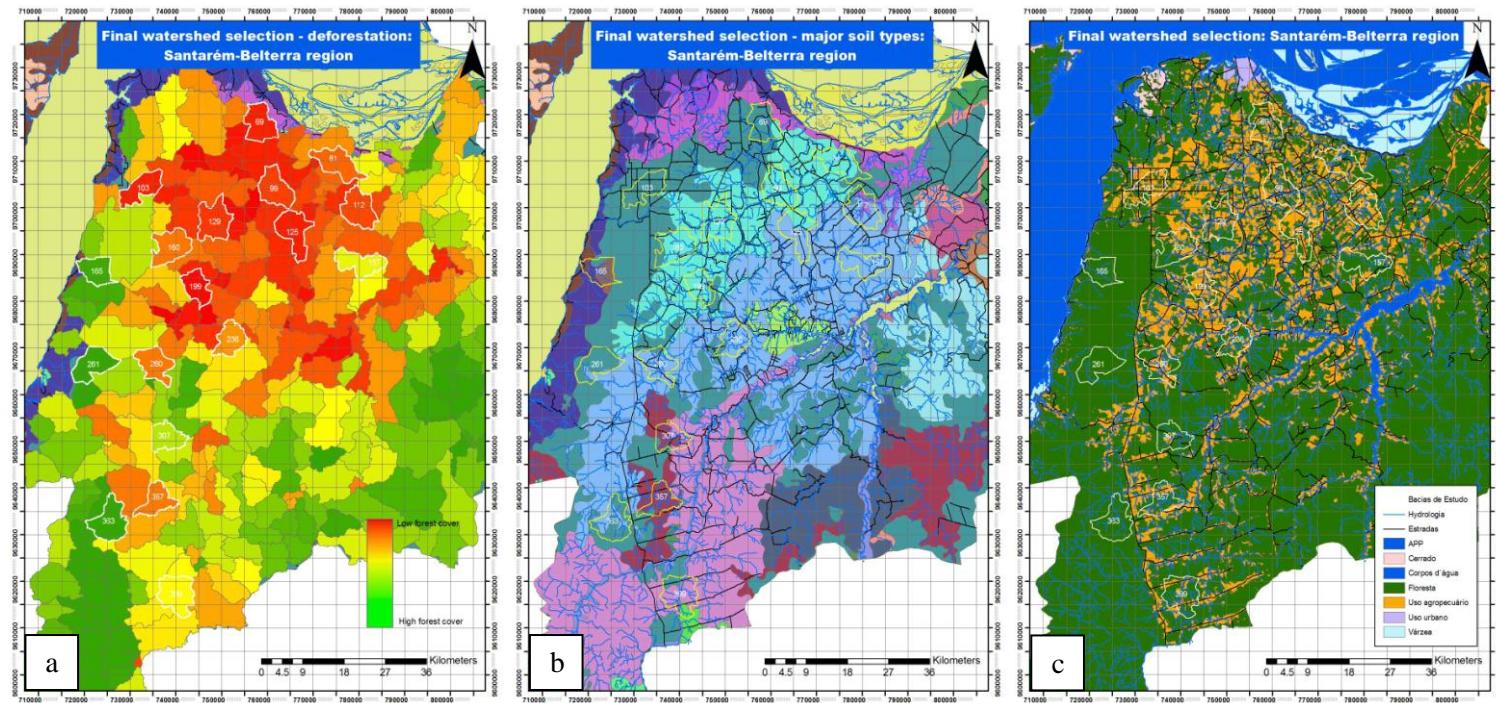


Figure 4 The micro watersheds studied in Santarem micro region were previously established according to (a) deforestation levels, (b) major soil types and (c) present day land-use.

Transects were distributed in each micro watershed at an even density (1 per 400 ha) and stratified with respect to total forest and non-forest area, whilst also maintaining a minimum between transect dispersion distance of 1500 m. This resulted in a range of 8 to 12 transects per micro watershed with an overall average of 11.2. In total, 82 transects were sampled in primary forest, 30 in secondary forest, 26 in pasture and 16 in agriculture. Three sampling points 150 m apart from each other were located along every 300 m transect, with three traps placed in each point (Figure 5). We defined primary forest as forests that has not been cleared, but may have been modified through activities such as selective logging and fire. The secondary forest consisted in naturally regenerating forest on abandoned land previously used for other purposes. The pasture was very heterogeneous, some areas presenting big and almost clean pastures (intensive), and other presenting abandoned pastures (with shrubs and dead trees). The agriculture consisted in areas of mechanized agriculture for soya, beans, corn or rice production.

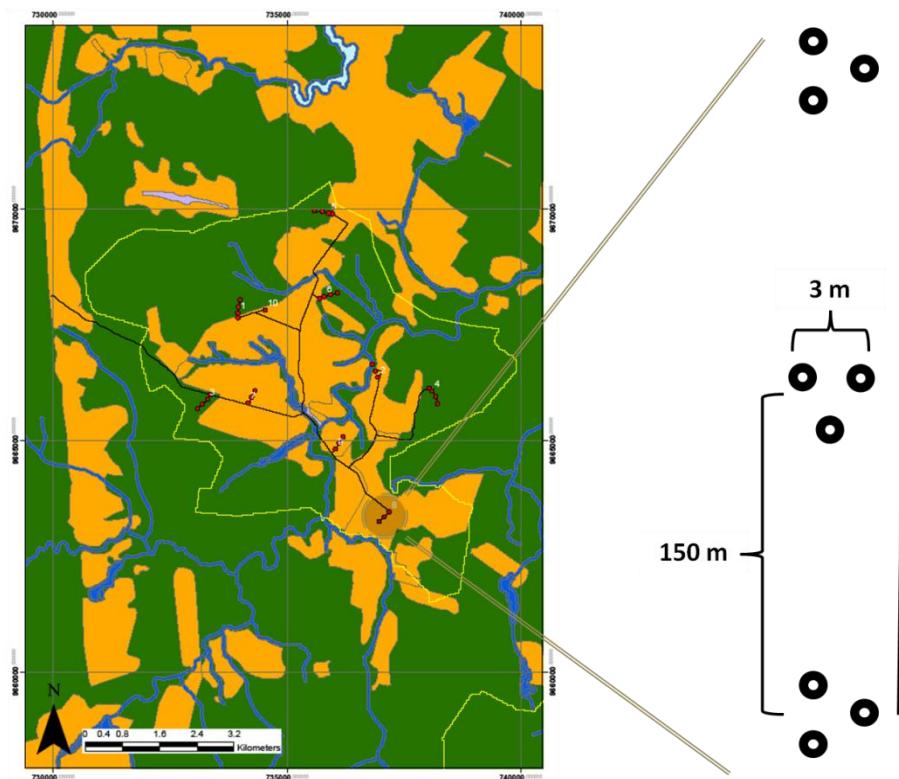


Figure 5 Representation of transect distribution. In the left, forested land-uses are represented in green, non-forested land-uses represented in yellow, water courses in blue and roads in black lines. The micro watershed is delimited by a yellow line. Red dots represent the points of each sampled transect. At the right side of the panel is shown the distribution of traps inside transects with black circles representing the individual traps

2.2 Dung beetle sampling

Sampling was conducted between April and June 2010, during the wet season. Although dung beetle richness and abundance variability are often associated to the rainfall in seasonal ecosystems (DAVIS, 1987; LOUZADA; LOPES, 1997; ANDRESEN, 2008), However, Gardner et al. (2008) showed that these attributes do not change significantly between seasons in Amazon rainforests. Gardner et al. (2008) found that despite the more individuals captured in wet *versus* dry season, the main effect of season was not significant across a land-use gradient of primary, secondary

and plantation forests. Thus, the interval between our first and last sample (three months, all within the main wet season) is unlikely to affect the overall patterns.

We used pitfall traps baited with approximately 50 g of dung bait (20% human dung, 80% pig dung). The traps were made of plastic containers (18 cm in diameter by 15 cm in height) with a bait holding recipient suspended in the middle and covered with a lid to protect from the rain (Figure 6). We filled the pitfall with 250 ml of water mixed with liquid detergent, used to break the water surface tension. After a period of 48 hours, all insects were collected, sorted and identified to the lowest taxonomic level possible. The identifications were validated by Fernando Vaz-de-Mello at the *Universidade Federal do Mato Grosso*. Voucher specimens were deposited at the Scarabaeinae collection of the *Laboratório de Ecologia e Conservação de Invertebrados/UFLA* and in the FZVM collection at *Universidade Federal do Mato Grosso*.



Figure 6 Pitfall trap baited with a mix of faeces (20% human dung and 80% pig dung) used for dung beetles sampling. The left-hand panel shows a pitfall trap in primary forest while the right-hand panel shows a trap after 48 hours in a pasture transect.

2.3 Data Analysis

2.3.1 Community structure

Sampling efficiency was assessed calculating the percentage of species caught in each land-use in relation to its estimated richness. The estimated richness was calculated by the average of three non-parametric richness estimators: ACE, Chao 1 and Jackknife 1. These estimators were chosen due to its different sensibilities. The ACE index is more sensible to species with abundances higher than 10 individuals, while Chao 1 is affected by the low occurrence species (e.g. singletons and doubletons). The Jackknife index is affected by the composition (presence/absence) of the communities sampled. The estimated richness was obtained using the EstimateS 8.2. software (COLWELL, 2010). Sampling efficiency was calculated due to the different sampling effort among the land-uses studied (considerably higher in primary forests). The relationship between number of species and sampling effort (individuals sampled) in each land-use was graphically expressed using species accumulation curves.

We plotted species rank-abundance distributions to visually compare patterns of species dominance in the different land-uses. We used non-metric multidimensional scaling (NMDS) to explore differences in dung beetle community structure. The NMDS was based on a similarity matrix constructed using the Bray-Curtis index on standardized and square-root transformed abundance and presence/absence matrix. We observed the robustness of NMDS solution by evaluating the stress level, with values below 0.2 considered as acceptable. Analysis of similarity (ANOSIM, CLARKE, 1993) was used to test significant differences in multivariate dung beetle community structure. ANOSIM is a non-parametric permutation test for similarity matrices that is analogous to an ANOVA. We then did a permutational analysis of multivariate dispersions (PERMDISP) for comparing the multivariate dispersions among the land-uses data. This test

was made by the comparison of the average of the distances among the groups of points (illustrated in the NMDS), using ANOVA. A *P*-value was then obtained using permutation of the observations. These analyses were conducted in Primer v.6 (CLARKE; GORLEY, 2006).

2.3.2 Conservation value

Conservation values of modified land-uses were defined as the proportion of primary forest species that they harbour. Thus, the more species the modified land-uses shares with primary forest, the greater their value to biodiversity conservation. Occasional species were defined as those that form the tail of the species abundance distribution in each land-use, which we arbitrarily decided as species with 10 or fewer records. For analysing how the modified land-uses conservation value varied following the sequential removal of different abundance classes, we follow the routine proposed by Barlow et al. (2010a). Two different metrics were compared:

- 1) The proportion of primary forest species that was shared with the modified land-uses, simultaneously removing occasional species from all-land uses. We so calculated the conservation value of each land-use type after removing species with one individual sampled in the land-use, then species with two individuals, then three until 10.
- 2) The proportion of primary forest species that was shared with modified land-uses, simultaneously removing occasional species from modified land-uses only. We so calculated the conservation value of each land-use type according to the first metric, but without removing occasional species of the primary forest.

Finally, to access the richness variation among transects of each land-use, we calculated the mean and the median of the richness found.

2.3.3 Sharing of species

We used a diagram and bars plots to express graphically the level of shared species among the land-uses. For accessing the relative importance of the primary forest richness to the total micro watershed richness we made a correlation, applying the Spearman's correlation coefficient. We did this correlation using the Bioestat 5.0 program (AYRES et al., 2007).

3 RESULTS

3.1 Community structure

We collected a total of 40,664 individuals and 99 species from 24 genera and six Neotropical tribes of Scarabaeinae beetles: Ateuchini (34 species / 6 genera), Canthonini (25 species / 7 genera), Coprini (14 species / 3 genera), Oniticellini (12 species / 1 genus), Onthophagini (6 species / 2 genera) and Phanaeini (8 species / 5 genera). We found a higher richness and abundance levels in primary forest (89 species / 22,285 individuals), followed by secondary forest (73 species / 5,982 individuals), pasture (24 species / 9,909 individuals) and agriculture (21 species / 2488 individuals). Species accumulation curves indicated significant differences between forested and non-forested areas (Figure 7).

The sampling can be considered satisfactory, since we caught around 89%, 90% and 90% of expected diversity for primary forest, secondary forest and pasture respectively. Although our sampling efficiency was lower in agriculture (68%), we considered the sampling as satisfactory too (Table 1). Due to the proximity of some agriculture transects to forested areas, the pitfall traps may have attracted species from these areas. Thus, as the estimated richness is based on the observed richness, the estimators overestimated the total richness of the agriculture.

Table 1 Sampling efficiency (Eff.) based on total richness (Obs.) of dung beetles sampled in primary forest, secondary forest, pasture and agriculture. The estimated richness was calculated using three non-parametric richness estimators (ACE, Chao 1, Jackknife 1).

Land-use	Obs.	ACE	Chao 1	Jack 1	Mean	Eff.
Primary forest	89	101.05	96.86	101.95	99.95	89%
Secondary forest	73	81.81	79.00	81.90	80.90	90%
Pasture	24	27.91	25.50	26.96	26.79	90%
Agriculture	21	29.99	36.00	26.88	30.96	68%

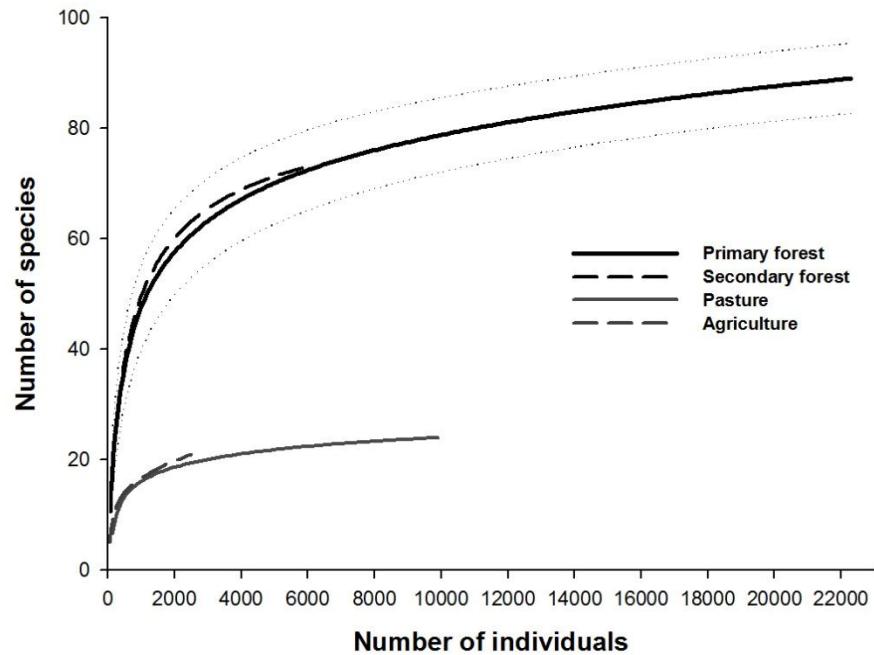


Figure 7 Individual-based rarefaction curves for dung beetles in primary forest, secondary forest, pasture and agriculture of 18 watersheds in the Santarem micro-region. Fitted dotted line indicates 95% confidence interval of expected richness in primary forest.

The patterns of species distribution varied among the land-uses, with communities showing low evenness in more degraded systems, since they visually presented more vertical abundance distributions in the species rank (Figure 8). Low similarity was found among the four most abundant species of the forested land-uses, except by *Canthon fulgidus*, the most common species in both primary and secondary forest. Regarding non-forested land-uses, *T. externepunktatum* and *P. xanthurum* were the most abundant species in agriculture and pasture, although they shifted their position in the rank.

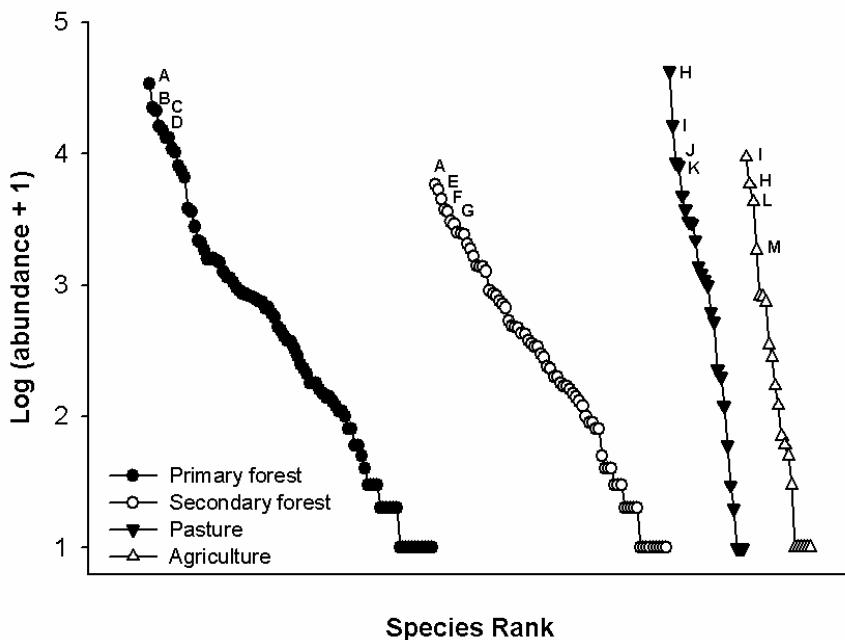


Figure 8 Rank of abundance curves comparing the species distribution in each land-use samples. Letter A=*Canthon fulgidus*, B=*Onthophagus* sp.1, C=*Eurysternus caribaeus*, D=*Canthidium* aff. *deyrollei*, E=*Canthon proseni*, F=*Eurysternus atrosericus*, G=*Canthidium* aff. *ardens*, H=*Trichilum externepunktatum*, I=*Pseudocanthon xanthurum*, J=*Dichotomius nisus*, K=*Canthidium barbacenicum*, L=*Canthon* aff. *acutus*, M=*Canthon* aff. *heyrowskyi*.

Dung beetle community structure was highly distinct when forested and non-forested land-uses were compared (Figure 9). Community structure was significantly different between primary and secondary forest, according to abundance data ($R_{ANOSIM}=0.411$; $p<0.001$) and presence/absence data ($R_{ANOSIM}=0.411$; $p<0.001$). There were no differences between pasture and agriculture, even according to abundance data ($R_{ANOSIM}=0.058$; $p<0.145$) or presence/absence data ($R_{ANOSIM}=0.058$; $p<0.138$). Patterns were similar using both transformed and untransformed data. Regarding to the multivariate dispersion among the land-use data, there were no differences among primary forest, agriculture and pasture. However, secondary forest was significantly different from all the other land-uses (Table 2)

Table 2 Results of the comparison of the multivariate dispersions (PERMDISP) among the land-uses data (* indicate significant differences).

Pairwise comparison	t	P(perm)
primary forest, secondary forest	5.4349	0.001*
primary forest, pasture	0.76941	0.470
primary forest, agriculture	0.46376	0.663
secondary forest, pasture	3.2226	0.002*
secondary forest, agriculture	2.6697	0.018*
pasture, agriculture	0.11792	0.907

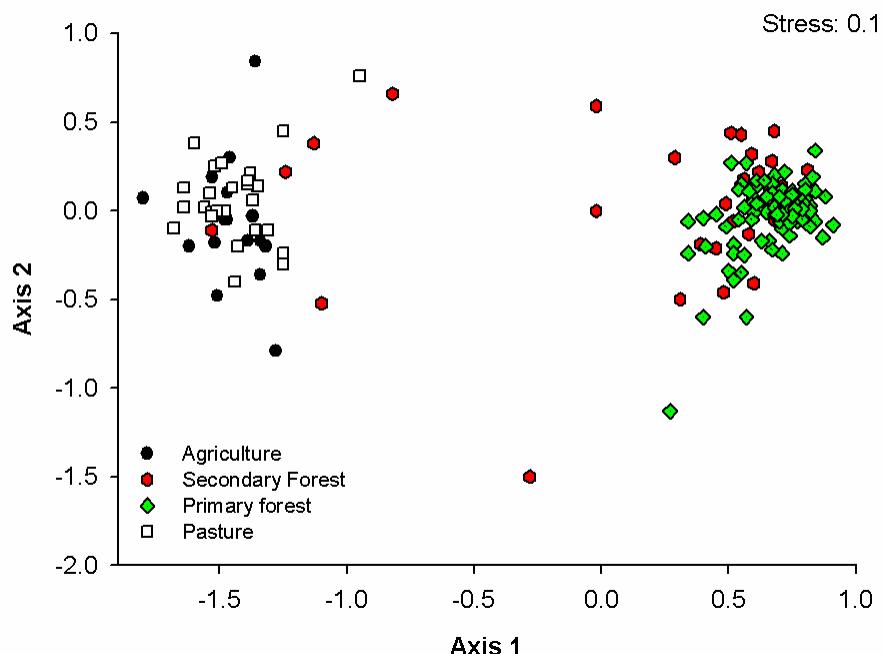


Figure 9 Non-metric Multidimensional Scaling (NMDS) ordination of dung beetle community structure across primary forest, secondary forest, pasture and agriculture based on abundance data. Patterns were similar using both transformed and untransformed (presented) data.

3.2 Conservation value

Overall, the removal of occasional species increased the proportion of species unique to primary forest, and decreased the conservation value of the modified land-uses. The conservation value of the non-forested land-uses

was indeed very low. However, it was lower when the occasional species were removed from all the land-uses (metric 1) (Figure 10) than when removed only from the modified land-uses (metric 2) (Figure 11). Opposing, we found higher values for secondary forest while excluding occasional species from all the land-uses.

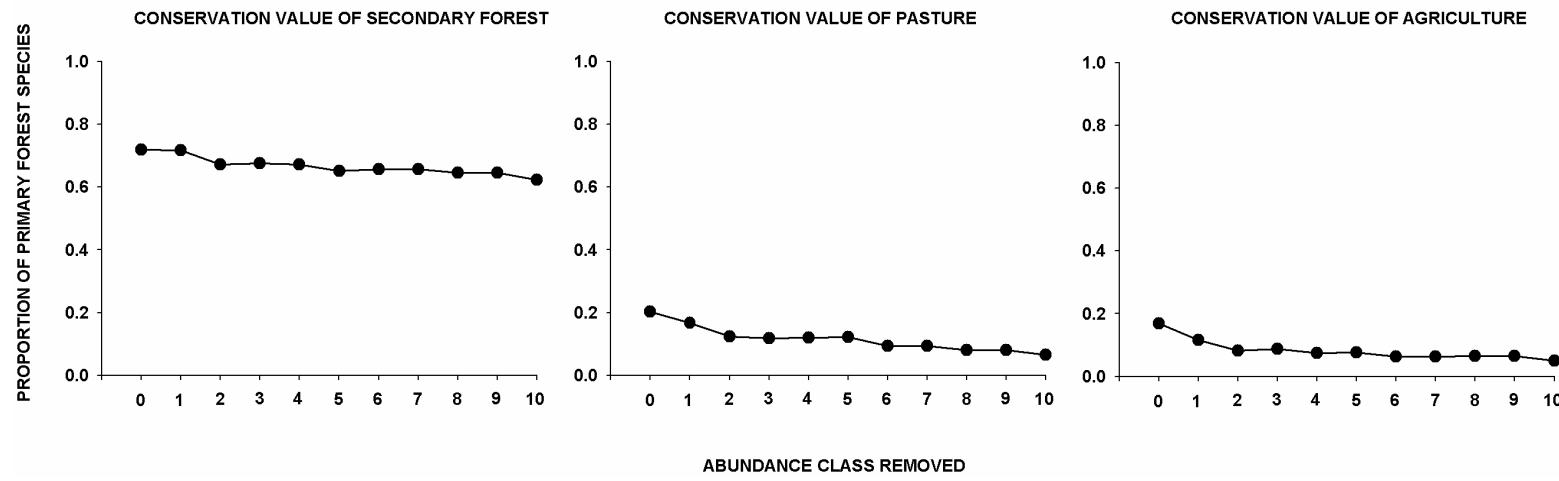


Figure 10 Metric 1: Conservation value of secondary forest, pasture and agriculture as an increasing number of abundance classes of occasional species are sequentially removed from all the land-uses.

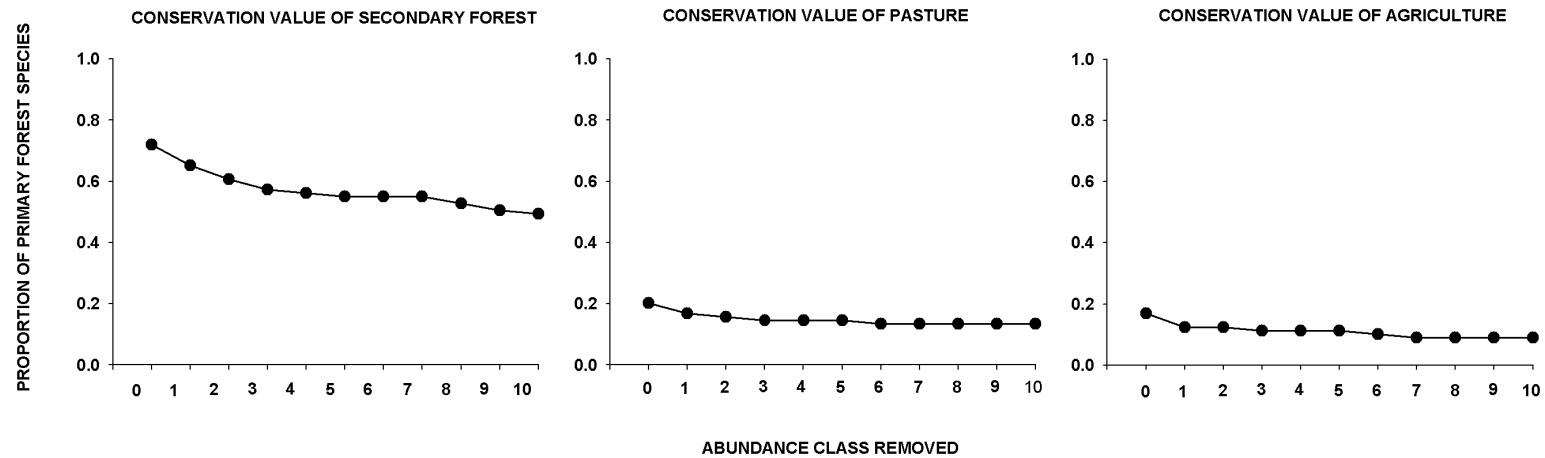


Figure 11 Metric 2: Conservation value of secondary forest, pasture and agriculture as an increasing number of abundance classes of occasional species are sequentially removed from the modified land-uses.

We found high variability on the richness found in all land-uses studied (Table 3)

Table 3 Richness variability of dung beetles sampled in primary forest (PF), secondary forest (SF), pasture (PA) and agriculture (AG) transects.

Land-use	PF	SF	PA	AG
Max	38.0	33.0	16.0	14.0
Min	10.0	6.0	4.0	3.0
Mean	23.5	18.3	10.1	7.9
Median	23.0	18.5	10.0	7.0

3.3 Sharing of species

The most abundant species were *Trichillum externepunktatum*, *Pseudocanthon* aff. *xanthurum*, *Canthon fulgidus*, *Onthophagus* sp.1 and *Eurysternus caribaeus* (Appendix A). Of these, only *T. externepunktatum* was sampled in all land-uses, as well as other 11 species (Table 4). The species *C. histrio* and *Canthidium* sp.1 were mostly collected in forested areas and none species was mostly abundant in agriculture (Appendix A). After removing the occasional species, only *C. barbacenicum*, *C. aff. ardens*, and *O. aff. hirculus* were shared among all land-uses.

Table 4 Abundance of species shared among primary forest (PF), secondary forest (SF), pasture (PA) and agriculture (AG).

Species	PF	SF	PA	AG	Total
<i>Canthidium (Canthidium) barbacenicum</i>	158	188	808	35	1189
<i>Canthidium (Canthidium) multipunctatum</i>	2	9	62	7	80
<i>Canthidium (Canthidium) sp.1</i>	381	86	2	1	470
<i>Canthidium (Eucanthidium) aff. ardens</i>	660	372	221	82	1335
<i>Canthon</i> aff. <i>Acutus</i>	1	49	484	429	963
<i>Canthon</i> aff. <i>Chalybaeus</i>	2	140	100	74	316
<i>Canthon</i> aff. <i>Hevrowskyi</i>	1	76	375	184	636
<i>Canthon histrio</i>	105	360	3	3	471
<i>Dichotomius nisus</i>	6	90	859	81	1036
<i>Ontherus appendiculatus</i>	2	17	304	6	329
<i>Onthophagus</i> aff. <i>hirculus</i>	12	13	110	28	163
<i>Trichillum externepunktatum</i>	10	67	4264	584	4925
TOTAL	1340	1467	7592	1514	11913

Of the 89 species found in the primary forest, 24 were exclusive of this land-use (Figure 9). Secondary forest areas presented only four exclusive species. One species, *Digitonthophagus gazella*, was restricted to pasture and agriculture, but we caught only one individual in the latter (Appendix A). Around 32% of primary forest species, 36% of secondary forest, 24% of pasture and 48% of agriculture species were sampled with 10 or less individuals, being considered as occasional. There was a high number of species shared between primary and secondary forest (Figure 12), and most of those shared among the other land-uses were characteristically non-forested species.

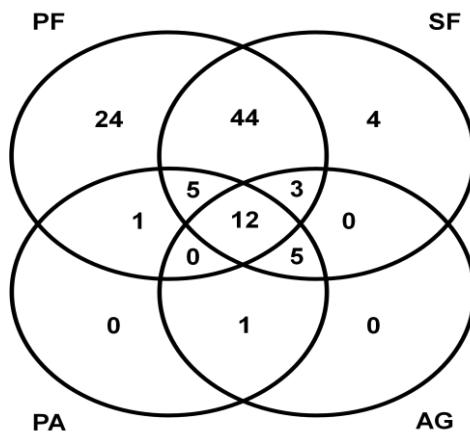


Figure 12 Diagram showing the sharing of species of dung beetles from the four land-uses sampled. PF = Primary Forest, SF= Secondary Forest, PA = Pasture, AG = Agriculture.

Primary forest fauna contributed with approximately 71% of the richness and 70% of the total abundance of dung beetles in agricultural areas. The values were higher regarding the other systems, with 75% richness/ 77% abundance for pasture and 88% richness / 97% abundance for secondary forests. However, after removing occasional species, these values decreased to approx. 38%/6% for agriculture, 37%/12% for pasture and 73%/90% for secondary forest (Figure 13).

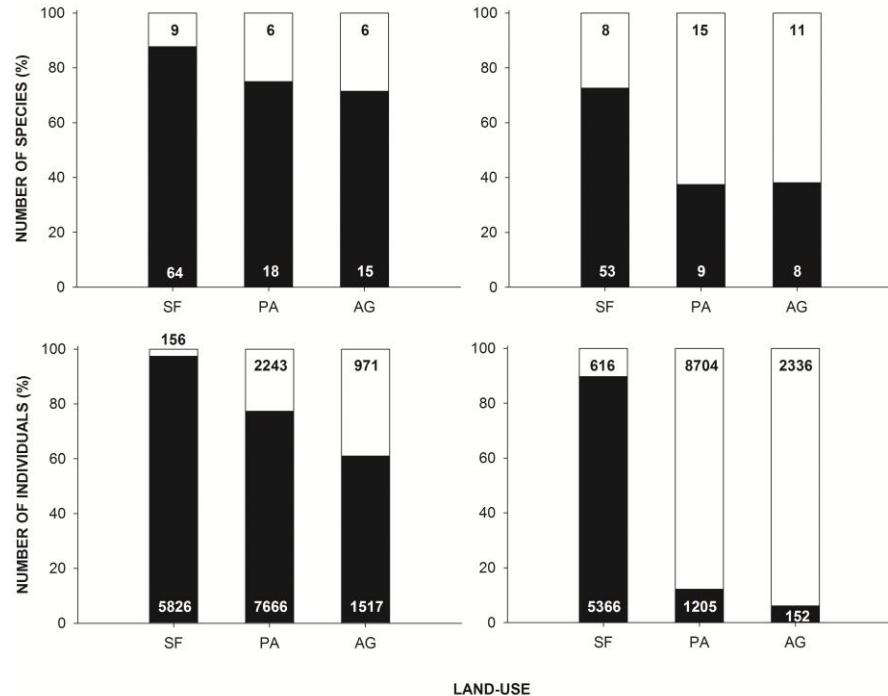


Figure 13 Percentage of total abundance and richness in secondary forest (SF), pasture (PA) and agriculture (AG) before (left) and after (right) the removal of occasional species. Black bars representing primary forest species and white bars non-forest species.

The high impact of the primary forest fauna on the total patterns of diversity found in the watershed was highlighted by the strong correlation between total watershed richness and primary forest richness ($r_{SPEARMAN}=0.7481$; $p=0.0003$) (Figure 14).

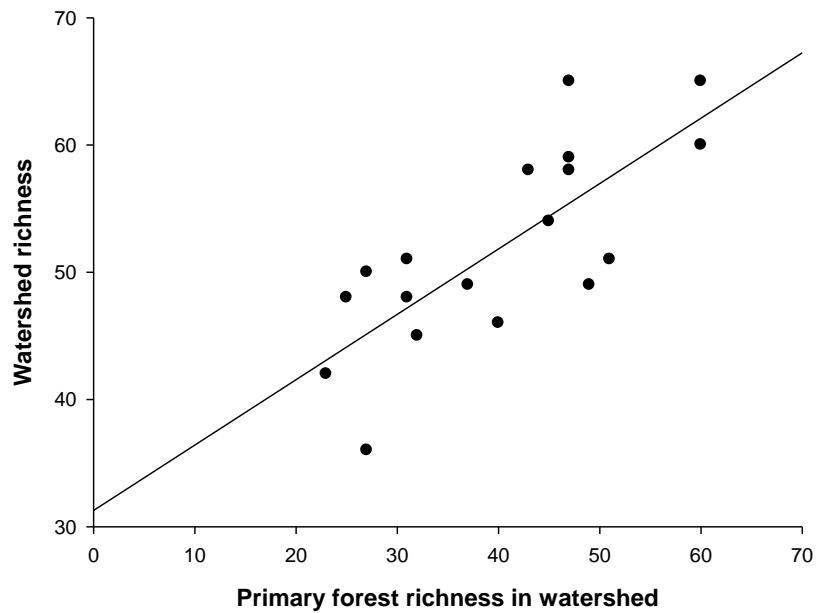


Figure 14 Correlation between the watersheds and primary forest richness.

4 DISCUSSION

In a recent review Bennet et al. (2006) highlighted the need of studies focused on understanding the importance of the landscape context, as it exerts a deeply and lasting influence on the structure, composition, and function of extant biota (GARDNER et al., 2010). Despite of the demand, data on biodiversity patterns at the meso-scale (10-100s km) are almost entirely absent from most regions (GARDNER et al., 2010). In the present work, we sampled dung beetle assemblages in different land-uses within 18 micro watersheds, and pooled the data to represent the watersheds as the unity of study. Although our analysis were made at transect level, this is the first work that presents genuine replicas at landscape level. Thus, our results contribute to a better understanding of the relative importance of landscape effects on observed biodiversity patterns.

4.1 Biodiversity responses to land-use intensification

As expected, dung beetle community richness, abundance and evenness decreased with increasing land-use intensification. The only exception to this overall pattern was the higher abundance of dung beetles in pasture when comparing to secondary forests.

Species responses to forest conversion and human induced disturbances are highly variable but largely negative (GARDNER et al., 2010). Many previous studies on dung beetles in tropical forests have shown important community changes in response to land-use intensification, including decreased species richness, abundance and evenness, and/or altered species composition (HORGAN, 2006; ANDRESEN, 2008; GARDNER et al., 2008; NEVES et al., 2010).

These patterns result from several interacting factors, including changes in fragment size, soil type, vegetation structure, microclimate and mammals abundance. The main sets of factors influencing dung beetles

populations are those associated to microclimate and to depletion of medium-large sized mammals and their associated dung resources (HALFFTER; MATTHEWS, 1966; NICHOLS et al., 2009). Since no adult Scarabaeinae is known to have mouthparts capable of chewing or cutting solid food, they need access to dung in a malleable or cuttable state (HALFFTER; MATTHEWS, 1966). With the forest cover loss, dung piles are deposited in sunnier and drier locations, and become quickly unavailable. Moreover, since dung beetles depend on vertebrates as dung suppliers, in particular mammals, consequently they are negatively affected by decreases in the population density of these animals (ANDRESEN; LAURANCE, 2007; NICHOLS et al., 2009; BARLOW et al., 2010b). The loss of medium-large sized mammals decreases the dung availability, and may disproportionately affect large bodied dung beetles, which are attracted and demand large sized dung patches (PECK; HOWDEN, 1984).

In addition to the decrease of dung beetle diversity, the land-use intensification result in two completely different communities, one associated to forested habitats and other to open habitats. Navarrete and Halffter (2008) found that the Scarabaeinae species from pastures penetrate only in the most perturbed forest fragments, and the presence of forested species in pastures is minimal, reduced to a few disturb-tolerant taxa. Since the canopy cover has a strong effect on dung beetle communities, forest removal produces a characteristic open-area species community, with fewer dung beetle species, lower community evenness, less biomass, and a greater abundance of small-bodied species (HALFFTER; ARELLANO, 2002; PINEDA et al., 2005; QUINTERO; ROSLIN, 2005). These patterns are strongly supported by our data, which showed no differences in species composition between agriculture and pasture, both exhibiting highly simplified communities. Non-forested areas presented two dominant small bodied species (*T. externepunktatum* and *P. xanthurum*), which together represented around 60% of the total abundance. The high abundance of *T. externepunktatum* in pasture may explain the higher abundance found in this

land-use when comparing to secondary forest. We sampled 5,982 dung beetles in secondary forest, and 4,264 *T. externe punctatum* in pasture.

Not surprisingly, species shared among all land-uses were mostly species known from open-area habitats, with low occurrence in primary forest, and the removal of occasional species from all land-uses severely decreased the amount of species shared. It is possible that the attractiveness of the bait may have been extended due to the high humidity and lower temperatures of the forest areas, increasing the pitfall effectively in these habitats. For dung beetles, bait attractiveness is strongly related to the water content in the dung. When the water content of dung falls below a certain level, it becomes unattractive to adult beetles (ERROUSSI et al., 2004). Since our pitfalls remained open for 48 hours in the field, it could have attracted ‘tourist species’ from neighbouring areas, depending on the distance to other land-uses.

We collected, for example, 4,264 individuals of *T. externe punctatum* in pasture, 654 in agriculture, and just 67 and 10 individuals in secondary and primary forest respectively. On the other hand, 105 individuals of *C. histrio* were found in primary forest, 360 in secondary forest, with just three individuals in pasture and agriculture. Thus, in spite of being collected very occasionally in primary forest, *T. externe punctatum* may be considered as open-area species. The same is true for the case of *C. histrio*. Understanding the reliability of inferences from field data is particularly challenging for a variety of reasons, including the spill-over effects across forest boundaries (GARDNER, 2010). Tourist species do not represent the native fauna of the landscape, as they are unlikely to establish viable populations (SCHMIDA; WILSON, 1985), and thus can lead to overestimates of diversity and conservation value of modified habitats (QUINTERO; HALFFTER, 2009).

4.2 Primary forest as source of species in human-modified land-uses

Dung beetles communities in the Neotropical region are very diverse (HANSKI; CAMBERFORT, 1991). In dry forest areas, total richness values are usually between 10 to 30 species, while in humid forest areas it can reach up than 80 species (GARDNER et al., 2008). In the present work, primary forest richness varied from 23 to 60 species among individual study transects, with a total richness of 99 for the entire landscape.

In contrast to the majority of studies concerning forest conversion, our study was carried in a forest matrix area, with a recent and disorderly colonization history (~50 yrs). The study landscape is composed of a mix of land-uses surrounded by forests in different levels of condition. We therefore expected a strong influence of primary forest areas on the spatial patterns of diversity distribution observed in our results. Indeed, our results show that primary forest is responsible for the majority of the region's dung beetle diversity and abundance.

Primary forest appears to be of limited importance as source of species to non-forested habitats. On first approach, primary forest appears to contribute more than 70% of total open-area habitat richness, although sharing only 15 and 18 species with agriculture and pasture, respectively. This would be noticeable, especially when compared to data collected by Vidaurre (2011). Studying introduced pastures and native systems across South America, Vidaurre (2011) found very low percentages of species occurring both in Amazon rainforest and introduced pastures. Vidaurre assigned this result to the low local colonization and to a lack of overlap with forest species. However, after we removed the occasional species, with abundance ≤ 10 individuals, the contribution of primary forest fauna to the overall non-forested land-use diversity decreased markedly to values around 40% of the abundance and 6 - 12% of dung beetle richness in the open-areas. This discrepancy is explained primarily by the forested species that were

collected in very low abundances in pasture and agriculture, and as such could represent non-viable populations from spill-over effects.

On the other hand, seven species predominantly abundant in non-forested land-uses were collected in primary forest with abundances ≤ 10 individuals. Most of these species are known independently as open-area species (Fernando Silva personal observations), and should not be considered in analyses of patterns of forest dung beetle diversity. We sampled, for example, only 10 individuals of *T. externepunktatum* in the 82 primary forest transects. In contrast, this species accounted for 43% of the total abundance of species found in pasture, and was the second most abundant species in agricultural areas. Thus, despite the fact that Vidaurre (2011) did not test the sensitivity of the patterns he observed to the inclusion or removal of occasional species, we can agree with his principal conclusions that open habitats are not (or very rarely) colonized by forest species, even if they are embedded within a forest matrix.

Since our study area is localized a far way from any Cerrado or other naturally open-habitat biome, the absence of representative natural open systems may hinder the occupation of disturbed areas by open-area species. This helps explain the low levels of species richness that we found in the non-forested land-uses, especially pasture, when comparing with other studies (MILHOMEM; VAZ-DE-MELLO; DINIZ, 2003; LOUZADA; CARVALHO-SILVA, 2009).

These findings highlight the importance of the proximity of naturally open areas in determining the diversity of disturbed areas, and help to reinforce the importance of taking account the geographic position of the study region before drawing any strong conclusions.

The ability to accurately determine the relative conservation values of undisturbed primary and human-modified environments is of particular importance in applied studies yet remains a major scientific challenge (BARLOW et al., 2010a). The high number of rare species, lack of ecological and biological information of those species, and the absence of

biodiversity data at meso-scale (for understanding the influence of the landscape in community properties) (SODHI, 2008; BARLOW et al., 2010a) may confound our interpretations, and lead to wrong decisions.

Overall, we showed that the removal of occasional species severely decreases the conservation value of the modified habitats (except for secondary forest). Accordingly to Barlow et al. (2010a), we found that the conservation value of secondary forest was lower when excluding species from the modified land-uses only. Because secondary forests share most of species with primary forest, and many of these species occur predominantly with low abundances, the removal of species with abundance ≤ 10 individuals has a marked effect, decreasing total secondary forest richness from 73 to 47 species and consequently its conservation value to regional biodiversity. However, the non-forested land-uses showed an opposite pattern of response to the species removal (although largely negative too), showing higher conservation values when excluding species only from the modified land-uses. Since the primary forest occasional species were not removed, the non-forested species which was shared among all the land-uses were considered as forested species too, overestimating the sharing of species between forested and non-forested land-uses. Furthermore most of the species shared among all the land-uses are removed from the primary forest when we remove the occasional species.

4.3 Conservation value of secondary forests

Our findings show a clear separation of dung beetle communities between forested and non-forested land-uses. Since dung beetles are very sensitive to environmental changes, the forest conversion into open-area agricultural habitats may be the most important factor responsible for species losses. The removal of canopy greatly affects, directly or indirectly, the microclimatic variables, vegetation structure, soil characteristics, and abundance of food resources (FINCHER, 1973; NEALIS, 1977;

LUMARET; KADIRI; BERTRAND, 1992; OSBERG; DOUBE; HANRAHAN, 1994; DAVIS, 1996; LUMARET; IBORRA, 1996; HALFFTER; ARELLANO, 2002; ANDRESEN, 2005), leading to a dramatic impoverishment of dung beetle communities.

Secondary forest harboured around 72% of the primary forest species and, after removing occasional species, there was little change in our measure of observed conservation value of this habitat. Nevertheless, it is still possible that this result represents a “false positive” and could overestimate the real importance of these habitats for biodiversity conservation. The high variance of species richness in secondary forests (median=18, max=31, min=6) illustrates how risky it is to make predictions based only on values of total richness, without considering the landscape effects. Depending on the site observed in our study area, one can conclude either that secondary forest is excellent for dung beetle conservation, or that it has almost no conservation value. Although recent studies show that maintaining a high degree of forest cover and relatively high complexity the forested land-uses can hold species-rich dung beetle communities similar to those found in intact areas (QUINTERO; ROSLIN, 2005; VULINEC; LAMBERT; MELLOW, 2006; NICHOLS et al., 2007), we show that some secondary forest areas – specially the newer and more distant to primary forests - can be characterized by impoverished dung beetle communities, being almost indistinguishable from open-area habitats. Moreover, dung beetle populations in secondary and plantation forests are often smaller and lack many of the larger bodied species that characterise assemblages in primary forest habitat (GARDNER et al., 2008). This fact has worrying implications for the maintenance of dung beetle-mediated services outside the primary forests (ANDRESEN; FEER, 2005).

Thus, as the effectiveness of secondary forests in maintaining biodiversity is highly context dependent, we agree with Gardner et al. (2008) that to be effective, management strategies of production landscapes need to emphasize the importance of protecting remaining areas of primary forest.

5 CONCLUSIONS

According to the results presented, we can draw the following conclusions:

- (1) Dung beetle communities structure are strongly affected by the forest cover, more than the land-use itself. Despite the differences in the communities' structure between primary and secondary forest, the values of richness and abundance of dung beetles drastically decreased in the non-forested land-uses. Moreover, the dung beetles communities of pasture and agriculture were almost completely different of the forest communities.
- (2) The conservation value of secondary forest, although higher than non-forested land-uses conservation value - is dependent of the landscape context, and highly sensitive to decisions regarding occasional species. We propose that conservation scientists consider the influence of occasional species in their results, and observe characteristics such as proximity to primary forest remaining and secondary forest age before taking conclusions.
- (3) Our hypothesis that primary forest biota dominates the make-up of dung beetles assemblages in non-forested Amazonian land-uses diversity was rejected. We can conclude that most of dung beetles are not capable of living in open-area habitats and are not able to colonize these areas.
- (4) The conservation value of the non-forested land-uses, when based on the proportion of primary forest species, is very low. Associating this fact with the low sharing of species between forested and non-forested habitats, and the absence of representative natural open systems near the study area, the continuous conversion of forested areas in open-areas in this region represents a great threat to biodiversity.

REFERENCES

ANDRESEN, E. Effects of season and vegetation type on community organization of dung beetles in a Tropical Dry Forest. **Biotropica**, v. 37, n. 2, p. 291-300, Jun. 2005.

_____. Short-term temporal variability in the abundance of tropical dung beetles. **Insect Conservation and Diversity**, v. 1, n. 2, p. 120-124, May. 2008.

ANDRESEN, E.; FEER, F. The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in Tropical Rainforests. In: FORGET, P. M. et al. (Eds.). **Seed fate**. Wallingford: CABI Publishing, 2005. p.331-349.

ANDRESEN, E.; LAURANCE, S. G. W. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. **Biotropica**, v. 39, n. 1, p. 141-146, Jan. 2007.

ASNER, G. P. et al. Selective logging in the Brazilian Amazon. **Science**, v. 310, n. 5747, p. 480-482, Oct. 2005.

AYRES, M. et al. **BioEstat**: aplicações estatísticas nas áreas das ciências biológicas e médicas. Belém: Sociedade Civil Mamirauá: MCT-CNPq, 2007. 364p.

BANG, H. S. et al. H. Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. **Applied Soil Ecology**, v. 29, n. 2, p. 165-171, Jun. 2005.

BARLOW, J. et al. Measuring the Conservation Value of Tropical Primary Forests: The Effect of Occasional Species on Estimates of Biodiversity Uniqueness. **Plos One**, v. 5, n. 3, p. 1-8, Mar. 2010a.

BARLOW, J. et al. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. **Journal of Applied Ecology**, v. 47, n. 4, p. 779-788, Aug. 2010b.

BASTOS, T. X. O estado atual dos conhecimentos das condições climáticas da Amazônia Brasileira. In: INSTITUTO DE PESQUISA AGROPECUÁRIA DO NORTE – IPEAN (Ed.). **Zoneamento agrícola da Amazônia: 1^a aproximação**. Belém: IPEAN, 1972. p.68-122. Boletim Técnico, 54.

BAWA, K. S. et al. Tropical ecosystems into the 21st century. **Science**, v. 306, n. 5694, p. 227-228, Oct. 2004.

BENNETT, A. F.; RADFORD, J. Q.; HASLEM, A. Properties of land mosaics: implications for nature conservation in agricultural environments. **Biological Conservation**, v. 133, n. 2, p. 250-264, Nov. 2006.

CLARKE, K. R. Non-parametric multivariate analysis of changes in community structure. **Australian Journal of Ecology**, v. 18, n. 1, p. 117-143, Mar. 1993.

CLARKE, K. R.; GORLEY, R. N. **Primer v6**: user manual/tutorial. Primer-E, Plymouth – UK. 2006. 192p.

COLWELL, R. K. **Estimates**: statistical estimation of species richness and shared species from samples. Version 8.2. User's guide and application. Published at: <<http://purl.oclc.org/estimates>>. Access: 20 Nov. 2010

DAILY, G. C. Ecological forecasts. **Nature**, v. 411, n. 6835, p. 245-245, May. 2001.

DAVIS, A. L. V. Geographical distribution of dung beetles (Coleoptera: Scarabaeidae) and their seasonal activity in south-western Cape Province. **Journal of The Entomological Society of South Africa**, v. 50, n. 2, p. 275-285. 1987.

DAVIS, A. L. V. Community organization of dung beetles (Coleoptera: Scarabaeidae): differences in body size and functional group structure between habitats. **African Journal of Ecology**, v. 34, n. 3, p. 258-275, Set. 1996.

DUMBRELL, A. J. et al. Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. **Journal of Applied Ecology**, v. 45, n. 5, p. 1531-1539, Oct. 2008.

ERROUSSI, F. et al. Effects of the attractiveness for dung beetles of dung pat origin and size along a climatic gradient. **Environmental Entomology**, v. 33, n. 1, p. 45-53, Feb. 2004.

FERRIER, S. et al. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. **Diversity and Distributions**, v. 13, n. 3, p. 252-264, May. 2007.

FINCHER, G. T. Nidification and reproduction of *Phanaeus* spp. in three textural classes of soil (Coleoptera: Scarabaeidae). **Coleopterist Bulletin**, v. 27, n. 1, p. 33-37. 1973.

FINCHER, G. T. Effect of dung beetle activity on the number of nematode parasites acquired by grazing cattle. **Journal of Parasitology**, v. 61, n. 4, p. 759-762. 1975.

GARDNER, T. A. et al. Predicting the uncertain future of tropical forest species in a data vacuum. **Biotropica**, v. 39, n. 1, p. 25-30, Jan. 2007.

GARDNER, T. A. et al. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. **Journal of Applied Ecology**, v. 45, n. 3, p. 883-893, Jun. 2008.

GARDNER, T. A. et al. Prospects for tropical forest biodiversity in a human-modified world. **Ecology Letters**, v. 12, n. 6, p. 561-582, Jun. 2009.

GARDNER, T. A. **Monitoring forest biodiversity:** improving conservation through ecologically-responsible management. London: Earthscan, 2010. 388p.

GARDNER, T. A. et al. A multi-region assessment of tropical forest biodiversity in a human-modified world. **Biological Conservation**, v. 143, n. 10, p. 2293-2300, Oct. 2010.

HALFFTER, G.; ARELLANO, L. Response of dung beetle diversity to human-induced changes in a tropical landscape. **Biotropica**, v. 34, n. 1, p. 144-154, Mar. 2002.

HALFFTER, G.; EDMONDS, W. D. **The nesting behavior of dung beetles (Scarabaeinae):** an ecological and evolutive approach. México DF: Instituto de Ecología, 1982. 242p.

HALFFTER, G.; MATTHEWS, E. G. The natural history of dung beetles of the subfamily Scarabaeinae. **Folia Entomológica Mexicana**, v. 12-14, p. 1-312. 1966.

HANSKI, I.; CAMBERFORT, Y. **Dung beetle ecology.** Princeton: Princeton University Press, 1991. 481p.

HAYASHI, S. et al. Boletim transparência florestal da Amazônia legal. Imazon, 2011. Disponível em: <<http://www.imazon.org.br/publicacoes/transparencia-florestal/transparencia-florestal-amazonia-legal/boletim-transparencia-florestal-da-amazonia-legal-abril-de-2011>>. Acesso em: 15 Mar. 2011.

HERRERA-MONTES, A.; BROKAW, N. Conservation value of tropical secondary forest: a herpetofaunal perspective. **Biological Conservation**, v. 143, n. 6, p. 1414-1422, Jun. 2010.

HORGAN, F. G. Burial of bovine dung by coprophagous beetles (Coleoptera : Scarabaeidae) from horse and cow grazing sites in El Salvador. **European Journal of Soil Biology**, v. 37, n. 2, p. 103-111, Apr-Jun. 2001.

_____. Aggregation and coexistence of dung beetles in montane rain forest and deforested sites in central Peru. **Journal of Tropical Ecology**, v. 22, n. 4, p. 359-370, Jul. 2006.

LINDENMAYER, D. B.; FRANKLIN, J. F. **Conserving biodiversity:** a comprehensive multiscaled approach. Washington: Island Press, 2002. 351p.

LOUZADA, J. N. C.; CARVALHO-SILVA, P. R. Utilisation of introduced Brazilian pastures ecosystems by native dung beetles: diversity patterns and resource use. **Insect Conservation and Diversity**, v. 2, n. 1, p. 45-52, Feb. 2009.

LOUZADA, J. N. C.; LOPES, F. S. A comunidade de Scarabaeidae copronecrófagos (Coleoptera) de um fragmento de Mata Atlântica. **Revista Brasileira de Entomologia**, v. 41, n. 1, p. 117-121, Mar. 1997.

LUMARET, J. P.; IBORRA, O. Separation of trophic niches by dung beetles (Coleoptera, Scarabaeidae) in overlapping habitats. **Pedobiologia**, v. 40, p. 392-404. 1996.

LUMARET, J. P.; KADIRI, N.; BERTRAND, M. Changes in resources: consequences for the dynamics of dung beetle communities. **Journal of Animal Ecology**, v. 29, n. 2, p. 349-356. 1992.

MALHI, Y. et al. Climate change, deforestation, and the fate of the Amazon. **Science**, v. 319, n. 5860, p. 169-172, Jan. 2008.

MILHOMEM, M. S.; VAZ-DE-MELLO, F. Z.; DINIZ, I. R. Técnicas de coleta de besouros copronecrófagos no Cerrado. **Pesquisa Agropecuária Brasileira**, v. 38, n. 11, p. 1249-1256, Nov. 2003.

MILLER, A. The mouthparts and digestive tract of adult dung beetles (Coleoptera: Scarabaeidae) with reference to the ingestion of helminth eggs. **Journal of Parasitology**, v. 47, n. 6, p. 735-744, Dec. 1961.

NAVARRETE, D.; HALFFTER, G. Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. **Biodiversity and Conservation**, v. 17, n. 12, p. 2869-2898, Nov. 2008.

NEALIS, V. G. Habitat associations and community analysis of south Texas dung beetles (Coleoptera: Scarabaeinae). **Canadian Journal of Zoology**, v. 55, n. 1, p. 138-147, Jan. 1977.

NEVES, F. D. et al. Successional and Seasonal Changes in a Community of Dung Beetles (Coleoptera: Scarabaeinae) in a Brazilian Tropical Dry Forest. **Natureza & Conservação**, v. 8, n. 2, p. 160-164, Dec. 2010.

NICHOLS, E.; GARDNER, T. A. Dung beetles as candidate study taxon in applied biodiversity conservation research. In: SIMMONS, L. W.;

RIDSDILL-SMITH, T. J. (Eds.). **Dung beetle ecology and evolution**. London: Blackwell, 2011. p. 267-291.

NICHOLS, E. et al Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. **Biological Conservation**, v. 137, n. 1, p. 1-19, Jun. 2007.

NICHOLS, E. et al. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. **Biological Conservation**, v. 141, n. 6, p. 1461-1474, Jun. 2008.

NICHOLS, E. et al. Co-declining mammals and dung beetles: an impending ecological cascade. **Oikos**, v. 118, n. 4, p. 481-487, Apr. 2009.

NORRIS, K. Agriculture and biodiversity conservation: opportunity knocks. **Conservation Letters**, v. 1, n. 1, p. 2-11, Apr. 2008.

OSBERG, D. C.; DOUBE, M.; HANRAHAN, S. A. Habitat specificity in African dung beetles: the effect of soil type on the survival of dung beetle immatures (Coleoptera: Scarabaeidae). **Tropical Zoology**, v. 7, n. 1, p. 1-10. 1994.

PALMER, M. et al. Ecology for a crowded planet. **Science**, v. 304, n. 5675, p. 1251-1252, May. 2004.

PECK, S. B.; HOWDEN, H. F. Response of a Dung Beetle Guild to Different Sizes of Dung Bait in a Panamanian Rainforest. **Biotropica**, v. 16, n. 3, p. 235-238, Sep. 1984.

PERES, C. A. et al. Biodiversity conservation in human-modified Amazonian forest landscapes. **Biological Conservation**, v. 143, n. 10, p. 2314-2327, Oct. 2010.

PINEDA, E. et al. Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. **Conservation Biology**, v. 19, n. 2, p. 400-410, Apr. 2005.

QUINTERO, I.; HALFFTER, G. Temporal changes in a community of dung beetles (Insecta: Coleoptera: Scarabaeinae) resulting from the modification and fragmentation of tropical rain forest. **Acta Zoológica Mexicana**, v. 25, n. 3, p. 625-649. 2009.

QUINTERO, I.; ROSLIN, T. Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. **Ecology**, v. 86, n. 12, p. 3303-3311, Dec. 2005.

REID, H.; HUQ, S. Climate change biodiversity and livelihood impacts. In: ROBLEDO, C.; KANNINEN, M.; PEDRONI, L. (Eds.). **Tropical Forest and Adaptation to Climate Change: in Search of Synergies**. Bogor: CIFOR, 2005. p.57-70.

SAYER, J.; MAGINNINS, S. **Forest in landscapes:** ecosystem approaches to sustainability. London: Earthscan, 2005. 268p.

SCHMIDA, A.; WILSON, M. Biological determinants of species diversity. **Journal of Biogeography**, v. 12, n. 1, p. 1-20, Jan. 1985.

SILVEIRA, F. A. O. et al. Predation on *Atta laevigata* (Smith 1958) (Formicidae Attini) by *Canthon virens* (Mannerheim 1829) (Coleoptera: Scarabaeidae). **Tropical Zoology**, v. 19, n. 1, p. 1-7, Jul. 2006.

SKOLE, D.; TUCKER, C. Tropical deforestation and habitat fragmentation in the Amazon satellite data from 1978 to 1988. **Science**, v. 260, n. 5141, p. 1905-1910, Dec. 1993.

SODHI, N. S. Invited views in basic and applied ecology - tropical biodiversity loss and people - a brief review. **Basic and Applied Ecology**, v. 9, n. 2, p. 93-99, Mar. 2008.

VAZ-DE-MELLO, F. Z. Estado atual de conhecimento dos Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) do Brasil. **Monografias Tercer Milênio**, v. 1, p. 183-195. 2000.

VIDAURRE, T. **Convergência ecológica em sistemas nativos e pastagens introduzidas da América do Sul, tomando como foco de estudo os Scarabaeinae (Coleoptera: Scarabaeidae)**. 2011. 76p. Dissertação (Mestrado em Ecologia) – Universidade Federal de Lavras, Lavras, MG.

VULINEC, K.; LAMBERT, J. E.; MELLOW, D. J. Primate and dung beetle communities in secondary growth rain forests: implications for conservation of seed dispersal systems. **International Journal of Primatology**, v. 27, n. 3, p. 855-879, Jun. 2006.

APPENDIX

APPENDIX A Dung beetles collected in four different Amazonian land-uses (primary forest, secondary forest, pasture and agriculture) in Santarém micro region (PA – Brazil), between April and June 2010.

Species	Land-use				Total
	PF	SF	PA	AG	
<i>Ateuchini tribe</i>					
<i>Anomiopus</i> aff. <i>latistriatus</i> (Canhedo 2006)		1			1
<i>Anomiopus</i> aff. <i>pictus</i> (Harold 1862)	2	1	1		4
<i>Anomiopus</i> <i>batesi</i> (Waterhouse 1891)	1				1
<i>Anomiopus</i> <i>brevipes</i> (Waterhouse 1891)	3				3
<i>Anomiopus</i> <i>parallelus</i> (Harold 1862)	1				1
<i>Ateuchus</i> aff. <i>candezei</i> (Harold 1868)	362	43			405
<i>Ateuchus</i> aff. <i>murrayi</i> (Harold 1868)	1319	83			1402
<i>Ateuchus</i> aff. <i>romani</i> (Boucamont 1927)	18				18
<i>Ateuchus</i> aff. <i>striatulus</i> (Borre 1886)		2			2
<i>Ateuchus</i> <i>connexus</i> (Harold 1868)	82	34			116

'Continue'...

Species	Land-use				Total
	PF	SF	PA	AG	
<i>Ateuchus</i> sp.1	74	36			110
<i>Ateuchus</i> sp.2	67	1			68
<i>Canthidium (Canthidium)</i> aff. <i>deyrollei</i> (Harold 1867)	1616	245			1861
<i>Canthidium (Canthidium)</i> aff. <i>gerswtcheri</i>	208	15			223
<i>Canthidium (Canthidium)</i> aff. <i>lentum</i> (Erichson 1847)	29	24		1	54
<i>Canthidium (Canthidium)</i> <i>barbacenicum</i> (Borre 1886)	158	188	808	35	1189
<i>Canthidium (Canthidium)</i> <i>multipunctatum</i> (Balthasar 1939)	2	9	62	7	80
<i>Canthidium (Canthidium)</i> sp.1	381	86	2	1	470
<i>Canthidium (Canthidium)</i> sp.2	85	20	53		158
<i>Canthidium (Canthidium)</i> sp.3	21	20			41
<i>Canthidium (Canthidium)</i> sp.4	125	47			172
<i>Canthidium (Canthidium)</i> sp.7	11	2			13
<i>Canthidium (Eucanthidium)</i> aff. <i>ardens</i> (Bates 1887)	660	372	221	82	1335
<i>Canthidium (Eucanthidium)</i> aff. <i>collare</i> (Castelnau 1840)	184	127			311
<i>Canthidium (Eucanthidium)</i> aff. <i>funebre</i> (Baltasar 1939)	4				4
<i>Canthidium (Eucanthidium)</i> sp.5	67	2			69
<i>Canthidium (Eucanthidium)</i> sp.6	5	9			14
<i>Canthidium (Eucanthidium)</i> sp.8	38	1			39

'Continue'...

Species	Land-use				Total
	PF	SF	PA	AG	
<i>Canthidium humerale</i> (Gemar, 1813)	8		12		20
<i>Eutrichillum</i> sp.1	3				3
<i>Trichillum externepunktatum</i> (Borre, 1880)	10	67	4264	584	4925
<i>Uroxys</i> sp.1	158	18	1		177
<i>Uroxys</i> sp.2	16				16
<i>Uroxys</i> sp.3	15	2			17
<i>Canthonini tribe</i>					
<i>Canthon</i> aff. <i>acutus</i> (Gemar 1813)	1	49	484	429	963
<i>Canthon</i> aff. <i>angustatus</i> (Harold 1867)	81	8			89
<i>Canthon</i> aff. <i>chalybaeus</i> (Harold 1867)	2	140	100	74	316
<i>Canthon</i> aff. <i>hevrowskyi</i> (Blanchard 1843)	1	76	375	184	636
<i>Canthon</i> aff. <i>quadrimaculatus</i> (Schmidt 1922)	91	243			334
<i>Canthon</i> aff. <i>sericatus</i> (Schmidt 1922)	78	17			95
<i>Canthon</i> aff. <i>simulans</i> (Schmidt 1922)		42	20	1	63
<i>Canthon</i> <i>fulgidus</i> (Martinez 1950)	3413	583			3996

'Continue'...

Species	Land-use				Total
	PF	SF	PA	AG	
<i>Canthon histrio</i> (Redtenbacher 1867)	105	360	3	3	471
<i>Canthon lituratus</i> (Audinet & Serville 1828)		30	295	17	342
<i>Canthon obscuriellus</i> (Gemar 1813)		4	138	5	147
<i>Canthon proseni</i> (Schmidt 1922)	1015	534			1549
<i>Canthon semiopacus</i> (Harold, 1868)		14			14
<i>Canthonella</i> sp.1		1			1
<i>Canthonella</i> sp.2		1			1
<i>Cryptocanthon pcorum</i> (Linnaeus 1767)	86	4			90
<i>Deltochilum amazonicum</i> (Bates 1887)	33	3			36
<i>Deltochilum carinatum</i> (Bates 1887)		1			1
<i>Deltochilum enceladum</i> (Westwood 1837)	113				113
<i>Deltochilum orbiculare</i> (Kolbe 1893)		76			76
<i>Deltochilum</i> sp.1	158	10			168
<i>Deltochilum</i> sp.2	806	137			943
<i>Pseudocanthon</i> aff. <i>xanthurum</i> (Arnaud 1984)		71	1645	935	2651
<i>Scybalocanthon</i> sp.1	23	3			26
<i>Sylvicanthon</i> sp.1	48	206		1	255

'Continue'...

Species	Land-use				Total
	PF	SF	PA	AG	
<i>Bdelyrus paranesis</i> (Cook 1998)	14				14
<i>Dichotomius aff. fortestriatus</i> (Linnaeus 1758)	736	252			988
<i>Dichotomius aff. lucasi</i> (Luederwaldt 1924)	1328	138	1		1467
<i>Dichotomius boreus</i> (Harold 1869)	1				1
<i>Dichotomius carinatus</i> (Olivier 1789)	154	34			188
<i>Dichotomius imitator</i> (Luederwaldt 1925)	25	23			48
<i>Dichotomius mamillatus</i> (Felsche 1901)	3	1			4
<i>Dichotomius melzeri</i> (Felsche 1901)	61	38			99
<i>Dichotomius nisus</i> (Luederwaldt 1922)	6	90	859	81	1036
<i>Dichotomius prietoi</i> (Olivier 1789)		1			1
<i>Dichotomius robustus</i> (Martinez & Martinez 1982)	18	3			21
<i>Dichotomius worontzowi</i> (Luederwaldt 1935)	147	48	1		196
<i>Ontherus appendiculatus</i> (Mannerheim, 1829)	2	17	304	6	329
<i>Ontherus carinifrons</i> (Mannerheim 1829)	41	16			57

'Continue'...

Species	Land-use				Total
	PF	SF	PA	AG	
<i>Oniticellini tribe</i>					
<i>Eurysternus arnaudi</i> (Fabricius 1787)	45	12			57
<i>Eurysternus atrosericus</i> (Génier 2009)	1501	447			1948
<i>Eurysternus balachowskyi</i> (Génier 2009)	57	14			71
<i>Eurysternus caribaeus</i> (Halfpter & Halfpter 1976)	2126	288			2414
<i>Eurysternus cayannensis</i> (Herbst 1789)	278	5			283
<i>Eurysternus cyclops</i> (Génier, 2009)	6				6
<i>Eurysternus haematicollis</i> (Génier 2009)	37	1			38
<i>Eurysternus howdeni</i> (Balthasar 1939)	1				1
<i>Eurysternus hypocrita</i> (Génier 2009)	18				18
<i>Eurysternus plebejus</i> (Balthasar 1939)	95	8			103
<i>Eurysternus vastiorum</i> (Harold 1880)	8				8
<i>Eurysternus wittmerorum</i> (Martinez 1988)	1088	165			1253
<i>Onthophagini tribe</i>					
<i>Digitonthophagus gazella</i> (Pereira 1942)			23	1	24
<i>Onthophagus aff. clypeatus</i> (Luederwaldt 1930)	1				1
<i>Onthophagus aff. hirculus</i> (Blanchard 1846)	12	13	110	28	163

'Continue'...

Species	Land-use				Total
	PF	SF	PA	AG	
<i>Onthophagus</i> aff. <i>onorei</i> (Mannerheim 1829)	2	1			3
<i>Onthophagus</i> <i>onthochromus</i> (Zunino & Halfter 1947)	1				1
<i>Onthophagus</i> sp.1	2232	304	6		2542
<i>Phanaeinae tribe</i>					
<i>Coprophanaeus degallieri</i> (Arnaud, 1997)	3				3
<i>Coprophanaeus jasius</i> (Arnaud 1977)	13				13
<i>Coprophanaeus lancifer</i> (Olivier 1789)	115	28			143
<i>Dendropaemon</i> aff. <i>refulgens</i> (Waterhouse, 1891)		1			1
<i>Diabroctis mimas</i> (Waterhouse 1891)		4	122	12	138
<i>Oxysternon macleayi</i> (Nevinson, 1892)	217	53			270
<i>Oxysternon silenus</i> (Nevinson 1892)	11	2			13
<i>Phanaeus alvarengai</i> (Castelnau 1840)		2			2
Total geral	22285	5982	9909	2488	40664