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RESPOSTAS DOS BESOUROS ESCARABEÍNEOS À MODIFICAÇÃO DE HABITAT EM FLORESTAS TROPICAIS

ILHÉUS- BAHIA

2019

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade da Universidade Estadual de Santa Cruz, para a obtenção do Título de Doutor em Ecologia e Conservação da Biodiversidade.

Orientador: Dr. Júlio Baumgarten

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Eu dedico essa tese a minha avó Minervina *(in memoriam)*

Dedicatória

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RESUMO

Com a intensificação das atividades antrópicas sobre as áreas naturais, principalmente nos trópicos, o uso de indicadores ambientais torna-se importante para verificar como a biodiversidade está respondendo a diferentes condições ambientais. O principal objetivo desta tese foi entender as respostas dos besouros escarabeíneos à modificação do habitat em floresta tropical. Para isso, subdividiram-se os seguintes objetivos: (Capítulo I) entender como redução de cobertura florestal influencia a comunidade de escarabeíneos; (Capítulo II) avaliar como diferentes preditores de paisagem - cobertura florestal, densidade de borda e matriz de pastagem - afetam diferentes subgrupos de escarabeíneos e (Capítulo III) resumir o estado atual de conhecimento sobre as variáveis respostas de escarabeíneos utilizadas em estudos de modificação de habitat em florestas tropicais. Para responder os dois primeiros objetivos, 16 paisagens localizadas na Floresta Atlântica do Nordeste brasileiro - *hotspot* de biodiversidade - foram selecionadas. Enquanto que para o terceiro objetivo, uma qualitativa e quantitativa revisão de literatura foi realizada com base em artigos publicados em revistas científicas exploradas a partir da plataforma 'Web of Knowledge'. Verificou-se que (1) a redução de cobertura florestal tem efeitos negativos sobre os escarabeíneos e a β diversidade aumentou em fragmentos com pouca cobertura florestal na paisagem; (2) a densidade de bordas foi a variável explicativa mais importante para mudanças na comunidade de escarabeíneos quando comparada com cobertura florestal e de pastagem em escala de paisagem. No entanto, tanto a cobertura florestal quanto a de pastagem influenciaram significativamente várias respostas no grupo, tais como redução de coprófagos e necrófagos; e (3) foram registrados 194 estudos de 1975 a 2018, desenvolvidos em florestas tropicais de 31 diferentes países e com pesquisadores concentrados principalmente no Brasil, Reino Unido e México. Nossos resultados destacam que as variáveis mais usadas para avaliar modificações de habitat foram em ordem crescente, 'abundância', 'riqueza/diversidade de espécies' e 'massa/tamanho corporal'. Em conjunto, esses resultados sugerem a necessidade de estratégias de conservação e manejo, por meio da recuperação da cobertura florestal e redução na cobertura de pastagem e densidade de borda em nível de paisagem. Como também, reforça a importância de aprimorar os estudos sobre as variáveis repostas de espécies indicadoras, visto que esse é um passo essencial para avaliar os efeitos da modificação de habitat na biodiversidade.

Palavras-Chave: Floresta tropical. Indicadores ecológicos. Mudança de habitat. Paisagens fragmentadas. Scarabaeinae.

ABSTRACT

With an intensification of anthropic activities on natural areas, mainly in the tropics, the use of ecological indicators becomes an essential task to verify how biodiversity is responding to different habitat condition. The main objective of this thesis was to understand the answers of dung beetle to habitat changes in tropical forests. For this, subdivided the following objectives: (Chapter I) to understand how reduction of forest cover influences the community of dung beetles; (Chapter II) to evaluate how different predictors of landscape - forest cover, edge density and pasture in the matrix - affect different subgroups of dung beetles and (Chapter III) to summarize the current state of knowledge on response variables of dung beetles in human-modified landscapes in tropical forests. To answer the first two objectives, 16 landscapes located in the Atlantic Forest of Northeast Brazil - biodiversity *hotspot* - were selected. While for the third objective, a qualitative and quantitative literature review was carried out based on articles published in scientific journals explored from the 'Web of Knowledge' platform. It was verified that (1) reduction of forest cover has negative effects on dung beetles and β diversity increased under low forest cover; (2) edge density was the most important explanatory variable to changes in the dung beetles communities when compared to forest and pasture cover at landscape scales. However, both forest and pasture cover also significantly influenced many of the dung beetle responses, such as reduction of coprophagous and necrophagous; and (3) we recorded 194 studies from 1975 to 2018, developed in tropical forests of 31 different countries and with researchers mostly concentrated in Brazil, United Kingdom and Mexico. Our results highlight that the highest ranked response variables used to assess habitat changes were 'abundance', followed by 'species richness/diversity' and 'body mass/size'. Taken together, these results suggest the need of conservation and management strategies focused through promotion the forest recovery and reduction in the pasture cover and edge density at the landscape-level. It also reinforces the importance of improving studies on response variables of ecological indicators, since this is an essential step to assess the effects of habitat changes on biodiversity.

Keywords: Ecological indicators. Fragmented landscape. Habitat change. Scarabaeinae. Tropical forest.

INTRODUÇÃO GERAL

A intensificação das atividades antrópicas sobre as áreas naturais, principalmente nos ecossistemas tropicais, tem levado pesquisadores a investigarem os efeitos das paisagens modificadas pelo homem sobre a biodiversidade e a definir estratégias de manejo dessas paisagens de modo a assegurar a conservação dos ecossistemas (BARLOW et al., 2018; MELO et al., 2013). O processo de modificação das paisagens conduzida pelo homem apresentou um acelerado crescimento nas últimas três décadas (LAMBIN & GEIST, 2006), baseado principalmente na expansão da agricultura, pecuária e urbanização (GEIST & LAMBIN, 2002; MAXWELL et al., 2016). As paisagens resultantes da perda e fragmentação de habitat podem apresentar além da quantidade de habitat original reduzida, fragmentos de diferentes tamanhos e com diferentes graus de isolamento, com influência do efeito de borda que varia de acordo com o tipo de matriz circundante (DELGADO et al., 2007; FAHRIG, 2003, 2013; LAURANCE, 2008).

A perda de habitat representa uma das maiores ameaças a biodiversidade, alterando a distribuição de espécies e enfraquecendo a funcionalidade dos ecossistemas (CARDINALE et al., 2012; PIMM & RAVEN, 2000). Com isso, os principais objetivos dos estudos em ecologia da conservação têm sido entender quais alterações ocorrem quando a dinâmica da paisagem é modificada (MURCIA, 1995; TABARELLI et al., 2012), as conseqüências destas alterações na manutenção da biodiversidade (GARDNER et al., 2008; NICHOLS et al., 2009) e como esses resultados podem gerar subsídios para políticas públicas de conservação da biodiversidade (CASTELLANO & SORRENTINO, 2012; JOLY et al., 2010).

Estudos têm comprovado empiricamente os impactos da perda de habitat em paisagens tropicais (FILGUEIRAS et al., 2016; NICHOLS et al., 2007; SÁNCHEZ-DE-JESÚS et al., 2015). Efeitos importantes como a formação de bordas em paisagens fragmentadas, podem causar uma redução da umidade relativa e aumento da incidência de temperatura (MURCIA, 1995; TURNER, 1996). Conseqüentemente, essas condições, afetam negativamente espécies tolerantes à sombra e favorecem espécies pioneiras (LAURENCE et al., 1998). Como também, os efeitos associados à formação de matrizes com diferentes composições vegetacionais e condições microclimáticas em relação à floresta (BARNES et al., 2014; FRANKLIN & LINDENMAYER, 2009), podem reduzir a conectividade entre paisagens e dificultar a dispersão dos organismos (FAHRIG & MERRIAM, 1994; METZGER & DECAMPS, 1997). Além disso, é importante destacar que os resultados da perda e fragmentação de habitat podem ser progressivos em longo prazo, levando conseqüências como o atraso de imigração e o débito de extinção e das funções do ecossistema (HADDAD et al., 2015).

As Florestas Tropicais são um dos mais diversos ecossistemas do mundo, com altas taxas de endemismo (MAYAUX et al., 2005). Todavia, estão associadas a uma alta incidência de perda e fragmentação de habitat, onde 70% das florestas estão dentro de 1 km ou menos de uma borda antropogênica (HADDAD et al., 2015). Dentro deste contexto, destaca-se a Floresta Atlântica do Brasil que tem 80% dos remanescentes florestais menores que 50 ha e aproximadamente metade da floresta existente está a menos de 100 m de uma área antropizada (RIBEIRO et al., 2009). A Floresta Atlântica abriga uma alta diversidade e taxa de endemismo de espécies (MYERS et al., 2000). Além disso, apresentam zonas de refúgios climáticos com alta diversidade genética (CARNAVAL & MORITZ, 2008; CARNAVAL et al., 2009; FONSECA, 1985), sendo um *hotspot* de biodiversidade (TABARELLI et al., 2005).

Desse modo, estudos que elucidem como os organismos estão respondendo a mudança de habitat podem estabelecer diretrizes para conservação da biodiversidade (BALMFORD et al., 2012; GARDNER et al., 2009). Uma forma de identificar modificações de habitat e qualificar os estudos ecológicos é através do uso de espécies que funcionam como indicadoras de alterações ambientais (MCGEOCH, 1998; MCGEOCH et al., 2002). A utilização de espécies indicadoras em ecossistemas terrestres aumentou a partir da década de 80 (MCGEOCH, 1998) e hoje, diversos grupos como borboletas, formigas e besouros têm sido classificados como efetivos indicadores terrestres (AGOSTI et al., 2000; BONEBRAKE et al., 2010; FREITAS et al., 2006; HALFFTER & FAVILA, 1993; UEHARA-PRADO et al., 2009).

Besouros da subfamília Scarabaeinae (Scarabaidae), popularmente conhecidos como escarabeíneos ou rola-bostas, são abundantes e diversos em florestas tropicais (HALFFTER & MATHHEWS, 1966; HANSKI & CAMBEFORT, 1991) e particularmente importantes para a manutenção de funções do ecossistema ligadas a ciclagem de nutrientes, dispersão secundária de sementes, aeração do solo e supressão de parasitas (NICHOLS et al., 2008). A comunidade de escarabeíneos é influenciada por diversos fatores, tais como cobertura florestal (HALFFTER & ARELLANO, 2002;

SÁNCHEZ-DE-JESÚS et al., 2015), tipo de solo (BEIROZ et al., 2017; FARIAS et al., 2015; GRIFFITHS et al., 2015), variáveis microclimáticas (OSBERG et al., 1994) e fontes de alimento (ESTRADA et al., 1999; NICHOLS et al., 2009). Desse modo, esses insetos têm sido largamente utilizados em avaliações sobre as conseqüências da perda e fragmentação em florestas tropicais (LARSEN et al., 2008; MARSH et al., 2018), contribuindo significativamente para a identificação de impactos negativos em habitats naturais (BARLOW et al., 2016; FILGUEIRAS et al., 2019).

As variações nas comunidades de escarabeíneos em resposta a perda e fragmentação nas florestas tropicais, incluem redução na riqueza e abundância de espécies florestais (BARRAGÁN et al., 2011; FILGUEIRAS et al., 2015), perda de guildas funcionais e mudanças no provimento das funções ecossistêmicas (AUDINO et al., 2017; BRAGA et al., 2013). Embora as variações descritas sejam em grande parte provenientes de estudos de pequena escala (NICHOLS et al., 2007), pesquisas recentes em nível de escala de paisagem também tem corroborado com esses padrões gerais de resposta (BARLOW et al., 2016; BRAGA et al., 2013; SOLAR et al., 2015).

Um passo fundamental para viabilizar o planejamento de ações de conservação efetivas em florestas tropicais é o desenvolvimento de pesquisas cujas análises forneçam uma compreensão de quais forças-motrizes da paisagem (*drivers*) alteram padrões e processos ecológicos e uma identificação clara sobre quais mudanças ocorrem nas comunidades biológicas. Visando esclarecer esta questão, meu principal objetivo nesta tese é entender os efeitos da modificação do habitat na comunidade de escarabeíneos tropicais e identificar quais variáveis respostas do grupo estão sendo utilizadas em estudos de alterações de habitat em florestas tropicais. Abordarei este assunto em três capítulos que foram escritos para publicação com co-autoria de pesquisadores do Brasil, Inglaterra e México, focando em diferentes aspectos de um tema central. Vale ressaltar que os três capítulos estão em formato de artigo e que a estrutura de cada um segue normas pré-estabelecidas pelas revistas às quais serão submetidos para publicação.

Capítulo I - Neste capítulo o enfoque é sobre como a redução de cobertura florestal (um *proxy* da perda de habitat) influencia a comunidade de besouros escarabeíneos, na Floresta Atlântica. Para alcançar esse objetivo, escarabeíneos foram coletados em 16 florestas distribuídas em duas regiões com diferentes porcentagens de cobertura florestal na Floresta Atlântica brasileira. As análises foram baseadas na abundância, riqueza e composição de espécies, grupos funcionais e índices de diversidade. Espera-se que a redução de cobertura florestal tenha efeitos negativos sobre a comunidade de escarabeíneos e a beta diversidade (β) apresente uma relação negativa com a porcentagem de cobertura florestal, com diferenciação na composição de escarabeíneos entre paisagens. Pretende-se submeter este trabalho à revista *Ecological Entomology.*

Capítulo II - Nesse capítulo buscamos entender as conseqüências da perda e fragmentação de habitat, em escala de paisagem, sobre a comunidade de escarabeíneos da Floresta Atlântica. Desse modo, duas questões principais foram levantadas: (1) A cobertura florestal contribui mais do que a densidade de bordas e a cobertura de pastagens para mudanças na comunidade de escarabeíneos? (2) Como esses preditores de paisagem afetam diferentes subgrupos de escarabeíneos e índices funcionais? Para responder a essas perguntas, selecionamos 16 paisagens separadas por pelo menos 1 km para evitar sobreposição. As espécies de escarabeíneos foram separadas em subgrupos com base em diferentes características (por exemplo, comportamento de recolocação de recursos, preferência alimentar, métricas morfológicas), que também foram consideradas para calcular índices distintos de diversidade funcional, para avaliar quão distintos os descritores em nível de paisagem (cobertura florestal, densidade de borda e cobertura de pastagem) afetam a biodiversidade florestal. Espera-se que a cobertura florestal tenha maior contribuição sobre as mudanças na comunidade de escarabeíneos. Como também, que diferentes subgrupos e índices funcionais apresentam respostas distintas a diferentes descritores de paisagem. Pretende-se submeter este trabalho à revista *Biological Conservation*.

Capítulo III – Visando organizar o estado atual de conhecimento de besouros escarabeíneos a respeito das variáveis respostas utilizadas em estudos sobre a modificação de habitat pelo homem em florestas tropicais e apontar caminhos para aprimorar o uso das métricas, uma ampla revisão de literatura baseada em 194 artigos publicados de 1975 a 2018 foi incluída nesse trabalho. Os principais objetivos desse capítulo foram: (1) Construir uma linha do tempo das publicações, bem como identificar principais revistas científicas e locais onde pesquisadores e trabalhos de campo estão concentrados; (2) Explorar os métodos que estão sendo utilizados para obtenção das variáveis respostas e a porcentagem de contribuição de cada variável para estudos de modificação de habitat (por exemplo, tamanho de fragmentos, efeitos de borda); (3) Destacar principais resultados obtidos, acrescentando recomendações para obtenção das variáveis e apontando lacunas para futuras pesquisas. Pretende-se submeter este trabalho à revista *Ecological Indicators*.

REFERÊNCIAS BIBLIOGRAFICAS

AUDINO, L.D.; MURPHY, S.J.; ZAMBALDI, L.; LOUZADA, J.; COMITA, L.S. Drivers of community assembly in tropical forest restoration sites: role of local environment, landscape, and space. **Ecological Applications** 27: 1731-1745, 2017.

AGOSTI, D.; MAJER, J.D.; ALONSO, L.E.; SCHULTZ, T.R. **Ants: standard methods for measuring and monitoring biodiversidade**. Washington, Smithsonian Institution Press, 2000.

BALMFORD, A.; GREEN, R.Ç; PHALAN, B. What conservationists need to know about farming. **Proceedings of the Royal Society B** 279: 2714-2724, 2012.

BARLOW, J.; LENNOX, G.D.; FERREIRA, J.; BERENGUER, E.; LEES, A.C.; MAC NALLY, R.; THOMSON, J.R.; FERRAZ, S.F.; LOUZADA, J.; OLIVEIRA, V.H.; PARRY, L.; SOLAR, R.R.; VIEIRA, I.C.; ARAGÃO, L.E.; BEGOTTI, R.A.; BRAGA R.F.; CARDOSO, T.M.; DE OLIVEIRA, R.C.; SOUZA, C.M.Jr.; MOURA, N.G.; NUNES, S.S.; SIQUEIRA, J.V.; PARDINI, R.; SILVEIRA, J.M.; VAZ-DE-MELLO, F.Z.; VEIGA, R.C.; VENTURIERI, A.; GARDNER, T.A. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. **Nature** 535: 144-147, 2016.

BARLOW, J.; FRANÇA, F.; GARDNER, T.A.; HICKS, C.C.; LENNOX, G.D.; BERENGUER, E.; CASTELLO, L.; ECONOMO, E.P.; FERREIRA, J.; GUÉNARD, B.; GONTIJO LEAL, C.; ISAAC, V.; LEES, A.C.; PARR, C.L.; WILSON, S.K.; YOUNG, P.J.; GRAHAM, N.A.J. The future of hyperdiverse tropical ecosystems. **Nature** 559: 517-526, 2018.

BARNES, A.D.; EMBERSON, R.M.; CHAPMAN, H.M.; KRELL, FRANK-T.; DIDHAM, R.K. Matrix habitat restoration alters dung beetle species responses across tropical forest edges. **Biological Conservation** 170: 28-37, 2014.

BARRAGÁN, F.; MORENO, C.E.; ESCOBAR, F.; HALFFTER, G.; NAVARRETE, D. Negative impacts of human land use on dung beetle functional diversity. **PLoS ONE** 6: e17976, 2011.

BEIROZ, W.; SLADE, E.M.; BARLOW, J. SILVEIRA, J.M.; LOUZADA, J.; SAYER, E. Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change. **Insect Conservation and Diversity** 10: 94-106, 2017.

BONEBRAKE, T.C.; PONISIO, L.C.; BOGGS, C.L.; EHRLICH, P.R. More than just indicators: A review of tropical butterfly ecology and conservation. **Biological Conservation** 143: 1831-1841, 2010.

BRAGA, R.F.; KORASAKI, V.; ANDRESEN, E.; LOUZADA, J. Dung beetle community and functions along a habitat-disturbance gradient in the amazon: a rapid assessment of ecological functions associated to biodiversity. **PLoS One** 8: e57786, 2013.

CARDINALE, B.J.; DUFFY, J.E.; GONZALEZ, A.; HOOPER, D.U.; PERRINGS, C.; VENAIL, P.; NARWANI, A.; MACE, G.M.; TILMAN, D.; WARDLE, D.A.; KINZIG, A.P.; DAILY, G.C.; LOREAU, M.; GRACE, J.B.; LARIGAUDERIE, A.; SRIVASTAVA, D.S.; NAEEM, S. Biodiversity loss and its impact on humanity. **Nature** 486: 59-67, 2012.

CARNAVAL, A.C.; HICKERSON, M.J.; HADDAD, C.F.B.; RODRIGUES, M.T.; MORITZ, C. Stability predicts genetic diversity in the Brazilian Atlantic Forest Hotspot. **Science** 323: 785-789, 2009.

CARNAVAL, A.C.; MORITZ, C. Historical climate modeling predicts patterns of current biodiversity in the Brazilian Atlantic forest. **Journal of Biogeography** 35: 1187-1201, 2008.

CASTELLANO, M; SORRENTINO, M. Participação em políticas públicas para conservação de matas ciliares no Estado de São Paulo. **Ambiente e Sociedade** 15: 53-69, 2012.

DELGADO, J.N.; ARROYO, N.L.; AREVALO, J.R.; FERNANDEZ-PALACIOS. J.M. Edge effects of roads on temperature, light, canopy closure, and canopy height in laurel and pine forests (Tenerife, Canary Islands). **Landscape and Urban Planning** 81: 328-340, 2007.

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** 48: 253-262, 1999.

FAHRIG, L Effects of habitat fragmentation on biodiversity. **Annual Review of Ecology, Evolution, and Systematics** 34: 487-515, 2003.

FAHRIG, L. Rethinking patch size and isolation effects: the habitat amount hypothesis. **Journal of Biogeography** 40: 1649-1663, 2013.

FAHRIG, L.; MERRIAM, G. Conservation of fragmented populations. **Conservation Biology** 8: 50-59, 1994.

FARÍAS, P.M.de; ARELLANO, L.; MEDINA HERNÁNDEZ, M.I.; LÓPEZ ORTIZ, S. Response of the copronecrophagous beetle (Coleoptera: Scarabaeinae) assemblage to a range of soil characteristics and livestock management in a Mexican tropical landscape. **Journal of Insect Conservation** 19: 947-960, 2015.

FILGUEIRAS, B.; TABARELLI, M.; LEAL, I.R; VAZ-DE-MELLO, F.Z.; IANNUZZI, L. Dung beetle persistence in human-modified landscapes: Combining indicator species with anthropogenic land use and fragmentation-related effects. **Ecological Indicators** 55: 65-73, 2015.

FILGUEIRAS, B.; TABARELLI, M.; LEAL, I.R; VAZ-DE-MELLO, F.Z.; PERES, C.A.; IANNUZZI, L. Spatial replacement of dung beetles in edge-affected habitats: biotic homogenization or divergence in fragmented tropical forest landscapes?. **Diversity and Distributions** 22: 400-409, 2016.

FILGUEIRAS, B.K.C; MELO, D.H.A.; ANDERSEN, A.N.; TABARELLI, M.; LEAL, I.R. Cross-taxon congruence in insect responses to fragmentation of Brazilian Atlantic forest. **Ecological Indicators** 98: 523-530, 2019.

FONSECA, G.A.B. The vanishing Brazilian Atlantic Forest. **Biological Conservation** 34: 17-34, 1985.

FRANKLIN, J.F.; LINDENMAYER, D.B. Importance of matrix habitats in maintaining biological diversity. **Proceedings of the National Academy of Sciences** 106: 349-350, 2009.

FREITAS, A.V.L.; LEAL, I.R.; UEHARA-PRADO, M.; IANNUZZI, L. **Insetos como indicadores de conservação da paisagem**. In: ROCHA, C.F.; BERGALO, H.; VAN SLUYS, M.; ALVES, M.A. (orgs.). Biologia da Conservação. Rio de Janeiro, Editora da UERJ, 2006. 201-225 p.

GARDNER, T.A.; BARLOW, J.; CHAZDON, R.; EWERS, R.M.; HARVEY, C.A.; PERES, C.A. et al. Prospects for tropical forest biodiversity in a human-modified world. **Ecology Letters** 12: 561-582, 2009.

GARDNER, T.A.; HERNANDEZ, M.I.M.; BARLOW, J.; PERES, C.A. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for Neotropical dung beetles. **Journal of Applied Ecology** 45: 883-893, 2008.

GEIST, H.J.; LAMBIN, E.F. Proximate causes and underlying driving forces of tropical deforestation. **Bioscience** 52: 143, 2002.

GRIFFITHS, H.M.; LOUZADA, J.; BARDGETT, R.D.; BEIROZ, W.; FRANÇA, F.; TREGIDGO, D.; BARLOW, J. Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. **Ecology** 96: 1607-1619, 2015.

HADDAD, N.M.; BRUDVIG, L.A.; CLOBERT, J.; DAVIES, K.F.; GONZALEZ, A.; HOLT, R.D.; LOVEJOY, T.E.; SEXTON, J.O.; AUSTIN, M.P.; COLLINS, C.D.; COOK, W.M.; DAMSCHEN, E.I.; EWERS, R.M.; FOSTER, B.L.; JENKINS, C.N.; KING, A.J.; LAURANCE, W.F.; LEVEY, D.J.; MARGULES, C.R.; MELBOURNE, B.A.; NICHOLLS, A.O.; ORROCK, J.L.; SONG, D.X.; TOWNSHEND, J.R. Habitat fragmentation and its lasting impact on Earth's ecosystems: **Science Advances** 1: e1500052, 2015.

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

HALFFTER, G.; FAVILA, M.E. The Scarabaeinae (Insecta: Coleoptera) an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. **Biology International** 27: 15-21, 1993.

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

HANSKI, I.; CAMBEFORT, Y. **Dung beetle ecology**. I. Hanski and Y. Cambefort (Eds.). Princeton University Press. 1991.

JOLY, C.A.; RODRIGUES, R.R.; METZGER, J. P.; HADDAD, C.F.B.; VERDADE, L. M.; OLIVEIRA, M.C.; BOLZANI, V.S. Biodiversity conservation research, training, and policy in São Paulo. **Science** 328: 1.358-1.359, 2010.

LAMBIN, E.F.; GEIST, H. **Land-use and land-cover change**. E.F. Lambin and H. Geist (Eds.). Springer Berlin Heidelberg, Berlin, Heidelberg. 2006.

LARSEN, T.H.; LOPERA, A.; FORSYTH, A. Understand trait dependent community disassembly: dung beetles, density functions and forest fragmentation. **Conservation Biology** 22: 1288-98, 2008.

LAURANCE, W.F. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. **Biological Conservation** 141: 1731-1744, 2008.

LAURANCE, W.F.; FERREIRA, L.V.; RANKIN-DE MÉRONA, J.; LAURANCE, S.G.; HUTCHINGS, R.G.; LOVEJOY, T.E. Effects of Forest fragmentation on recruitment patterns in Amazonian tree communities. **Conservation Biology** 12: 460-464, 1998.

MARSH, C.J.; FEITOSA, R.M.; LOUZADA, J. EWERS, R.M. Is β-diversity of Amazonian ant and dung beetles communities elevated at rainforest edges?. **Journal of Biogeography** 45: 1966-1979, 2018.

MAYAUX, P.; HOLMGREN, P.; ACHARD, F.; EVA, H.; STIBIG, .H-J.; BRANTHOMME, A. Tropical forest cover change in the 1990s and options for future monitoring. **Philosophical transactions of the Royal Society of London B** 360: 373-84, 2005.

MAXWELL, S.L.; FULLER, R.A.; BROOKS, T.M.; WATSON, J.E. The ravages of guns, nets and bulldozers. **Nature** 536: 143-145, 2016.

MCGEOCH, M. The selection, testing and application of terrestrial insects as bioindicators. **Biological Reviews** 73: 181-201, 1998.

MCGEOCH, M.A.; VAN RENSBURG, B.J; BOTES, A. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. **Journal of Applied Ecology** 39: 661-672, 2002.

MELO, F.P.L.; ARROYO-RODRÍGUEZ, V.; FAHRIG, L.; MARTÍNEZ-RAMOS, M.; TABARELLI, M. On the hope for biodiversity-friendly tropical landscapes. **Trends in Ecology and Evolution** 28: 462-468, 2013.

METZGER, J.P.; DÉCAMPS, H. The structure connectivity theshold: on hypothesis in conservation biology at the landscape scale. **Acta Ecologica** 18: 1-12, 1997.

MURCIA, C. Edge effectes in fragmented forests; application for conservation. **Trends in Ecology and Evolution** 10: 58-62, 1995.

MYERS, N.; MITTERMEIER, R.A.; MITTERMEIER, C.G.; FONSECA, G.A.B.; KENT, J. Biodiversity hotspots for conservation priorities. **Nature** 403: 853-855, 2000.

NICHOLS, E.; GARDNER, T.A.; PERES, C.A.; SPECTOR, S. Co-declining mammals and dung beetles: an impending ecological cascade. **Oikos** 118: 481-487, 2009.

NICHOLS, E.; LARSEN, T.; SPECTOR, S.; DAVIS, A.L.; ESCOBAR, F.; FAVILA, M.; VULINEC, K. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. **Biological Conservation** 137: 1-19, 2007.

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

PIMM, S.L.; RAVEN, P. Extinction by numbers. **Nature** 403: 843-845, 2000.

RIBEIRO, M.C.; METZGER, J.P.; MARTENSEN, A.C.; PONZONI, F.J.; HIROTA, M.M. The Brazilian Atlantic Forest: how much is left, and howis the remaining forest distributed? Implications for conservation. **Biological Conservation** 142: 1141-1153, 2009.

SÁNCHEZ-DE-JESÚS, H.A.; ARROYO-RODRÍGUEZ, V.; ANDRESEN, E.; ESCOBAR, F. Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. **Landscape Ecology** 31: 843-854, 2015.

SOLAR, R.R.C.; BARLOW, J.; FERREIRA, J.; BERENGUER, E.; LEES, A.C.; THOMSON, J.R.; LOUZADA, J.; MAUÉS, M.; MOURA, N.G.; OLIVEIRA, V.H.F.; CHAUL, J.C.M.; SCHOEREDER, J.H.; VIEIRA, I.C.G.; MAC NALLY, R.; GARDNER, T.A. How pervasive is biotic homogenization in human-modified tropical forest landscapes?. **Ecology Letters** 18: 1108-1118, 2015.

TABARELLI, M.; PERES, C.A.; MELO, F.P.L. The “few winners and many losers” paradigm revisited: Emerging prospects for tropical forest biodiversity. **Biological Conservation** 155: 136-140, 2012.

TABARELLI, M.; PINTO, L.P.; SILVA, J.M.C.; HIROTA, M.M.; BEDÊ, L.C. Challenges and opportunities for biodiversity conservation in the Brazilian Atlantic Forest. **Conservation Biology** 19: 695-700, 2005.

TURNER, I.M. Species loss in fragments of tropical rain forest: a review of the evidence. **Journal of Applied Ecology** 33: 200-209, 1996.

UEHARA-PRADO, M,; FERNANDES, J.O.; BELLO, A.M.; MACHADO, G.; SANTOS, A.J.; VAZ-DE-MELLO, F.Z.; FREITAS, A.V.L. Selecting terrestrial arthropods as indicators of small-scale disturbance: A first approach in the Brazilian Atlantic Forest. **Biological Conservation** 142: 1220-1228, 2009.

Capítulo I

Loss of ecological diversity with forest loss in a global hotspot in the neotropics

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Loss of ecological diversity with forest loss in a global hotspot in the neotropics

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Abstract. 1. Habitat loss represents one of the most pervasive threats to tropical forests. As such, understanding the effects of forest cover loss (a *proxy* of habitat loss) on biodiversity is strategic for conservation of biodiversity.
2. Dung beetles have been frequently adopted as indicators of forest changes, and by analyzing their diversity it is possible to predict the trends of biodiversity which inhabit threatened ecosystems tropical forests.
3. In the present study, we evaluated dung beetles sampled in 16 different landscapes across two regions with different amount of forest cover in the Brazilian Atlantic Forest. We evaluated the abundance, richness and species composition, functional groups, and diversity numbers. We measured β-diversity across the landscapes, and decomposed into turnover and nestedness components.
4. Our findings provide novel empirical evidence that species richness, abundance and functional groups (i.e. coprophagous, necrophagous, generalists, tunnelers and rollers) decreased with the decrease of forest cover. Furthermore, β-diversity increases in landscapes with decreasing forest cover, promoting compositional differentiation between landscapes.
5. Taken together, these results suggest that to preserve dung beetles and their key functional roles in the ecosystem, conservation initiatives should promote the conservation of forest cover in the current fragmented landscape of the neotropics.

Key-words: anthropocene, biodiversity, conservation, deforestation, human-modified landscape, scarabaeinae.

Introduction

Habitat loss represents one of the main causes of biodiversity loss in tropical forest (Bender *et al*., 1998; Brooks *et al*., 2002; Fahrig, 2013). Changes on patterns and ecological processes due to habitat loss have been shown empirically by several studies (e.g. Morante-Filho *et al*., 2015; Pessoa *et al*., 2016; Rocha-Santos *et al*., 2016; Benchimol *et al*., 2017). Therefore, understanding how biodiversity is affected by habitat loss has been suggested as essential for developing effective conservation strategies are required to safeguard tropical forest (Gardner *et al*., 2009; Balmford *et al*., 2012; Barlow *et al*., 2016).

Forest cover at the landscape scale have been considered a good *proxy* for habitat loss due relationships observed between the amount of forest and species diversity (Fahrig, 2003; Pardini *et al*., 2010; Estavillo *et al*., 2013; Fahrig, 2013). Studies shown that the reduction of forest cover has caused alterations in the local forest structure, leading to early successional stages, such as an increase in the canopy openness and reduction in the overall basal area (Rocha-Santos *et al*., 2016), negative effects over shade-tolerant species (Laurence *et al*., 1998). Besides the decrease of taxonomic biodiversity, the reduction of forest cover may act as a barrier in ecological communities, filtering specific traits of the species and consequently jeopardizing ecosystem functioning (Hooper *et al.*, 2005; Flynn, 2009).

Dung beetles have been frequently adopted as indicators of forest changes, because of their sensitivity to environmental changes (Spector, 2006; Gardner *et al*., 2008), stable and well-defined taxonomy (Philips *et al*., 2004; Vaz de Mello *et al*., 2011), and good cost-effectively of sampling when compared to other taxa (Larsen & Forsyth, 2005; Gardner *et al*., 2008). The responses of dung beetle to ecosystem transformations may help to predict health status of ecological communities (Favila & Halffter, 1997; Spector, 2006), presenting cues of biodiversity trends to forest loss. Besides, these insects are particularly important for the maintenance of ecosystem functions and processes, because they are linked to nutrient cycling, secondary seed dispersal, soil aeration and parasite suppression (Nichols *et al*., 2008). Furthermore, is important to highlight that ecological services performed by dung beetles are strictly dependent on functional properties, which may be analyzed through resource-relocation behavior and diet preference (Slade *et al*., 2007; Barragán *et al*., 2011).

The chronological land-use trajectory of Brazilian Atlantic Forest serves an excellent model to examine how habitat loss can shape biodiversity. The Atlantic Forest is a mega-diverse tropical forest (Myers *et al*., 2000; Silva & Tabarelli, 2000) and currently over 80% of the forest fragments are smaller than 50 ha and almost half of the remaining forests are less from 100 m from its edge (Ribeiro *et al*., 2009). Studies encompassing responses of dung beetle community structure towards habitat loss usually focus on coarse diversity metrics (e.g. species richness, abundance, and diversity numbers) (Almeida *et al*., 2011; Martello *et al*., 2016). The partition of β diversity into turnover and nestedness components may shed light under ecological consequences of habitat loss that are still poorly known (Filgueiras *et al*., 2016; Morante-Filho *et al*., 2016). Moreover, through ecological studies focusing on diversity of functional groups, it is possible to analyze, at a finer scale, what are the sensible groups that are being filtered with the processes of habitat loss.

Here, we evaluated the consequences of forest cover loss (a *proxy* of habitat loss) for abundance, species composition, and diversity of dung beetles in the Brazilian Atlantic Forest. Considering that native forested ecosystem encompasses diverse communities within large portions of forest fragments (Laurance *et al*., 2002; Herrmann *et al*., 2005), we predict that forest cover loss would decrease abundance, and diversity of dung beetles. In addition, we expect that β-diversity is positively related to the decrease of forest cover, promoting distinct community structure between landscapes with different levels of deforestation (Laurance *et al*., 2007; Arroyo-Rodrıguez *et al*., 2013; Solar *et al*., 2015).

Material and methods

Study area

The study was conducted in the Atlantic Forest of southern region of Bahia state, which is located in north-eastern Brazil (15°280 S, 39°150 W, WGS84). This region is dominated by Tropical Lowland Rainforest and it is located within the hot and humid region without a distinct dry season (*Af* Köppen classification), with mean annual temperature of 24°C and ~2000 mm annual rainfall (Thomas *et al*., 1998). Land-use changes were particularly severe within large tracts of previously continuous forests, which were converted to small fragments of different successional stages and embedded in a mosaic of different monocultures, such as cocoa plantations, rubber trees, and cattle pastures (Pardini *et al*., 2009).

Sampling design and explanatory variables

We worked in two regions with landscapes presenting contrasting percentage of forest cover: 1) High forest cover (HFC) landscapes with 40-100% of forest cover; and 2) Low forest cover (LFC) landscapes with 3-63% of forest cover (Fig. 1). Both regions have similar soil, topography and floristic composition (Thomas *et al*., 1998). The selection of landscapes was based on high resolution satellite images (RapidEye® from 2009 to 2010, QuickBird® and WorldView® from 2011). We mapped the landscapes by manually digitizing land cover features as visually interpreted at a scale of 1:10.000, and polygons were classified as forest fragments and different land-uses (e.g. pasture and agriculture) according to the *Instituto Brasileiro de Geografia e Estatıstica* (IBGE, 2006) and using ArcGIS 10.2 software (ESRI, 2011). After intensive ground-validation, we mapped the forest fragments and land-uses within a study area of 3,500 km^2.

The percentage of forest cover was calculated based forest fragments within a 1-km radius from the center of each landscape, since it represents the longest movement distance recorded for dung beetle species in Brazilian Atlantic Forest within a 48-h period (Silva & Hernández, 2015). The center of each landscape was preferably in forest fragment with mature forest within the least degraded part and without any slash-and-burn evidence. In each region, we selected 8 non-overlapping landscapes separated by at least 1 km, to assure that each landscape represented independent dung beetle samples (Silva & Hernández, 2015) (Fig. 1). In the region of HFC had one landscape completely covered by old growth forest that is included within one federally protected conservation unit (Una Biological Reserve).

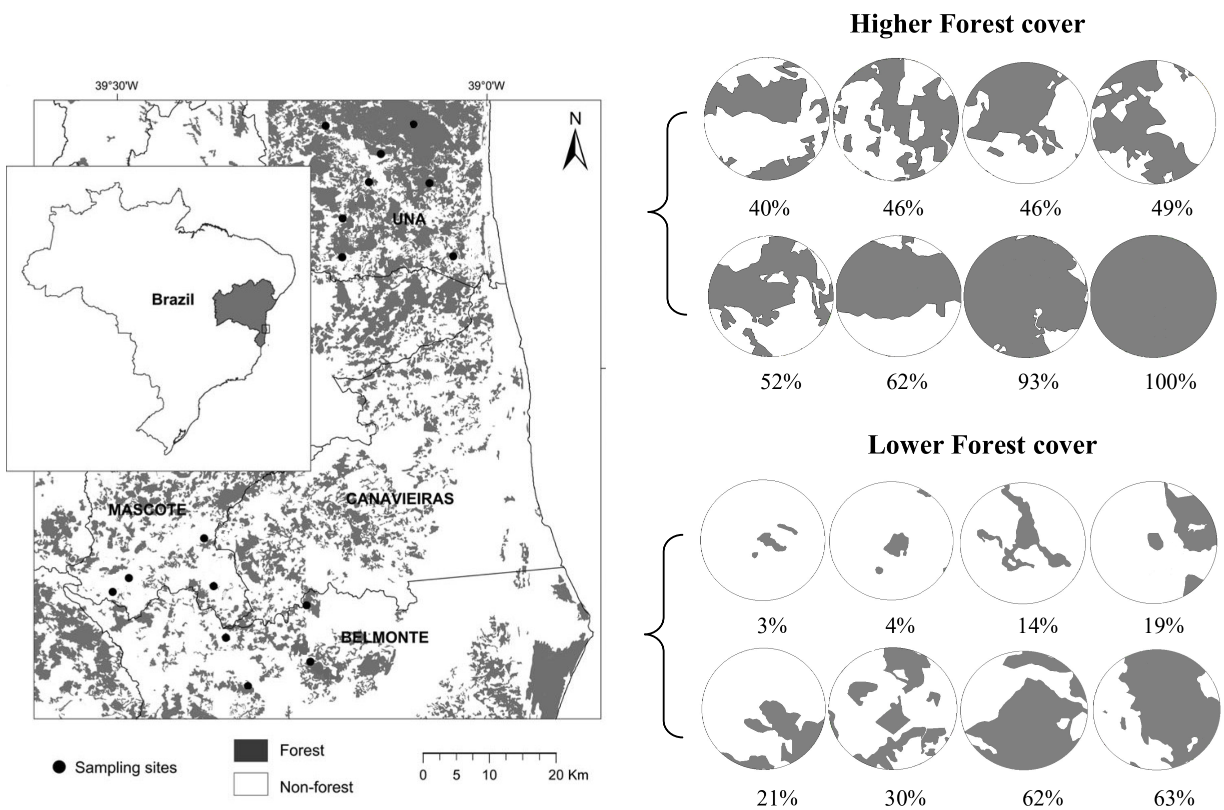

Fig. 1. Map of the study area showing the spatial distribution of Atlantic Forest remnants in Bahia state, Brazil. We show the location of region with higher forest cover (HFC), with 40 to 100% of remaining forest cover, and the region with lower forest cover (LFC), with 3 to 63% of remaining forest cover. The black dots indicate the landscape within each region.

Dung beetle sampling

Dung beetles were sampled three times at each one of 16 landscapes during the rainy season (April-June) in 2017. We used pitfall traps, which consisted of a plastic container (15 cm in diameter and 13 cm in height) buried with an opening at ground level and with a small recipient (3 cm in diameter by 4.8 cm in height) where fresh human feces or decomposed meat were placed as bait (ca. 30 g of bait). Pitfalls were filled with ca. 250 ml of killer solution (saline solution with detergent) and were covered by a plastic lid to protect sampled material from the rain.

We established three sets of pitfalls traps, spaced 100 m apart (Silva & Hernández, 2015) in the center of each landscape. Each set contained three pitfalls disposed at the vertices of a 5-m equilateral triangle, each trap with a different bait-treatment (fresh human feces, decomposed meat, or non-baited) that was randomly distributed within each pitfall set. Traps were exposed in the field during 48h, and sampled dung beetles were taken to the Applied Ecology and Conservation Lab at the Universidade Estadual de Santa Cruz (UESC). Dung beetles were identified to species level when possible, and voucher specimens were deposited in the entomological collections of the Laboratório de Entomologia (UESC) and the Seção de Entomologia da Coleção Zoológica, Universidade Federal de Mato Grosso (UFMT), both in Brazil.

Dung beetle functional groups

We separated dung beetles according with their resource-relocation behaviour (tunneler, rollers and dwellers) and diet preference (coprophagous, necrophagous or generalists). See below for details.

RESOURCE-RELOCATION BEHAVIOUR: This attribute is related to dung manipulation for feeding and reproduction (Halffter & Edmonds, 1982). Species were grouped as tunnelers, rollers and dwellers. Tunneler species are those that dig tunnels in the soil immediately under, or very close to the resource; rollers usually make resource balls and roll them to some distance from the original dung patch; dwellers remain within the resource patches (Halffter & Edmonds, 1982; Hanski & Cambefort, 1991).

DIET PREFERENCE: Following Beiroz *et al*. (2017), we considered dung beetle species as coprophagous or necrophagous when > 75% of the individuals of a given species were sampled in dung- or meat-baited traps, respectively. Species with < 75% of their individuals collected per bait type were classified as generalists. For species with less than five individuals, we sought the advice of the Neotropical dung beetle specialist Dr. Fernando Z. Vaz-de-Mello. We excluded all undefined species from the analyses. The selected diets are commonly reported for Neotropical dung beetles (Hanski & Cambefort, 1991).

Statistical analysis

We used the coverage estimator recommended by Chao & Jost (2012) to estimate the accuracy of inventories in each landscape, considering observed and expected species richness, based on coverage-based extrapolations performed with the *entropart* package in R software version 3.2.0 (R Core Team, 2017) to avoid any potential bias in our results due to differences in sample coverage among landscapes. Sample coverage was satisfactory in the landscapes (75-99 % of the species recorded), indicating that our sampling effort was adequate.

To describe and analyze dung beetle diversity in each landscape, we used spatially decomposed diversity, using alpha (Dα) diversity (Jost, 2006). We considered the species richness (^{0}D) and Shannon diversity (^{1}D) to evaluate the Dα, through Hill numbers (Hill, 1973; Jost, 2006). Species richness does not consider the abundance of the species for diversity analysis, while Shannon considers the relative abundance of each species. Dα was analyzed for each landscape and $^{0}D\alpha$ indicates the mean number of species richness, $^{1}D\alpha$ indicates the number of abundant species in the dung beetle community.

To understand the processes shaping the dung beetle community in the whole landscape of the study, we decomposed β-diversity using Jaccard-dissimilarity (Dj) (Baselga, 2010; Legendre, 2014). Dj represents the total β-diversity, and consists of species turnover, which consider species replacement, and nestedness. We performed the decomposition of β-diversity considering species composition of the dung beetle community. We performed this analysis using Vegan and Betapart libraries in R software version 3.2.0 (R Core Team, 2017).

To test whether the loss of forest cover affected dung beetle community, we performed linear models to analyze Dα ($^{0}D\alpha$ and $^{1}D\alpha$), β-diversity using Jaccard-dissimilarity (Dj), nestedness and turnover components of Dj. Generalized linear models (GLMs) with Poisson error distributions for species richness and abundance (Crawley, 2013). Besides, we also performed GLMs to evaluate the effect of forest cover loss on distribution of functional groups (i.e. resource relocation behavior, diet preference) over dung beetle community. The normality of residuals of the models was analyzed visually from normal q-q plots, and the presence of outliers was evaluated through Cook's distance, and homogeneity of variances was tested with bptest (Hothorn *et al*., 2015). If the Poisson GLMs presented overdispersion (Zuur *et al*., 2009), we used negative binomial distribution. Outliers (Cook's distance > 1) were excluded from the models; if excluding outliers did not adjust the model, data were log transformed. Data were analyzed in R software version 3.2.0 (R Core Team, 2017).

To a fine understanding of the species turnover process, as well as the similarity of dung beetle community between landscapes, we performed Jaccard similarity index. We conducted a similarity profile permutation (SIMPROF) to evaluate whether dung beetle assemblages differed according to the landscapes. In addition, we performed a map for a visual representation of beetle species occurrence in the each landscape. Jaccard similarity index and SIMPROF were conducted in Primer software version 6.0 (Clarke & Gorley, 2006).

Results

A total of 3,944 individuals from 16 genera and 37 species and were recorded in the studied Atlantic Forest considering both regions (see Table S1 in supplementary material). All community parameters that were significantly influenced by percentage of forest cover presented a negative relation with the increase of forest loss (Table 1).

Table 1. Models exhibiting the effects of the percentage of forest cover on dung beetle community parameters and functional groups. All the variables that were statistically related are in bold.

	Percentage of forest cover (%)		
Community parameters	**X^2/F**	**P**	**R^2**
Total species richness	**$X^2_{1,14} = 18.740$**	**0.003**	**0.315**
Total abundance	**$X^2_{1,13} = 16.170$**	**<0.001**	**0.547**
Total ^{0}D alpha	$F_{1,13} = 2.678$	0.125	0.170
Total ^{1}D alpha	$F_{1,13} = 0.006$	0.936	<0.001
Jaccard beta diversity	**$F_{1,14} = 4.620$**	**0.049**	**0.259**
Species nestedness	$F_{1,13} = 1.707$	0.214	0.116
Species turnover	$F_{1,14} = 0.023$	0.880	0.001
Functional groups			
Diet preference			
Coprophagous species richness	**$X_{1,14} = 17.394$**	**0.008**	**0.297**

	Percentage of forest cover (%)		
Community parameters	**X^2/F**	**P**	**R^2**
Coprophagous abundance	$X_{1,14}$ = 15.024	0.296	0.398
Necrophagous species richness	$X_{1,14}$ = 9.085	0.06	0.289
Necrophagous abundance	**$X_{1,14}$ = 16.820**	**<0.001**	**0.365**
Diet-generalist species richness	$X_{1,13}$ = 3.4272	0.065	0.547
Diet-generalist abundance	**$X_{1,14}$ = 18.258**	**0.003**	**0.455**
Resource relocation behavior			
Dweller species richness	$X_{1,14}$ = 10.814	0.328	0.099
Dweller abundance	$X_{1,14}$ = 2.320	0.358	0.024
Roller species richness	$X_{1,14}$ = 17.774	0.157	0.136
Roller abundance	**$X_{1,14}$ = 6.748**	**<0.001**	**0.390**
Tunneler species richness	$X_{1,13}$ = 9.923	0.466	0.268
Tunneler abundance	**$X_{1,14}$ = 2.286**	**0.038**	**0.234**

Species richness and abundance of dung beetles were affected by the loss of forest cover (Fig. 2). However, Dα based on species richness (^{0}Dα) and Shannon diversity (^{1}Dα) were not significantly related to the loss of forest cover. The species richness of coprophagous, abundance of necrophagous and diet-generalists dung beetles were negatively affected by the loss of forest cover (Fig. 2). Abundance of coprophagous and species richness of necrophagous and diet-generalists were not significantly affected by the percentage of forest cover. According to the resource relocation behavior, abundance of rollers and tunnelers presented a significant relation with the loss of forest cover. Species richness and abundance of dweller beetles, as well as species richness of roller and tunneler beetles were not significantly related to the percentage of forest cover.

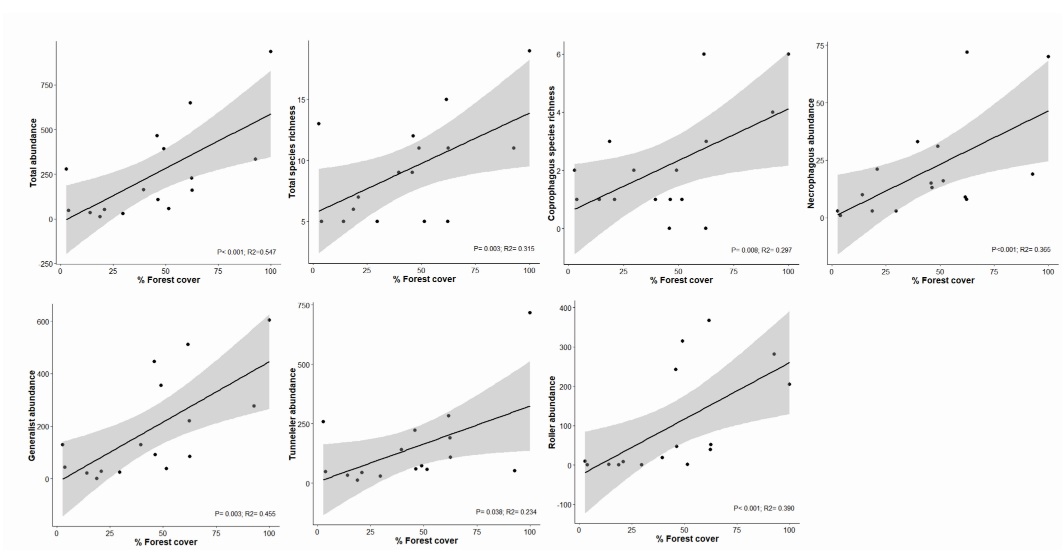

Fig. 2. Influence of percentage of forest cover at landscape scale on dung beetle: total species richness, total abundance and functional groups (i.e. coprophagous, necrophagous, generalists; rollers and tunnelers) in Atlantic Forest, Bahia, Brazil. Only significant relations with the percentage of forest cover were presented.

There was a negative relation between forest cover and β-diversity (Table 1). The lowest value (B= 0.70) was observed in the landscapes with highest forest cover, while the highest values (B= 0.95) were observed in landscapes with low forest cover (19% and 30%). The beta diversity of the landscape was mainly affected by species turnover than by species nestedness (Bturnover= 0.932; Bnestedness= 0.068). When decomposing beta diversity of each landscape, neither Bturnover or Bnestedness were significantly related to the percentage of forest cover (Table 1).

According to SIMPROF and Jaccard similarity index, the dung beetle assemblages were segregated in three significantly distinct groups ($p < 0.05$), according to the landscape (Fig. 3). One of the clusters with highest similarity (37%) was composed by seven landscapes, encompassing areas with more than 39% of forest cover, as well as the most conserved site (Una Biological Reserve – 100% of forest cover). The two other clusters grouped five and three landscapes, presenting 37 and 25% of similarity, respectively. Such clusters encompassed landscapes with contrasting percentage of forest cover, ranging between 18 and 62% of forest cover in the cluster with 37% of similarity, and ranging between 2 and 62% of forest cover in the cluster with 25% of similarity.

Dung beetle clustered eight significantly distinct groups, based on species distribution (Fig. 3). Three clusters were composed by species with narrow distribution, which were recorded in only one or two of the 16 landscapes (*Canthon staigi*, *Canthon prasinus* and *Canthidium* sp6 clustered with 50% of similarity; *Uroxys* sp1 and *Canthidium* sp2 clustered with 50% of similarity; *Canthidium* sp9, *Ateuchus voluxemi* and *Dichotomius depressicolis* clustered with 100% of similarity). One cluster was composed by species with wide distribution, and each species was recorded in ≥50% of landscapes (*Deltochilum* aff. *calcaratum, Ateuchus vigilans, Dichotomius iannuzzae, Coprophanaeus dardanus, Ateuchus oblongus, Canthonella silphoides*, clustered with 57% of similarity). Two clusters were composed by species distributed mainly in landscapes with high percentage of forest cover (≥45%). Such clusters were composed by *Onthophagus haemotopus, Canthidium* sp4, *Phanaeus splendidulus, Canthidium flavipes* (clustered with 33% of similarity); and *Holocephalus sculptus*, *Deltochilum brasiliensis, Deltochilum* sp1*, Anomiopus* sp1*, Dichotomius mormon, Anomiopus* sp2 and *Paracanthon* sp1 (clustered with 14% of similarity).

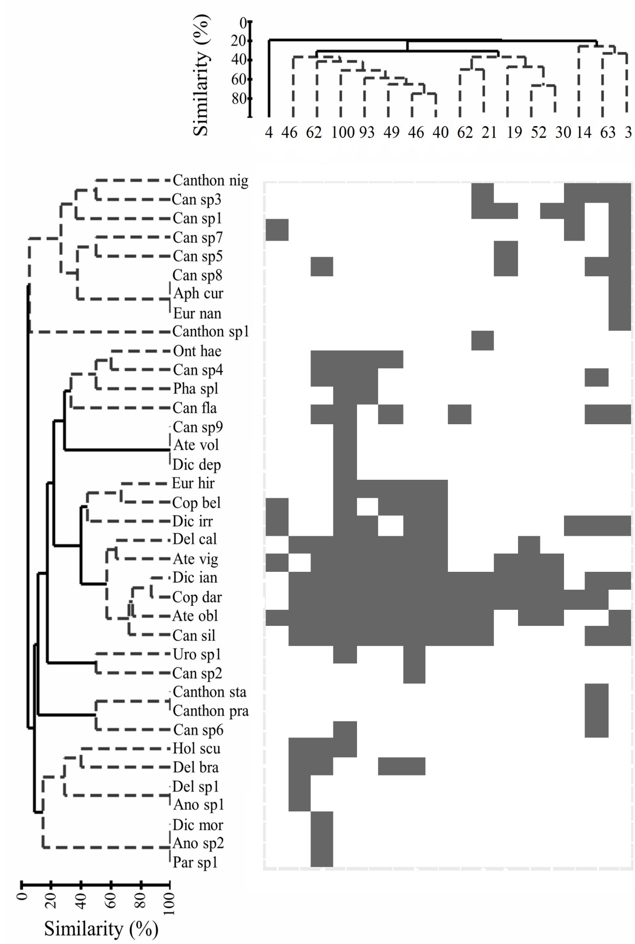

Fig. 3. Dendrogram clustering dung beetles, according to Jaccard similarity index and map of occurrence to dung beetles species recorded in the landscapes of Atlantic Forest, Bahia, Brazil. Solid lines represent statistical differences between groups, based on SIMPROF analyses ($p < 0.05$). Numbers represent the percentage of forest cover of each landscape.

Discussion

Dung beetles are an excellent model to understand the effects of habitat transformation over biodiversity (Halffter & Favila, 1993; Gardner *et al.*, 2008b). We found that the process of forest cover loss in Neotropical rainforests affect different subgroups of dung beetle and generates a more heterogeneous community. Coprophagous, necrophagous and diet-generalist beetles have their communities negatively affected by the decrease of forest cover. Likewise, roller and tunneler dung beetles were negatively affected the loss of forest cover. The simplification of functional groups is one of the consequences of the habitat loss and forest fragmentation, a representative scenario that is disseminated throughout the landscapes of the Anthropocene (Girão *et al.*, 2007; Santos *et al.*, 2008; Sattler *et al.*, 2010). Forest disturbance in the tropics negatively affects dung beetle diversity (Nichols *et al.*, 2007; Gardner *et al.*, 2008), what may also erodes its ecological diversity. Dung beetle diversity is driven by the availability of different food types, and habitats high species richness are related to a high diversity of mammal species, the main food providers for these insects (Andresen & Laurence, 2007; Culot *et al*., 2013; Nichols *et al*., 2013). In the same way, dung beetle abundance is related to the food availability, and habitats with higher food amount may hold abundant beetle communities (Nichols *et al*., 2009). Therefore, our results give cues that with forest loss there is a decline in food diversity and availability for diet-specific and diet-generalist dung beetles.

In addition, the decrease of beetle abundance based on resource removal strategies is surprising, considering that both rollers and tunnelers were negatively affected by forest loss. Usually, rollers and tunnelers present contrasting results to forest structure, or there is a clear response of one of them to habitat transformation (Lumaret & Kirk, 1987; Krell *et al*., 2003; Barragán *et al*., 2011). Our results prove that in Atlantic Forest, the loss of forest cover is affecting the whole dung beetle community, reducing ecological diversity. This is in accordance to other literature data that points the habitat loss and fragmentation as effects that drastically reduces the biodiversity of the dung beetle communities (Klein, 1989; Estrada *et al*., 1998; Nichols *et al*., 2007). With the decrease and extinction of determined functional groups, ecosystem functions (e.g. nutrient cycling, seed dispersal, parasite control) related with primary functions of dung beetles (dung burial and removal) will be drastically reduced.

The increase of forest cover was a significantly related to the decrease in β-diversity. Contrasting and heterogeneous communities' results in elevated beta diversity, as a consequence of the turnover in species composition and species abundances (Wilson & Shmida, 1984; Harbone *et al*., 2006; Melo *et al*., 2009). Tropical forests are diverse ecosystems, and more conserved environments are related to higher microclimatic conditions and dung beetle species richness, as a consequence of the wide food supply (Estrada *et al*., 1999; Fleury & Galetti, 2006; Nichols *et al*., 2007). Although there is a higher alpha diversity in more forested landscapes, our data suggests that dung beetle community has a higher evenness in this environment. Ecosystems with a more heterogeneous landscape may favor the occurrence of species with different habitat requirements, increasing the β-diversity. Previous studies present the same pattern observed in this study (Didham *et al*., 1998; Filgueiras *et al*., 2019), suggesting that the lower β-diversity is related to more conserved tropical forests. Therefore, we suggest that future studies carefully evaluate the mean of high values of β-diversity, since it may represent disturbed environmental conditions in tropical landscapes.

Landscapes with higher forest cover sustained dung beetle community with species that were absent from the more disturbed areas. Based on the SIMPROF results, two clusters with a total of 11 species (ca. 30 % of total species richness of the study) were mostly observed in conserved areas. Such species belonged to eight genera, which present contrasting functional groups, as diet and resource relocation behavior (Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Scholtz *et al*., 2009). Although there is a relevant number of studies regarding how environmental parameters may filter determined traits in ecological communities (Coelho *et al*., 2018; Ulrich *et al*., 2018a, b), in the fragmented landscape of the Atlantic forest this knowledge is still incipient. However, with the decrease in diversity of functional groups in the landscapes with reduced forest cover, there is a lower resilience against negative consequences of environmental change (Loreau, 2004; Hooper *et al*., 2005; Fischer, 2006).

This work provides a baseline for the effects of forest loss over dung beetle ecological diversity in the Atlantic Forest, one of the main global hotspots for biological conservation (Myers *et al*., 2000). As a consequence of the decrease of forest cover, the loss of species from distinct functional groups provides signals that deforestation does not filter dung beetle of specific groups, and negatively affects the whole community. Based on our results, the increase of forest cover seems to be the crucial parameter to recover the ecological diversity of key insects, as the dung beetles.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of dung beetle species, as well as resource-relocation behavior, diet preference and total abundance, sampled in fragmented forests in the Atlantic forest, northeastern Brazil.

References

Almeida, S., Louzada, J., Sperber, C. & Barlow, J. (2011). Subtle land-use change and tropical biodiversity: dung beetle communities in Cerrado grasslands and exotic pastures. Biotropica **43**: 704-710.

Andresen, E. & Laurance, S.G. (2007). Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica **39**: 141-146.

Arroyo-Rodríguez, V., Ros, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M. & Chazdon, R. (2013). Plant b-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. Journal of Ecology **6**: 1449-1458.

Balmford, A., Green, R. & Phalan, B. (2012). What conservationists need to know about farming. Proceedings of the Royal Society **279**: 2714-2724.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., MacN Nally, R., Thomson, J.R., Ferraz, S.F.B., Louzada, J., Oliveira, V.H.F., Parry, L., Solar, R.R.C., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.B., Cardoso, T.M., Oliveira, R.C.J., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F., Veiga, R.C.S., Venturieri, A. & Gardner, T.A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature **535**: 144-147.

Barragán, F., Moreno, C.E., Escobar, F., Halffter, G. & Navarrete, D. (2011). Negative impacts of human land use on dung beetle functional diversity. PLoS One **6**: e17976.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography **19**: 134-143.

Beiroz, W., Slade, E.M., Barlow, J., Silveira, J.M., Louzada, J. & Sayer, E. (2017). Dung beetle community dynamics in undisturbed Tropical forests: implications for ecological evaluations of land-use change. Insect Conservation and Diversity **10**: 94-106.

Benchimol, M., Mariano-Neto, E., Faria, D., Rocha-Santos, L., Pessoa, M.S. Gomes, S.F., Talora, D.C. & Cazetta, E. (2017). Translating plant community responses to habitat loss into conservation practices: Forest cover matters. Biological Conservation **209**: 499-507.

Bender, D.J., Contreras, T.A. & Fahrig L. (1998). Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology **78**: 517-533.

Brooks, T.M.R., Mittermeier, C.G. Mittermeier, G.B. Da Fonseca, A.B., Rylands, W.R. Konstant, P., Flick, J., Pilgrim, S., Oldfield, G., Magin, C. & Hilton-Taylor. (2002). Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology **16**: 909-923.

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology **93**: 2533-2547.

Clarke, K.R. & Gorley, R.N. (2006). Primer v6: user manual/tutorial. Plymouth: Primer-e.

Coelho, M.S., Carlos, P.P., Pinto, V.D., Meireles, A., Negreiros, D., Morellato, L.P.C., & Fernandes, G.W. (2018). Connection between tree functional traits and environmental parameters in an archipelago of montane forests surrounded by rupestrian grasslands. Flora **238**: 51-59.

Crawley, M. (2013). The R book (2nd edition). London, UK: Wiley & Sons.

Culot, L., Bovy, E., Vaz-de-Mello, F.Z., Guevara, R. & Galetti, M. (2013). Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation **163**: 79-89.

Didham, R. K., Hammond, P.M., Lawton, J. H., Eggleton, P. & Stork, N. (1998). Beetle species responses to tropical forest fragmentation. Ecological Monographs **68**: 295-323.

Estavillo, C., Pardini, R., Rocha & P.L.B. (2013). Forest loss and the biodiversity threshold: an evaluation considering species habitat requirements and the use of matrix habitats. PLoS One **8**: e82369.

Estrada, A., Anzures, A. & Coates-Estrada, R. (1999). Tropical rain forest fragmentation, Howler Monkeys (*Alouatta palliata*) and dung beetles at Los Tuxtlas, Mexico. American Journal of Primatology **48**: 253-262.

Estrada, A., Coates-Estrada, R., Dadda, A.A. & Cammarano, P. (1998). Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. Journal of Tropical Ecology **14**: 577-593.

Environmental Systems Research Institute (ESRI). (2011). ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Fahrig, L. (2003). Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecological Applications **12**: 346-353.

Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. Journal of Biogeography **40**: 1649-1663.

Favila, M.E. & Halffter, G. (1997). The use of indicator groups for measuring biodiversity as related to community structure and function. Acta Zoologica Mexicana **72**: 1-25.

Filgueiras B.K.C, Tabarelli, M., Leal, I.R., Vaz-de-Mello, F., Peres, C.A. & Iannuzzi, L. (2016). Spatial replacement of dung beetles in edge-affected habitats: biotic homogenization or divergence in fragmented tropical forest landscapes? Diversity and Distributions **22**: 400-409.

Filgueiras, B.K.C, Melo, D.H.A., Andersen, A.N., Tabarelli, M. & Leal, I.R. (2019). Cross-taxon congruence in insect responses to fragmentation of Brazilian Atlantic forest, Ecological Indicators **98**: 523-530.

Fischer, J., Lindenmayer, D.B. & Manning, A.D. (2006). Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in the Ecology and the Environment **4**: 80-86.

Fleury, M. & Galetti, M. (2006). Forest fragment size and microhabitat effects on palm seed predation. Biological Conservation **131**: 1-13.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. & DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters **12**: 22-33.

Gardner, T.A., Barlow. J., Sodhi, N.S. & Peres, C.A. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. Biological Conservation **143**: 2293-2300.

Gardner, T.A., Hernández, M.I., Barlow, J., & Peres, C.A. (2008). Understanding the biodiversity consequences of habitat change: The value of secondary and plantation forests for Neotropical dung beetles. Journal of Applied Ecology **45**: 883-893.

Gardner, T.A., Barlow, J., Chazdon, R.L., Ewers, R., Harvey, C.A., Peres, C.A. & Sodhi, N. (2009). Prospects for tropical forest biodiversity in a human-modified world. Ecology Letters **12**: 561-582.

Gardner, T.A., Barlow, J., Araújo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcom, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Overal, W.L., Parry, L., Peters, S.L., Ribeira-Junior, M.A., Silva, M.N.F., Motta, C.S. & Peres, C.A. (2008b). The cost-effectiveness of biodiversity surveys in Tropical forests. Ecology Letters **11**: 139-150.

Girão, L.C., Lopes, A.V., Tabarelli, M. & Bruna, E.M. (2007). Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. PLoS One **9**: e908.

Halffter, G. & Matthews, E.G. (1966). The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). Folia Entomológica Mexicana **12**: 1-312.

Halffter, G. & Edmonds, W.D. (1982). The nesting behaviour of dung beetles (Scarabaeinae): an ecological and evolutive approach. Instituto de Ecologia, Mexico City, Mexico.

Halffter, G. & Favila, M.E. (1993). The Scarabaeinae (Insecta: Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. Biology International **27**: 15-21.

Hanski, I. & Cambefort, Y. (1991). Dung beetle ecology. Princeton University Press, Princeton, p. 481.

Harborne, A R., Mumby, P.J., ZŻychaluk, K., Hedley, J.D. & Blackwell, P.G. (2006). Modeling the beta diversity of coral reefs. Ecology **87**: 2871-2881.

Herrmann, B.C., Rodrigues, E. & Lima, A. (2005). A paisagem como condicionador de fragmentos florestais. Floresta **35**: 13-22.

Hill, M.O. (1973). Diversity and evenness: a unifying notation and its consequences. Ecology **54**: 427-431.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., SetSlS, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs. **75**: 3-35.

Hothorn, T., Zeileis, A., Farebrother, R.W., Cummins, C., Millo, G., Mitchell, D. (2015). lmtest: Testing Linear Regression Models. R package version 0.9-34, URL https://cran.r-project. org/package=lmtest.

Instituto Brasileiro de Geografia e Estatística (IBGE). (2006). Censo Agropecuário: Brasil, Grandes Regiões e Unidades da Federação, pp. 775.
Jost, L. (2006). Entropy and Diversity. Oikos **113**: 363-375.

Klein, B.C. (1989). Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology **70**: 1715-1725.

Krell, F., Krell-Westerwalbesloh, S., Weiß, I., Eggleton, P. & Linsenmair, K.E. (2003). Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae). Ecography **26**: 210-222.

Larsen, T.H. & Forsyth, A. (2005). Trap spacing and transect design for dung beetle biodiversity studies. Biotropica **37**: 322-325.

Laurance, W.F., Ferreira, L.V., Rankin-de Mérona, J., Laurance, S.G., Hutchings, R.G. & Lovejoy, T.E. (1998). Effects of Forest fragmentation on recruitment patterns in Amazonian tree communities. Conservation Biology **12**: 460-464.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology **16**: 605-618.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M. & Harms, K.E., Luizão, R.C.C., Ribeiro, J.E. (2007). Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLoS One **2**: e1017.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography **23**: 1324-1334.

Loreau, M. (2004). Does functional redundancy exist? Oikos **104**: 606-611.

Lumaret, J.P. & Kirk, A. (1987). Ecology of dung beetles in the French Mediterranean region (Col. Scarabaeinae). Acta Zoológica Mexicana **24**: 1-55.

Martello, F., Andriolli, F., Souza, T.B., Dodonov. & Ribeiro, M.C. (2016). Edge and land use effects on dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in Brazilian cerrado vegetation. Journal of Insect Conservation **20**: 957-970.

Martini, A.M.Z., Fiaschi, P., Amorim, A.M. & da Paixão, J.L. (2007). A hot-point within a hot-spot: a high diversity site in Brazil's Atlantic Forest. Biodiversity and Conservation **16**: 3111-3128.

Melo, A.S., Rangel, T.F. & Diniz-Filho, J.A. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. Ecography **32**: 226-236.

Morante-Filho, J.C., Faria, D., Mariano-Neto, E. & Rhodes, J. (2015). Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the Brazilian Atlantic Forest. PLoS One **10**: e0128923.

Morante-Filho, J.C., Arroyo-Rodríguez, V. & Faria, D. (2016). Patterns and predictors of b-diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of forest specialist and generalist birds. Journal of Animal Ecology **85**: 240-250.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature **403**: 853-858.

Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M. & Network T.S.R. (2007). Global dung beetle response to tropical forest modiication and fragmentation: a quantitative literature review and meta-analysis. Biological Conservation **137**:1-19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E. & Network, T.S.R. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation **141**: 1461-1474.

Nichols, E., Gardner, T.A., Peres, C.A., Spector, S. & Network, T.S.R. (2009). Co-declining mammals and dung beetles: an impending ecological cascade. Oikos **118**: 481-487.

Nichols, E., Uriarte, M., Peres, C.A., Louzada, J., Braga, R.F., Schiffler, G., Endo, W., & Spector, S.H. (2013). Human-induced trophic cascades along the fecal detritus pathway. PLoS One **8**: e75819.

Pardini, R., Faria, D., Accacio, G.M., Laps, R.R., Mariano-Neto, E., Paciencia, M.L.B., Dixo, M. & Baumgarten, J. (2009). The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. Biological Conservation **142**: 1178-1190.

Pardini, R., Bueno, A.A., Gardner, T.A., Prado, P.I. & Metzger, J.P. (2010). Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscape. PLoS One **5**: 1-10.

Pessoa, M.S., Rocha-Santos, L., Talora, D.C., Faria, D., Mariano-Neto, E., Hambuckers, A. & Cazetta, E. (2016). Fruit biomass availability along a forest cover gradient. Biotropica **49**: 45-55.

Philips, T.K., Pretorius, E. & Scholtz, C.H. (2004). A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. Invertebrate Systematics **18**: 53-88.

R Core Team. (2017). R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009). The Brazilian Atlantic Forest: how much is left, and how is the remaining Forest distributed? Implications for conservation. Biological Conservation, **142**: 1141-1153.

Rocha-Santos, L., Pessoa, M.S., Cassano, C.R., Talora, D.C., Orihuela, R.L.L., Mariano-Neto, E., Morante-Filho, J.C., Faria, D. & Cazetta, E. (2016). The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure. Biological Conservation **196**: 1-9.

Santos, B.A., Peres, C.A., Oliveira, M.A., Grillo, A., Alves-Costa, C.P. & Tabarelli M. (2008). Drastic erosion in functional attributes of tree assemblages in Atlantic Forest fragments of Northeastern Brazil. Biological Conservation **141**: 249-260.

Sattler, T., Duelli, P., Obrist, M.K., Arlettaz, R. & Moretti, M. (2010). Response of arthropod species richness and functional groups to urban habitat structure and management. Landscape Ecology **25**: 941-954.

Scholtz, A.D.L., Davis, A.L. & Kryger, U. (2009). Evolutionary biology and conservation of dung beetles. Pensoft Publishers, Sofia.

Slade, E.M., Mann, D.J., Villanueva, J.F. & Lewis, O.T. (2007). Experimental evidence for the efects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. Journal of Animal Ecology **76**:1094-1104.

Silva, J.M.C. & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature **404**: 72-73.

Silva, P.G. & Hernández, M.I.M. (2015). Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. PLoS One **10**: e0126112.

Solar, R.R.C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R., Louzada, J., Maués, M., Moura, N.G., Oliveira, V.H.F., Chaul, J.C.M., Schoereder, J.H., Vieira, I.C.G., Mac Nally, R. & Gardner, T.A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecology Letters **18**: 1108-1118.

Spector, S. (2006). Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation.Coleopterists Bulletin **60**: 71-83.

Thomas, W.W., Carvalho, A.M.V., Amorim, A.M., Garrison, J. & Arbeláz A.L. (1998). Plant endemism in two forests in southern Bahia, Brazil. Biodiversity and Conservation **7**: 311-322.

Ulrich, W., Banks-Leite, C., De Coster, G., Habel, J. C., Matheve, H., Newmark, W. D., Tobias, J.A. & Lens, L. (2018a). Environmentally and behaviourally mediated co-occurrence of functional traits in bird communities of tropical forest fragments. Oikos **127**: 274-284.

Ulrich, W., Kubota, Y., Piernik, A. & Gotelli, N.J. (2018b). Functional traits and environmental characteristics drive the degree of competitive intransitivity in European saltmarsh plant communities. Journal of Ecology **106**: 865-876.

Vaz-de-Mello, F.Z., Edmonds, W.D., Ocampo, F.C. & Schoolmeesters, P. (2011). A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). Zootaxa **2854**: 73p.

Wilson, M.V. & Shmida, A. (1984). Diversity with presence-absence data. Journal of Ecology **72**: 1055-1064.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). Mixed effects models and extensions in ecology with R. Springer: New York.

Supporting Information

Table S1. List of dung beetle species, as well as resource-relocation behavior, diet preference and total abundance, sampled in fragmented forests in the Atlantic forest, northeastern Brazil.

Species	Relocation behavior	Diet preference	Abundance
Anomiopus sp.1	Tunneler	Undefined	1
Anomiopus sp.2	Tunneler	Undefined	1
Aphengium curtum Silva & Vaz-de-Mello 2015	Tunneler	Generalist	8
Ateuchus oblongum (Harold, 1883)	Tunneler	Generalist	205
Ateuchus vigilans (Van Lansberge, 1874)	Tunneler	Coprophagous	19
Ateuchusvolxemi (Borre, 1886)	Tunneler	Undefined	3
*Canthidium flavipes*Harold, 1867	Tunneler	Generalist	78
Canthidium sp.1	Tunneler	Generalist	14
Canthidium sp.2	Tunneler	Undefined	1
Canthidium sp.3	Tunneler	Coprophagous	98
Canthidium sp.4	Tunneler	Coprophagous	101
Canthidium sp.5	Tunneler	Coprophagous	56
Canthidium sp.6	Tunneler	Coprophagous	10
Canthidium sp.7	Tunneler	Undefined	2
Canthidium sp.8	Tunneler	Undefined	1
Canthidium sp.9	Tunneler	Undefined	1
Canthon nigripennis Van Lansberge, 1874	Roller	Necrophagous	10
*Canthon prasinus*Klug, 1833	Roller	Necrophagous	9
Canthon sp.1	Roller	Undefined	2
Canthon staigi(Pereira, 1953)	Roller	Necrophagous	38
*Canthonella silphoides*Harold, 1867	Roller	Generalist	1470
Coprophanaeus bellicosus (Olivier, 1789)	Tunneler	Necrophagous	43
Coprophanaeus dardanus(MacLeay, 1819)	Tunneler	Necrophagous	147
Deltochilum brasiliense (Castelnau, 1840)	Roller	Necrophagous	16
Deltochilum próx. *calcaratum*Bates, 1870	Roller	Necrophagous	40
Deltochilum sp.1	Roller	Undefined	1
Dichotomius depressicollis (Harold, 1867)	Tunneler	Undefined	1
Dichotomius iannuzziae Valois, Vaz-de-Mello & Silva 2017	Tunneler	Generalist	914
Dichotomius irrinus (Harold, 1867)	Tunneler	Generalist	303
Dichotomius mormon Ljungh, 1799	Tunneler	Undefined	2
Eurysternus nanus Génier, 2009	Dweller	Generalist	10
Eutrichillum hirsutum (Boucomont, 1928)	Dweller	Necrophagous	24
Holocephalus sculptus (Gillet, 1907)	Tunneler	Undefined	3
Onthophagus haematopus Harold 1875	Tunneler	Coprophagous	300
Paracanthon sp.1	Roller	Undefined	2
Phanaeus splendidulus (Fabricius, 1781)	Tunneler	Undefined	5
Uroxys sp.1	Tunneler	Undefined	5

Capítulo II

Effects of forest loss and fragmentation on dung beetle communities: Assessing the relative influence of landscape attributes in the Brazilian Atlantic Forest

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Effects of forest loss and fragmentation on dung beetle communities: Assessing the relative influence of landscape attributes in the Brazilian Atlantic Forest

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ABSTRACT

Habitat loss is classified as most pervasive threats to biodiversity worldwide. As such, identifying as drivers are shaping biological communities in fragmented tropical landscapes is crucial for enhancing conservation strategies. We address this using a hybrid patch-landscape approach design and a multimodel inference approach to test the relative impact of forest loss and increase de edge density and pasture cover on different functional traits of dung beetles in the Atlantic Forest, Brazil. Our findings provide novel empirical evidence that edge density was the most important explanatory variable to changes in the dung beetles communities when compared to forest and pasture cover at landscape scale. However, both forest and pasture cover also significantly influenced many of the dung beetle responses, supporting the idea that biological communities are negatively affected by habitat loss and fragmentation. Contrary to expectations, we found that dung beetle body size, protibia area and metatibia length was unexpectedly higher in landscapes with increase edge density, reinforces the need for studies to better understand which mechanisms could favor the presence of larger dung beetles in tropical human-modified landscapes. Taken together, these results suggest the need of conservation and management strategies focused on the protection of the remaining Atlantic Forest fragments, and the promotion the forest recovery and reduction in the pasture cover and edge density at the landscape-level.

Keywords: Anthropogenic edge, Forest Cover, Invertebrate, Land-use, Matrices, Tropical Forest.

1. Introduction

Habitat loss represents one of major threats to tropical biodiversity, altering species distribution and weakening ecosystem functionality (Cardinale et al., 2012; Pimm and Raven, 2000). Reduction in available native core habitat, modifications in the forest microclimate (Didham and Lawton, 1999) and in the vegetation structure (Laurance et al., 2006) are the main suggested pathways by which fragmentation can affect species persistence and community structure (Didham et al., 1998). Given that around 70% of the world's remaining forests are within 1 km or less from an anthropogenic edge (Haddad et al., 2015), understanding the underlying drivers of biodiversity in fragmented landscapes is crucial for enhancing conservation strategies (Balmford et al., 2012; Gardner et al., 2009).

The historical and current land-use trajectory of Brazilian Atlantic Forest offers an excellent opportunity to examine how habitat loss and fragmentation can shape tropical biodiversity. This forest hotspot is one of the most diverse ecosystems in the world (Myers et al., 2000; Silva and Tabarelli, 2000), and has experienced high deforestation rates since the 16th century (Tabarelli et al., 2010). Currently, over 80% of the forest fragments are < 50 ha and almost half of the remaining forests are < 100 m from its edge (Ribeiro et al., 2009). In particular, deforestation and fragmentation of the Atlantic forest led to profound changes in faunal richness (Filgueiras et al., 2011), species composition (Campos and Hernández, 2015), biomass (Filgueiras et al., 2015), and functional and phylogenetic diversity (Audino et al., 2014; Morante-Filho et al., 2017). These biological changes are more alarming when involving the loss of species and further cascade extinctions that can bring severe ecological implications (Eklof and Ebenman, 2006; Koh et al., 2004). For example, mammal extinctions are expected to negatively influence dung beetles (Raine et al., 2018), and reported co-declines in mammal and dung beetle communities (Nichols et al., 2009) are, therefore, likely to result in cascade effects for dung beetle-mediated ecological processes (Culot et al., 2013; Nichols et al., 2013).

Dung beetles (Coleoptera: Scarabaeinae) are considered as a responsive and cost-effective model system for evaluating the impacts from human activities on tropical ecosystems (Gardner et al., 2010; Larsen et al., 2005; Nichols et al., 2007), and have been widely used to assess the impacts from habitat loss and fragmentation (Audino et al., 2017; Gardner et al., 2008). These detritivore insects also perform several key ecological processes associated with the nutrient cycling, improvement of physical and chemical properties of soil, parasite suppression and secondary seed dispersion (Nichols et al., 2007; 2008). The ecological functions provided by dung beetles and their sensitivity to environmental changes have been shown to be influenced by a set of functional traits such as resource-relocation behaviour, body size, and diet and habitat preference (Barragán et al., 2011; Gardner et al., 2008; Leite et al., 2018; Nichols et al., 2009). While larger dung beetle species are expected to relocate more soil and dung (Carvalho et al., 2018; Gregory et al., 2015), dung beetle resource-relocation behaviours has been shown to influence the efficiency secondary seed dispersal. The horizontal movement promoted by roller species, for example, may decrease the probability of density-dependent seed or seedling mortality (Lawson et al., 2012) and the vertical burial by tunnelers can provide a better microenvironment for seed germination (Andresen, 2001; Andresen and Levey, 2004). The combined effect of the dwellers and tunnelers can also stimulate soil microbial activity (Menéndez et al., 2016), increasing the concentration of foliar nutrients (Santos-Heredia et al., 2016).

Although dung beetles have been extensively used to evaluate the impacts of human activities on forest biodiversity (Beiroz et al., 2018; França et al., 2016a), few studies have evaluated how the contribution of different landscape descriptors may vary for different dung beetle functional groups. Previous research shows that smaller and isolated fragments have impoverished communities (Filgueiras et al., 2011), but appear to serve as refuges for some forest species and at the same time provide habitat for pasture species (Arellano et al., 2008). It has also been found that forest cover loss affect dung beetle groups according to their habitat preference (Leite et al., 2018). Yet, these studies do not consider morphological traits and/or functional diversity indices that may advance our understanding on how biodiversity respond to environmental changes (McGill et al., 2006). In addition, when landscape descriptors (e.g. patch size and shape, distance among fragments and forest cover) have been used to explain changes in dung beetle communities (Campos and Hernández, 2015; Costa et al., 2013; Filgueiras et al., 2011), these were analyzed individually and/or at a patch scale (but see Filgueiras et al., 2015; Sánchez-de-Jesús et al., 2015) or for other type of forests (Arellano et al., 2008).

Here, we address these knowledge gaps by evaluating the consequences of the Atlantic forest loss and fragmentation for dung beetles. We surveyed 16 landscapes and separated beetle species into subgroups based on different traits (e.g. resource-relocation behavior, diet preference, morphological traits), which were also considered to calculate distinct functional diversity indices, to assess how distinct landscape-level descriptors (forest cover, edge density and pasture cover) affect forest biodiversity. We ask the following questions: (1) Does forest cover contribute more than edge density and pasture cover for changes in dung beetle communities? (2) How these landscape predictors affect different dung beetle functional groups and functional diversity? We expected forest cover to drive the most pervasive effects on dung beetle responses, as previous research highlights its importance when compared to other landscape metrics (Fahrig, 2003; 2013; Nichols et al., 2007; Pardini et al., 2010). We also expected that distinct dung beetle subgroups, community metrics and functional indices to respond differently to distinct landscape descriptors (Beiroz et al., 2017; Martello et al., 2016). Taken together, our analyses provide a quantitative understanding of the landscape spatial attributes that affect of the persistence and loss of dung beetle communities in one of the most species-rich tropical forests and can provide a basis for predicting the biological consequences of future deforestation on other tropical regions.

2. Methods

2.1 Study area

The study was conducted in the southern region of Bahia state, north-eastern Brazil (15°280S, 39°150W, WGS84). This region is hot and humid region without a distinct dry season (*Af* Köppen classification), with mean annual temperature and rainfall of 24°C and ca. 2000 mm, respectively and dominated by tropical lowland rainforest (Thomas et al., 1998). Land use changes were particularly severe within large tracts of previously continuous forests, which were converted to small fragments in different succession stages and embedded within a mosaic of different monocultures such as cocoa plantations, rubber trees, and cattle pastures (Pardini et al., 2009).

2.2 Sampling design and explanatory variables

We selected 16 non-overlapping sampling landscapes (Figure 1) based on a hybrid patch-landscape approach (Tischendorf and Fahrig, 2000). The selection of landscapes was based on high resolution satellite images (RapidEye® from 2009 to 2010, QuickBird® and WorldView® from 2011). We mapped the landscapes by manually digitizing land cover features as visually interpreted at a scale of 1:10.000, and polygons were classified as forest fragments and different land-uses (e.g. pasture and agriculture) according to the *Instituto Brasileiro de Geografia e Estatıstica* (IBGE, 2006) and using ArcGIS 10.2 software (ESRI, 2011). After intensive ground-validation, we mapped the forest fragments and land-uses within a study area of 3,500 km^2.

The percentage of forest cover (FC) was calculated based forest fragments within a 1-km radius from the center of each landscape and forest cover varied from 3 to100%. The landscape completely covered by old growth forest and with absence of edge density and pasture cover is included within one federally protected conservation unit (Una Biological Reserve), while other landscapes are located within private properties. We used scale of 1-km because it represents the longest movement distance recorded for dung beetle species in Atlantic Forest within a 48-h period (Silva and Hernández, 2015). The center of each landscape was selected preferably in forest fragment with mature forest within the least degraded part and without any slash-and-burn evidence. The landscapes were separated by at least 1-km to assure that each landscape represented independent dung beetle samples (Silva and Hernández, 2015).

Figure 1.

2.3 Dung beetle sampling

Dung beetles were sampled three times at each of the 16 landscapes during the rainy season (April-June) in 2017. We used pitfall traps, which consisted of a plastic container (15 cm in diameter and 13 cm in height) buried with an opening at ground level and with a small recipient (3 cm in diameter by 4.8 cm in height) where human feces or decomposed meat were placed as bait (*ca*. 30 g of bait). Pitfalls were filled with ca. 250 ml of a killer solution (saline solution with detergent) and were covered by plastic lid to protect sampled material from the rain.

We established three sets of pitfalls, spaced 100 m apart (Silva and Hernández, 2015) in the center of each landscape. Each set contained three pitfalls disposed at the vertices of a 5-m equilateral triangle, each trap with a different bait-treatment (fresh human feces, or decomposed meat, or non-baited) that was randomly distributed within each pitfall set. Traps were exposed in the field for 48h, and sampled dung beetles were taken to the Applied Ecology and Conservation Lab at the Universidade Estadual de Santa Cruz (UESC). Dung beetles were identified to species level, whenever possible. Voucher specimens were deposited in the entomological collections of the Laboratório de Entomologia (UESC) and the Seção de Entomologia da Coleção Zoológica, Universidade Federal de Mato Grosso, Cuiabá, both in Brazil.

2.4 Dung beetles functional groups

We classified dung beetles according to functional groups in resource-relocation behavior, diet preference and morphological traits, which were also used for estimating functional diversity metrics. See below for details.

RESOURCE-RELOCATION BEHAVIOUR: This attribute is related to dung manipulation for feeding and reproduction (Halffter and Edmonds, 1982). Species were grouped as tunnelers, rollers and dwellers. Tunneler species are those that dig tunnels in the soil immediately under or very close to the resource, whereas rollers usually make resource balls and roll them to some distance from the original dung patch and dwellers remain within the resource deposits (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991)

DIET PREFERENCE: Following Beiroz et al. (2017), we considered dung beetles species as coprophagous and necrophagous when > 75% of the individuals of a given species was sampled in dung- or meat-baited traps, respectively; and as generalists those species with lower percentages. For species with less than five individuals, we sought the advice of the Neotropical dung beetle specialist Dr. Fernando Z. Vaz-de-Mello. We excluded all undefined species from the analyses. The selected diets are commonly reported for Neotropical dung beetles (Hanski and Cambefort, 1991).

MORPHOLOGICAL TRAITS: We examined morphological traits relevant to soil excavation and dung burial activities (Nichols et al., 2008; Petchey and Gaston, 2006). We used a Leica M250 microscope and Life Measurement software (Leica, Wetzlar, Germany) to measure the body size (sum of pronotum and elytra length), protibia area, and metatibia lenght of a maximum of 30 individuals to abundant species captured in the study (*N total* = 1450, see Griffiths et al., 2016a).

FUNCTIONAL DIVERSITY METRICS: We used the FD package (Laliberté et al., 2012) in R (R Core Team 2017) to calculate four functional metrics: Functional richness (FRic), Functional evenness (FEve), (3) Functional divergence (FDiv) and Functional dispersion (FDis). See Villéger et al. (2008) and Laliberté and Legendre (2010) for description of each of these metrics, which considered dung beetle resource-relocation behaviour (roller, tunneler, or dweller), diet preference (coprophagous, necrophagous or generalists) and morphological traits (body size and mass and adjusted-metatibia length) during the calculation. Following Griffiths et al. (2015), we opted to divide the protibia area and metatibia length by the body size of the same individual (body size-adjusted traits) because these were co-related traits (Cadotte et al., 2011; Naeem and Wright, 2003); and used trait's medians rather than means because their distribution did not follow a normal curve (Griffiths et al., 2015). All traits were given equal weighting and species were weighted by their relative abundance for the calculation of each of the functional indices.

2.5 Statistical analyses

All statistical analyses were performed in the software R (R Core Team, 2017). We used the coverage estimator recommended by Chao and Jost (2012) to estimate the accuracy of inventories:

Eq. 1

where f_1 and f_2 are the number of species represented by one and two individuals, respectively, and *n* is the total number of individuals in the sample. We considered not only the observed values of species richness, but also the expected values based on coverage-based extrapolations performed with the *entropart* package (Marcon and Hérault, 2015). We estimated the variance inflation factor (VIF) using the *car* package (Fox and Weisberg, 2011) to assess collinearity among explanatory variables. Values of VIF should be < 2.5 in order to avoid the collinearity effect (Zuur et al., 2009).

We performed a hierarchical partitioning analysis (HP) to computes the independent contribution of each explanatory variable in order to assess their relative importance (Mac Nally, 2000; Murray and Conner, 2009). Competing models were evaluated based on R^2 goodness of fit statistic, which allowed us to interpret the independent effects as proportion of explained variance. Significance ($\alpha = 0.05$) of independent effects of each predictor was calculated using a randomization test with 1000 interactions (Mac Nally, 2002; Walsh and Nally, 2013). To assess the effects of the explanatory variables (forest cover, edge density and pasture cover) on the response variables (second question), we used an information-theoretic approach based on the selection of the most parsimonious models (Burnham and Anderson, 2002) using the *MuMIn* package (Bartón, 2017). For each response metric, we built full models representing all combinations of explanatory variables. For each model, we computed the Akaike's information criterion corrected for small samples (AICc) and selected the most parsimonious models (ΔAICc < 4 when compared to the best model; Burnham & Anderson 2002). From the complete set of possible models, we averaged coefficients of models within ΔAICc < 4, thus capturing greater uncertainty in the final set of candidate variables (Vierling et al., 2013).

We fixed a Gaussian distribution for continuous response variables (e.g. functional richness) after verifying for normality using the function *shapiro.test* from *stats* package (R Core Team, 2017); and used Poisson distribution, corrected for over-dispersion if required, when response variables did not follow a normal distribution (Zuur et al., 2009). We assessed the distribution suitability and model fit through residual analysis, and semivariograms were checked to detect any spatial correlation trends (Crawley, 2012; Diggle and Ribeiro, 2007). For better interpreting our results, we constructed heatmap using *ggplot2* package (R Core Team, 2017) with rank-abundance normalized to see differences in species' dominance and rarity among study sites.

3. Results

We sampled 3944 dung beetles from 16 genera and 37 species in the 16 landscapes (see Table S1 in supplementary material). Sample coverage was high in all landscapes (75-99% of the species recorded), indicating that our sampling effort was adequate. Landscape metrics were not correlated (VIF < 2.5), which allowed us to independently evaluate their effects on dung beetle communities.

Overall, edge density was the most important explanatory variable (accounting for 48% of the explanation and nine contributions with significant effects, $\alpha = 0.05$), followed by forest cover (26%) and pasture cover (26%). We also found edge density influencing all subgroups of dung beetle when considering the independent contribution from each explanatory variable in complete models that showed the highest percentage of explained deviance (Figure 2). Addressing our second question, distinct dung beetle responses were affected by different sets of explanatory variables (Table 1).

Figure 2.

RESOURCE-RELOCATION BEHAVIOUR – Model selection revealed strong support for the influence of edge density and pasture cover for all resource-relocation behaviours, and from forest cover on roller species (Table 1, Figure 3). We found that tunneler abundance and richness declined with increase of pasture cover and edge density (e.g. *Uroxys* sp.1, *Holocephalus sculptus* and *Canthidium flavipes;* Figure S2). Abundance of roller dung beetles declined in landscapes with lower forest cover (e.g. *Canthon staigi* and *Canthon* *prasinus;* Figure S2), and when the interaction of larger edges and pasture (ED + PC) was present. Model selection supported the importance of edge density and pasture cover for dweller species, which had reduced abundances in landscapes with higher edge densities and pasture cover (e.g. *Eutrichilum hirsutum*).

Table 1.

DIET PREFERENCE – Forest cover had a strong influence on all diet-based dung beetle groups (Table 1, Figure 3). The abundance of coprophagous beetles declined with increased edge density and pasture cover at landscape-level, while their richness declined with increase of edge density increased with forest cover (e.g. *Phanaeus splendidulus*, *Onthophagus haemotopus* and *Dichotomius depressicolis*). We found necrophagous abundance and richness declining with forest loss and increases in pasture cover, respectively (e.g. *Eutrichilum hirsutum* and *Canthon prasinus*). The abundance of generalist beetles was positively affected by the amount of forest cover (e.g. *Canthidium flavipes* and *Ateuchus voluxemi*).

MORPHOLOGICAL TRAITS – We found strong support for the influence from edge density on all examined traits, while body size and protibia area were affected by pasture cover, and protibia area by forest cover (Table 1, Figure 3). Dung beetle body size was unexpectedly higher in landscapes with increase edge density (e.g. *Deltochilum* prox. *calcaratum*), and when the interaction of larger edges and pasture (ED + PC) was present. Landscapes with greater edge density also had species with higher protibia area, which was also positively related with the interaction of larger edges and pasture (ED + PC) and negatively related with the interaction of larger edges and forest cover (ED + FC). Lastly, landscapes presenting more edge density also had species with higher metatibia length.

FUNCTIONAL DIVERSITY INDICES – We found no evidence of functional diversity being affected by any of the landscape descriptors.

Figure 3.

4. Discussion

This study contributes to our understanding on the drivers of change in dung beetle communities within fragmented tropical landscapes. Two findings deserve special attention. First, in a broader perspective, changes in the dung beetle community structure were strongly influenced by edge effects rather than by forest and pasture cover at the landscape scale. Second, all measured landscape attributes played a role in determining the dung beetle responses, supporting the idea that biological communities are negatively affected by some landscape attributes in the Brazilian Atlantic Forest.

THE RELATIVE IMPORTANCE OF LANDSCAPE ATTRIBUTES: Our results strongly support the notion that edge density at landscape scale is an important determinant of changes in dung beetle communities in the Brazilian Atlantic Forest. This finding contributes to previous evidence demonstrating the negative edge effects on dung beetle abundance, richness, species composition and body conditions (Filgueiras et al., 2015; 2016; Martello et al., 2016; Salomão and Iannuzzi, 2017; Spector and Ayzama, 2003).

The decline in dung beetle groups due to the effects of forest loss and increased edge density and pasture cover might be explained by two non-exclusive hypotheses: (1) changes in the vegetation structure (Gardner et al., 2010; Hanski and Camberfort, 1991; Halffter and Arellano, 2002; Nichols et al., 2007) and (2) lack of vertebrate dung resources (Andresen and Laurance, 2007; Barlow et al., 2010; Bogoni et al., 2016). Previous research in the same region have revealed that forest remnants in more deforested landscapes shows early successional attributes and increased canopy openness (Rocha-Santos et al., 2016), and dung beetles are known for their high sensitivity to even small changes in forest structure (Silva and Hernández, 2016) and low-level forest disturbances (Bicknell et al., 2014). In addition, medium and large-sized mammals – the main providers of resource for dung beetles (Halffter and Matthews, 1966) – had been locally extinct in the most of Atlantic Forest fragments (Canale et al., 2012), while the open matrix at this region also may acts as a barrier for primate movement (Estrada et al., 1999). However, not all dung beetles were negatively affected by fragmentation, as we also found species with higher abundances in landscapes with increased edge density and pasture cover (e.g. *Canthidium* sp.3 and *Canthidium* sp.5). These species are likely to be matrix- or even edge-specialists (Filgueiras et al., 2015; Peyras et al., 2013; Scheffler, 2005).

RESOURCE-RELOCATION BEHAVIOURS: Our results demonstrated that all resource-relocation groups were negatively affected by increase of edge density, and that pasture cover and forest loss had negative effects particularly on roller beetles, reinforcing the negative ecological impacts from habitat loss and fragmentation (Barlow et al., 2010; Escobar, 2004; Gardner et al., 2008; Martello et al., 2016).

The different resource-relocation behaviour in dung beetles is considered as a strategy to facilitate species coexistence (Hanski and Cambefort, 1991) through coping with the rates of dung dissection and reducing competition for food resources – which are key factors influencing the survivorship of tropical dung beetles (Halffter and Edmonds, 1982). Forest fragments usually have increased canopy openness (see Arroyo-Rodríguez et al., 2013; Rocha-Santos et al., 2016), and microclimatic changes caused by higher light incidence and decreased soil humidity can be limiting factors for adult and larvae beetles, which depend of ephemeral resources that become unusable when desiccated (Peck and Forsyth, 1982; Sowig, 1995). Larvae of roller species are more prone to suffer with soil desiccation because these beetles usually dig shallower nests (Davis et al., 2010; Hanski and Cambefort, 1991; Osberg et al., 1993).

Resource scarcity is likely to create a competitive hierarchy for dung beetle resource-relocation behaviours, in which rollers and fast tunnelers are stronger competitors than slow tunnelers, which are then followed by dweller species (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Scholtz et al., 2009). This hierarchy (rollers > tunnelers > dwellers) is combined with increasing energetic costs (Krell et al., 2003), where stronger competitors such as roller beetles need more energy and, consequently, more resources (Krell et al., 2003; Halffter and Edmonds, 1982). The relocation and use of energy reserves to roll the food resource away in a short time span may therefore cause a reduction in individual fitness – mainly when food resources are scarce – through affecting beetles' physiological integrity (França et al., 2016a; Salomão et al., 2018), immune system and reproduction (Cotter et al., 2007; Halffter and Edmonds, 1982; Van Praet et al., 2014).

DIET PREFERENCE: We found the abundance and richness of necrophagous and coprophagous beetles decreasing in landscapes with higher values of forest loss, edge densities and pasture cover, while more generalist beetle individuals were sampled in landscapes with more forest cover. Dung beetles' diet preference can be influenced by different resource characteristics such as the physical and chemical characteristics (Gittings and Giller, 1998), shape (Gordon and Cartwright, 1974), water and/or fibre content (Verdú and Galante, 2004; Arellano et al., 2015), size (Peck and Howden, 1984), and nutritional value (Verdú and Galante, 2004; Arellano et al., 2015). Irrespective of their diet preference and resource characteristics, our results are probably related to the fact that landscapes with higher forest cover sustain greater environmental and resource heterogeneity, thus supporting more dung beetle species and individuals (Morante-Filho et al., 2016; Navarrete and Halffter, 2008; Tscharntke et al., 2012). In addition, landscapes dominated by pasturelands are also more likely to have herbivores dung (Steinfeld et al., 2006), affecting negatively necrophagous dung beetles, which compete with others insect groups for carcasses (Jong and Chadwick, 1999; Mohamed and Mashaly, 2017), a less frequent and spatially and temporally limited resource (Halffter and Matthews, 1966).

MORPHOLOGICAL TRAITS: Overall, it has been shown that dung beetles decrease in body size and within tropical disturbed forests (França et al., 2016b; 2017; Halffter et al., 1992; Scheffler, 2005; Spector and Ayzama, 2003). However, we unexpectedly found increased body size, protibia area and metatibia length within landscapes with higher values of edge density and pasture cover. While providing support to the findings from recent study with dung beetles in Mexican forest landscapes (Salomão et al., 2018), these patterns could be a result of reduced intraspecific competition caused by the lower abundance conspecifics. This was previously observed for *Anoplotrupes stercorosus* (Geotrupidae) beetles in Europe, which had larger body sizes in sites where the species was less abundant (Byk and Semkiw, 2010). Nevertheless, we highlight that further research is needed to better understand the mechanisms by which intraspecific competition and other environmental factors could favor the presence of larger dung beetles in tropical human-modified landscapes.

5. Conclusion

The current forest cover of the Brazilian Atlantic Forest is only about 11% of its original extent (Ribeiro et al., 2009), and considered as one of the hotspots of biodiversity (Myers et al., 2000). The remnants within our study region in Bahia State (*ca*. 17% of its original) are among the most preserved areas in Brazil (Ribeiro et al., 2009), considered as a hotspot within Atlantic rainforest that provides refuge for biodiversity (*Bahia* *refugium*; Carnaval et al., 2009). If expected increases in forest loss, fragmentation and degradation continue in this region (Ribeiro et al., 2009), not only dung beetle diversity will be lost, but also significant short and long-term implications will occur for functioning processes in remaining fragments. This group of insects with its primary functions mediate many key ecosystem functions such as nutrient cycling, soil bioturbation, parasite suppression and secondary seed dispersal (Andresen and Feer, 2005; França et al., 2018; Nichols et al., 2008). The loss of dung beetles is therefore likely to result in cascading effects, for example affecting the spatial distribution and demography of plant communities, with important implications for tropical forest regeneration and conservation (Lawson et al., 2012). In particular, the observed declines in roller and coprophagous beetles may lead to a reduction in secondary seed dispersal (Hosaka et al., 2014) – mainly horizontally – and, consequently, increases in the probability of seed competition (Andresen, 1999; Andresen and Levey, 2004) or density-dependent predation (Beaune et al., 2012; Estrada and Coates-Estrada, 1991) where dung with seeds are still being produced by existing mammals.

Our research assessed the influence of three distinct landscape attributes for dung beetle communities from the Brazilian Atlantic forest hotspot (Myers et al., 2000). We found edge density as the main driver of biological changes, but both forest and pasture cover also significantly influenced many of the dung beetle responses. We therefore call for conservation and management strategies focused on the protection of the remaining Atlantic Forest fragments, and the promotion the forest recovery and reduction in the pasture cover and edge density at the landscape-level. This will be beneficial not only for dung beetles, which perform several key ecological processes (França et al., 2018; Nichols et al., 2007), but also for the other groups that usually respond similarly to human-induced forest disturbances in tropical regions such as birds and plants (e.g. Barlow et al., 2016; Ferreira et al., 2018). Nevertheless, given that tropical ecosystems are subject to multiple sources of stress such as climate change and local disturbance (Barlow et al., 2018), conservation efforts will also require multiple but interdependent management actions at landscape level in order to attain long-term success.

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References

Andresen, E., 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rainforest. Biotropica 31, 145–158. https://doi.org/10.1111/j.1744-7429.1999.tb00125.x.

Andresen, E., 2001. Effects of dung presence, dung amount, and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. J. Tropical Ecol. 17, 61–78. https://doi.org/10.1017/S0266467401001043.

Andresen, E., Levey, D.J., 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia 139, 145–154. https://doi.org/10.1007/s00442-003-1480-4.

Andresen, E., Feer, F., 2005. The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In P.-M. Forget, J. E. Lambert, P. E. Hulme, & S. B. Vander Wall (Eds.), Seed fate (pp. 331–349). Wallingford: CABI Publishing.

Andresen, E., Laurence, S.G.W., 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica 39. https://doi.org/10.1111/j.1744-7429.2006.00239.x.

Arellano, L., León-Cortés, J., Halffter G., 2008. Response of dung beetle assemblages and their conservation in remnant natural and modified habitats in southern Mexico. Insect Conserv. Diver. 1, 253-262. https://doi.org/10.1111/j.1752-4598.2008.00033.x.

Arellano, L., Castillo-Guevara, C., Huerta, C., Germán-García, A., Lara, C., 2015. Effect of using different types of animal feces in the feeding and nesting on the dung beetle *Onthophagus lecontei* (Coleoptera: Scarabaeinae). Can. J. Zool. 93, 337–343. https://doi.org/10.1139/cjz-2014-0226

Arroyo-Rodríguez, V., Ros, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M., Chazdon, R., 2013. Plant b-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. J. Ecol. 6, 1449–1458. https://doi.org/10.1111/1365-2745.12153.

Audino, L.D., Louzada, J., Comita, L., 2014. Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity? Biol. Conserv. 169, 248–257. https://doi.org/10.1016/j.biocon.2013.11.023.

Audino, L.D., Murphy, S.J., Zambaldi, L., Louzada, J., Comita, L.S., 2017. Drivers of community assembly in tropical forest restoration sites: role of local environment, landscape, and space. Ecol. Appl. 27, 1731–1745. http://dx.doi.org/10.1002/eap.1562.

Balmford, A., Green, R., Phalan, B., 2012. What conservationists need to know about farming. Proc. R. Soc. 279, 2714–2724. https://doi.org/10.1098/rspb.2012.0515.

Barragán, F., Moreno, C.E., Escobar, F., Halffter, G., Navarrete, D., 2011. Negative impacts of human land use on dung beetle functional diversity. PLoS One 6, e17976. https://doi.org/10.1371/journal.pone.0017976.

Barlow, J., Louzada, J., Parry, L., Hernández, M.I.M., Hawes, J., Peres, C.A., Vaz-de-Mello, F.Z., Gardner, T.A., 2010. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. J. Appl. Ecol. 47, 779–788. http://dx.doi.org/10.1111/j.1365-2664.2010. 01825.x.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., MacN Nally, R., Thomson, J.R., Ferraz, S.F.B., Louzada, J., Oliveira, V.H.F., Parry, L., Solar, R.R.C., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.B., Cardoso, T.M., Oliveira, R.C.J., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535, 144–147. https://doi.org/10.1038/nature18326.

Barlow, J.; França, F.; Gardner, T.A.; Hicks, C.C.; Lennox, G.D.; Berenguer, E.; Castello, L.; Economo, E.P.; Ferreira, J.; Guénard, B.; Gontijo Leal, C.; Isaac, V.; Lees, A.C.; Parr, C.L.; Wilson, S.K.; Young, P.J.; Graham, N.A.J., 2018. The future of hyperdiverse tropical ecosystems. Nature 559, 517–526. https://doi.org/10.1038/s41586-018-0301-1.

Bartón, K., 2017. MuMIn *package*. https://cran.r-project.org/web/packages/MuMIn/index.html.

Beaune, D., Bollache, L., Bretagnolle, F., Fruth, B., 2012. Dung beetles are critical in preventing postdispersal seed removal by rodents in Congo rain forest. J. Trop. Ecol. 28, 507–510. https://doi.org/10.1017/S0266467412000466.

Beiroz, W., Slade, E.M., Barlow, J., Silveira, J.M., Louzada, J., Sayer, E., 2017. Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change. Insect Conserv. Divers. 10, 94–106. https://doi.org/10.1111/icad.12206.

Beiroz, W., Sayer, E., Slade, E.M., Audino, L., Braga, R.F., Louzada, J., Barlow, J., 2018. Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape. Ecol. Indic. 95, 518–526. https://doi.org/10.1016/j.ecolind.2018.07.062.

Bicknell, J.E., Phelps, S.P., Davies, R.G., Mann, D.J., Struebig, M.J., Davies, Z.G., 2014. Dung beetles as indicators for rapid impact assessments: evaluating best practice forestry in the neotropics. Ecol. Indic. 43, 154–161. http://dx.doi.org/10.1016/j. ecolind.2014.02.030.

Bogoni, J.A., Graipel, M.E., Castilho, P.V., Fantacini, F.M., Kuhnen, V.V., Luiz, M.R., Maccarini, T.B., Marcon, C.B., Texeira, C.S.P., Tortato, M.A., Vaz-de-Mello, F.Z., Hernández, M.I.M., 2016. Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodivers. Conserv. 25, 1661–1675. https://doi.org/10.1007/s10531-016-1147-1.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York. http://dx.doi.org/10.1007/b97636.

Byk, A., Semkiw, P., 2010. Habitat preferences of the forest dung beetle Anoplotrupes stercorosus (Scriba, 1791) (Coleoptera: Geotrupidae) in the Białowieża forest. Acta Sci. Pol. 9, 3–4.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance ofecological processes and services. J. Appl. Ecol. 48, 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x.

Canale, G.R., Peres, C.A., Guidorizzi, C.E., Gatto, C.A., Kierulff, M.C., 2012. Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. PLoS One 7, e41671. https://doi.org/10.1371/journal.pone.0041671.

Campos, R.C., Hernández, M.I.M., 2015. Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. Ecol. Indic. 49, 216–227. https://doi.org/10.1016/j.ecolind.2014.09.043.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/0.1038/nature11148.

Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T., Moritz, C., 2009. Stability predicts genetic diversity in the Brazilian Atlantic Forest Hotspot. Science 323, 785–789. https://doi.org/10.1126/science.1166955.

Carvalho, R.L., Frazão, F., Ferreira–Châline, R.S., Louzada, J., Cordeiro, L., França, F., 2018. Dung burial by roller dung beetles (Coleoptera: Scarabaeinae): An individual and specific-level study. Int. J. Trop. Insect. Sci. 38, 373–380. https://doi.org/10.1017/S1742758418000206.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecol. 93, 2533–2547. https://doi.org/10.1890/11-1952.1.

Costa, F., Pessoa, K.K., Liberal, C.N., Filgueiras, B.K.C., Salomão, R.P., Iannuzzi, L., 2013. What is the importance of open habitat in a predominantly closed forest area to the dung beetle (Coleoptera, Scarabaeinae) assemblage? Rev. Bras. Entomol. 57, 329–334. http://dx.doi.org/10.1590/S0085-56262013000300012.

Crawley, M.J., 2012. The R Book. second ed. Wiley, London, UK.

Culot, L., Bovy, E., Vaz-de-Mello, F.Z., Guevara, R., Galetti, M., 2013. Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biol. Conserv. 163, 79–89. https://doi.org/10.1016/j.biocon.2013.04.004.

Davis, A.L., Scholtz, C.H., Kryger, U., Deschodt, C.M., Strumpher, W.P., 2010. Dung beetle assemblage structure in Tswalu Kalahari Reserve: responses to a mosaic of landscape types, vegetation communities, and dung types. Environ. Entomol., 39, 811–820. https://doi.org/10.1603/EN09256.

Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P., Stork, N., 1998. Beetle species responses to tropical forest fragmentation. Ecol. Monogr. 68, 295–323. https://10.1890/0012-9615(1998)068[0295: BSRTTF]2.0.CO;2.

Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31, 17–30. https://doi.org/10.1111/j.1744-7429.1999.tb00113.x.

Diggle, P.J., Ribeiro, P.J.J., 2007. Model-based Geostatistics. 230 p.

Environmental Systems Research Institute (ESRI)., 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Eklof, A., Ebenman, B., 2006.Species loss and secondary extinctions in simple and complex model communities? J. Anim. Ecol. 75, 239–246. https://doi.org/10.1111/j.1365-2656.2006.01041.x.

Escobar, F., 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. Trop. Zool. 17, 123–136. https://doi.org/10.1080/03946975.2004.10531202.

Estrada A., Coates-Estrada, R., 1991 Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. J. Trop. Ecol. 7, 459–474. https://doi.org/10.1017/S026646740000585X.

Estrada, A., Anzures, D.A., Coates-Estrada, R., 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. Am. J. Primat. 48, 253–262. https://doi.org/10.1002/(SICI)1098-2345(1999)48:4<253::AID-AJP1>3.0.CO;2-D.

Fahrig, L., 2003. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecol. Appl. 12, 346–353. https://doi.org/10.2307/3060946.

Fahrig, L., 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. J. Biogeogr. 40, 1649–1663. https://doi.org/10.1111/jbi.12130.

Ferreira, J., Lennox, G.D., Gardner, T.A., Thomson, J.R., Lees, A.C., Mac Nally, R., Aragão, L.E.O.C., Ferraz, S.F.B., Louzada, J., Moura, N.G., Oliveira, V.H.F., Pardini, R., Solar, R.C., Vieira, I.C.G., Barlow, J., 2018. Carbon-focused conservation may fail to protect the most biodiverse tropical forests. Nat. Clim. Change 8, 744–749. https://doi.org/10.1038/s41558-018-0225-7

Filgueiras, B. K., Iannuzzi, L., Leal, I.R., 2011. Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biol. Conserv. 144, 362–369. https://doi.org/10.1016/j.biocon.2010.09.013.

Filgueiras, B.K., Tabarelli, M., Leal, I.R., Vaz-de-Mello, F.Z., Iannuzzi, L., 2015. Dung beetle persistence in human-modified landscapes: Combining indicator species with anthropogenic land use and fragmentation-related effects. Ecol. Indic. 55, 65–73. https://doi.org/10.1016/j.ecolind.2015.02.032.

Filgueiras B.K.C, Tabarelli, M., Leal, I.R., Vaz-de-Mello, F., Peres, C.A., Iannuzzi, L., 2016. Spatial replacement of dung beetles in edge-affected habitats: biotic homogenization or divergence in fragmented tropical forest landscapes? Divers. Distrib. 22, 400–409. https://doi.org/10.1111/ddi.12410.

França, F., Barlow, J., Araújo, B., Louzada, J., 2016a. Does selective logging stress tropical forest invertebrates? Using fat stores to examine sublethal responses in dung beetles. Ecol. Evol. 6, 8526–8533. http://dx.doi.org/10.1002/ece3.2488.

França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J.M., Barlow, J., 2016b. Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. J. Appl. Ecol. 53, 1098–1105. http://dx.doi. org/10.1111/1365-2664.12657.

França, F.M., Frazão, F.S., Korasaki, V., Louzada, J., Barlow, J., 2017. Identifying thresholds of logging intensity on dung beetle communities to improve the sustainable management of Amazonian tropical forests. Biol. Conserv. 216, 115–122. http://dx.doi.org/10.1016/j.biocon.2017.10.014.

França, F., Louzada, J., Barlow, J., 2018. Selective logging effects on 'brown world' faecal-detritus pathway in tropical forests: A case study from Amazonia using dung beetles. Forest Ecol. Manag. 410, 136–143.https://doi.org/10.1016/j.foreco.2017.12.027.

Fox, J., Weisberg, S. 2011. An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Gardner, T.A., Hernández, M.I.M., Barlow, J., Peres, C.A., 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. J. Appl. Ecol. 45, 883–893. http://dx.doi.org/10.1111/j.1365-2664.2008.01454.x.

Gardner, T.A., Barlow, J., Chazdon, R.L., Ewers, R., Harvey, C.A., Peres, C.A., Sodhi, N., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x.

Gardner, T.A., Barlow, J., Sodhi, N.S., Peres, C.A., 2010. A multi-region assessment of tropical forest biodiversity in a human-modified world. Biol. Conserv. 143, 2293–2300. https://doi.org/10.1016/j.biocon.2010.05.017.

Gittings, T., Giller, P.S., 1998. Resource quality and the colonization and sucession of coprophagous dung beetles. Ecography 21, 581–592. https://doi.org/10.1111/j.1600-0587.1998.tb00550.x.

Gordon, R.D., Cartwright, O.L., 1974. Survey of food preferences of some North American Canthonini (Coleoptera: Scarabaeidae). Entomol. News 85, 181–185.

Gregory, N., Gómez, A., Oliveira, T.M.F. de S., Nichols, E., 2015. Big dung beetles dig deeper: trait-based consequences for faecal parasite transmission. Int. J. Parasitol. 45, 101–105. http://dx.doi.org/10.1016/j.ijpara.2014.10.006.r.

Griffiths, H.M., Louzada, J., Bardgett, R.D., Beiroz, W., França, F., Tregidgo, D., Barlow, J., 2015. Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. Ecol. 96, 1607–1619. http://dx.doi.org/10.1890/14-1211.1.

Griffiths, H.M., Louzada, J., Bardgett, R.D., Barlow, J., 2016. Assessing the importance of intraspecific variability in dung beetle functional traits. PLoS One 11, e0145598. http://dx.doi.org/10.1371/journal.pone.0145598.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O. Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052. http://dx.doi.org/10.1126/sciadv.1500052.

Halffter, G., Matthews, E. G., 1966. The natural history of dung beetles of the subfamily Scarabaeinae. Fol. Entom. Mex. 12–14: 1Đ312.

Halffter, G., Edmonds, W.D., 1982. The nesting behaviour of dung beetles (Scarabaeinae): an ecological and evolutive approach. Instituto de Ecologia, Mexico City, Mexico.

Halffter, G., Favilla, M., Halffter, V., 1992. A comparative study of the structure of the scarab guild in MexicanTropical rain forests and derived ecosystems. Fol. Entom. Mex. 84, 131–156.

Halffter, G., Arellano, L., 2002. Response of dung beetle diversity to human–induced changes in a tropical landscape. Biotropica 34, 144–154. https://doi.org/10.1111/j.1744-7429.2002.tb00250.x.

Hanski, I., Cambefort, Y., 1991. Dung beetle ecology. I.Hanski and Y. Cambefort, editors. Princeton UniversityPress, Princeton, New Jersey, USA.

Hosaka T., Ninno, M., Kon, M., Ochi, T., Yamada, T, Fletcher, C., Okuda, T., 2014. Effects of logging road networks on the ecological functions of dung beetles in peninsular Malaysia. Forest Ecol. Manag. 326, 18–24. https://doi.org/10.1016/j.foreco.2014.04.004.

Instituto Brasileiro de Geografia e Estatística (IBGE)., 2006. Censo Agropecuário: Brasil, Grandes Regiões e Unidades da Federação, pp. 775.

Jong, D.G.D, Chadwick, J.W., 1999. Decomposition and arthropod succession on exposed rabbit carrion during summer at high altitudes in Colorado, USA. J. Med. Entomol. 36, 833–845. https://doi.org/10.1093/jmedent/36.6.833.

Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S., 2004. Species coextinctions and the biodiversity crisis? Science 305, 1632–1634. https://doi.org/10.1126/science.1101101.

Krell, F.T., Krell-Westerwalbesloh, S., Weiß, I., Eggleton, P., Linsenmair, K.E., 2003. Spatial separation of Afrotropical dung beetle guilds: a trade-of between competitive superiority and energetic constraints (Coleoptera: Scarabaeidae). Ecography 26, 210–222. https://doi.org/10.1034/j.1600-0587.2003.03278.x.

Laliberté, E., Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecol. 91, 299–305. https://doi.org/10.1890/08-2244.1.

Laliberté, E., Shipley, B., Laliberté, M.E. 2012. FD *package*. http://cran.r-project.org/web/packages/FD/.

Larsen, T., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning? Ecol. Lett. 8, 538–547. https://doi.org/10.1111/j.1461-0248.2005.00749.x.

Larsen, T.H., Lopera, A., Forsyth, A., Génier, F., 2009. From coprophagy to predation: a dung beetle that kills millipedes. Biol. Lett. 5, 152–155. https://doi.org/10.1098/rsbl.2008.0654.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P., Lovejoy, T.E., Condit, R., Chave, J., Harms, K.E., D'Angelo, S., 2006. Rapid decay of tree-community composition in Amazonian forest fragments. PNAS 103, 19010–19014. https://doi.org/10.1073/pnas.0609048103.

Lawson, C.R., Mann D.J., Lewis, O.T., 2012. Dung Beetles Reduce Clustering of Tropical Tree Seedling. Biotropica 44, 271–275. https://doi.org/10.1111/j.1744-7429.2012.00871.x.

Leite, C. M.P., Mariano-Neto, E., Rocha, P.L., 2018. Biodiversity thresholds in invertebrate communities: The responses of dung beetle subgroups to forest loss. PLoS One 13, e0201368. https://doi.org/10.1371/journal.pone.0201368.

Mac Nally, R., 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’ models. Biodivers. Conserv. 9, 655–671. https://doi.org/10.1023/A:1008985925162.

Mac Nally, R., 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodivers. Conserv. 11, 1397–1401. http://dx.doi.org/10.1023/A:1016250716679.

Marcon, E., Hérault, B. 2015., Entropart *package*. https://doi.org/10.18637/jss.v067.i08.

Martello, F., Andriolli, F., Souza, T.B., Dodonov, P., Ribeiro, M.C., 2016. Edge and land use effects on dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in Brazilian cerrado vegetation. J. Insect Conserv. 20, 957–970. https://doi.org/10.1007/s10841-016-9928-0.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Tree 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002.

Menéndez, R., Webb, P., Orwin, K.H., 2016. Complementarity of dung beetle species with different functional behaviours influence dung e soil carbon cycling. Soil Biol. Biochem. 92, 142–148. https://doi.org/10.1016/j.soilbio.2015.10.004.

Mohamed, A., Mashaly, A., 2017. Carrion beetles succession in three different habitats in Riyadh, Saudi Arabia. Saudi J. Biol. Sci. 24, 430–435. https://doi.org/10.1016/j.sjbs.2016.02.015.

Morante-Filho, J.C., Arroyo-Rodríguez, V., Lohbeck, M., Tscharntke, T., Faria, D., 2016. Tropical forest loss and its multitrophic effects on insect herbivory. Ecol. 97, 3315–3325. https://doi.org/10.1002/ecy.1592.

Morante-Filho, J.C., Arroyo-Rodríguez, V., de Andrade, E.R., Santos, B.A., Cazetta, E., Faria, D., 2017. Compensatory dynamics maintain bird phylogenetic diversity in fragmented tropical landscapes. J. App. Ecol. 55, 256–266. https://doi.org/10.1111/1365-2664.12962.

Murray, K., Conner, M.M., 2009. Methods to quantify variable importance: implications for the analysis of noisy ecological data. Ecol. 90, 348–355. https://doi.org/10.1890/07-1929.1.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Naeem, S., Wright, J.P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecol. Lett. 6, 567–579. https://doi.org/10.1046/j.1461-0248.2003.00471.x.

Navarrete, D., Halffter, G., 2008. 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. Biodivers. Conserv. 17, 2869–2898. https://doi.org/10.1007/s10531-008-9402-8.

Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M., Network, T.S.R., 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biol. Conserv. 137, 1–19. https://doi.org/10.1016/j.biocon.2007.01.023.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E., Network, T.S.R., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biol. Conserv. 141, 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011.

Nichols, E., Gardner, T.A., Peres, C.A., Spector, S., Network, T.S.R., 2009. Co-declining mammals and dung beetles: an impending ecological cascade. Oikos 118, 481–487. https://doi.org/10.1111/j.1600-0706.2009.17268.x.

Nichols, E., Uriarte, M., Peres, C.A., Louzada, J., Braga, R.F., Schiffler, G., Endo, W., Spector, S.H., 2013. Human-induced trophic cascades along the fecal detritus pathway. PLoS One 8, e75819. doi:10.1371/journal.pone.0075819.

Osberg, D.C., Doube, B.M., Hanrahan, S.A., 1993. Habitat specificity in African dung beetles: the effect of soil type on dung burial by two species of ball-rolling dung beetles (Coleoptera Scarabaeidae). Trop. Zool. 6, 243–251. https://doi.org/10.1080/03946975.1993.10539225.

Pardini, R., Faria, D., Accacio, G.M., Laps, R.R., Mariano-Neto, E., Paciencia, M.L.B., Dixo, M., Baumgarten, J., 2009. The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. Biol. Conserv. 142, 1178–1190. https://doi.org/10.1016/j.biocon.2009.02.010.

Pardini, R., Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscape. PLoS One 5: 1–10. https://doi.org/10.1371/journal.pone.0013666.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.

Pimm, S.L., Raven, P., 2000. Extinction by numbers. Nature 403, 843–845. https://doi.org/10.1038/35002708.

Peck, S.B., Forsyth, A., 1982. Composition, structure, and competitive behavior in a guild of Ecuadorian rain forest dung beetles (Coleptera; Scarabaeidae). Cann. J. Zool. 60, 1624-1634. https://doi.org/10.1139/z82-213.

Peck, S.B., Howden, H.F., 1984. Response of a dung beetle guild to different sizes of dung bait in a Panamanian rainforest. Biotropica 16, 235–238.

Peyras, M., Vespa, N.I., Bellocq, M.I., Zurita, G.A., 2013. Quantifying edge efects: the role of habitat contrast and species specialization. J. Insect Conserv. 17, 807–820. https://doi.org/10.1007/s10841-013-9563-y.

Raine, E.H., Mikich, S.B, Lewis, O.T., Riordan, P., Vaz-de-Mello, F.Z., Slade, E.M., 2018. Extinctions of interactions: quantifying a dung beetle–mammal network Echosphere 9, e02491. https://doi.org/10.1002/ecs2.2491.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput, Vienna, Austria.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining Forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021.

Rocha-Santos, L., Pessoa, M.S., Cassano, C.R., Talora, D.C., Orihuela, R.L.L., Mariano-Neto, E., Morante-Filho, J.C., Faria, D., Cazetta, E., 2016. The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure. Biol. Conserv. 196, 1–9. https://doi.org/10.1016/j.biocon.2016.01.028.

Salomão, R.P., Iannuzzi, L., 2017. How do regeneration stages of caatinga forests influence the structure of dung beetle (Coleoptera: Scarabaeidae) assemblage? Coleopterists Bull. 71, 578–588. https://doi.org/10.1649/0010-065X-71.3.578.

Salomão, R.P., González-Tokman, D., Dátillo, W., López-Acosta, C., Favila, M.E., 2018. Landscape structure and composition define the body condition of dung beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rainforest. Ecol. Indic. 88, 144–151. https://doi.org/10.1016/j.ecolind.2018.01.033.

Sánchez-de-Jesús, H., Arroyo-Rodríguez, V., Andresen, E., Escobar, F., 2015. Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. Landsc. Ecol. 31, 843–854. https://doi.org/10.1007/s10980-015-0293-2.

Santos-Heredia, C., Andresen, E., Del-Val, E., Zarate, D.A., Mendoza, M.N., Jaramillo, V.J., 2016. The activity of dung beetles increases foliar nutrient concentration in tropical seedlings. Biotropica 48, 565–567. https://doi.org/10.1111/btp.12364.

Scheffler P.Y., 2005. Dung beetle (Coleoptera: Scarabaeinae) diversity and community structure across three disturbance regimes in eastern Amazonia. J. Trop. Ecol. 21, 9–19. https://doi.org/10.1017/S0266467404001683.

Scholtz, A.D.L., Davis, A.L., Kryger, U., 2009. Evolutionary biology and conservation of dung beetles. Pensoft Publishers, Sofia.

Silva, J.M.C., Tabarelli, M., 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404, 72–73. https://doi.org/10.1038/35003563.

Silva, P.G., Hernández, M.I.M., 2015. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. PLoS One 10, e0126112. http://dx.doi.org/10.1371/journal.pone.0126112.

Silva, P.G., Hernández, M.I.M., 2016. Spatial variation of dung beetle assemblages associated with forest structure in remnants of southern Brazilian Atlantic Forest. Rev. Bras. Entomol. 60, 73–81. http://dx.doi.org/10.1016/j.rbe.2015.11.001.

Sowing, P., 1995. Habitat selection and offspring survival rate in three paracoprid dung beetles: The influence of soil type and soil moisture. Ecography 18, 147–154. https://doi.org/10.1111/j.1600-0587.1995.tb00335.x.

Spector, S., Ayzama, S., 2003. Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian Neotropical forest-savanna ecotone. Biotropica 35, 394–404. https://doi.org/10.1646/02102.

Steinfeld, H., Gerber, P., Wassenaar, T., Castel, V., Rosales, M., Haan, C., 2006. Livestock's long shadow: environmental issues and options, food and agriculture organization of the United Nations: Rome, p. 414.

Tabarelli, M., Aguiar, A.V., Ribeiro, M.C., Metzger, J.P., Peres, C.A., 2010. Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human modified landscapes. Biol. Conserv. 143, 2328–2340. https://doi.org/10.1016/j.biocon.2010.02.005.

Tscharntke, T., Tylianakis, M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Frund, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Linden-Mayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies C, Van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x.

Thomas, W.W., Carvalho, A.M.V., Amorim, A.M., Garrison, J., Arbeláz A.L., 1998. Plant endemism in two forests in southern Bahia, Brazil. Biodivers. Conserv. 7, 311–322. https://doi.org/10.1023/A:1008825627656.

Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. Oikos 90, 7–19. https://doi.org/10.1034/j.1600-0706.2000.900102.x.

Verdú, J.R., Galante, E., 2004. Behavioral and morphological adaptations for a low-quality resource in semi-arid environments: dung beetles (Coleoptera, Scarabaeoidea) associated with the European rabbit (*Oryctolagu cuniculus* L.). J. Nat. Hist. 38, 705–715. https://doi.org/10.1080/0022293021000041707.

Villéger, S., Mason, N.W.H., Mouillot, D.. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1.

Vierling, L.A., Vierling, K.T., Adam, P., Hudak, A.T., 2013. Using satellite and airborne LiDAR to model woodpecker habitat occupancy at the landscape scale. PLoS One 8, e80988. https://doi.org/10.1371/journal.pone.0080988.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer: New York.

Walsh, C., Nally, R.M., 2013. Hier.part *package*. https://cran.r-project.org/web/packages/hier.part/hier.part.pdf.

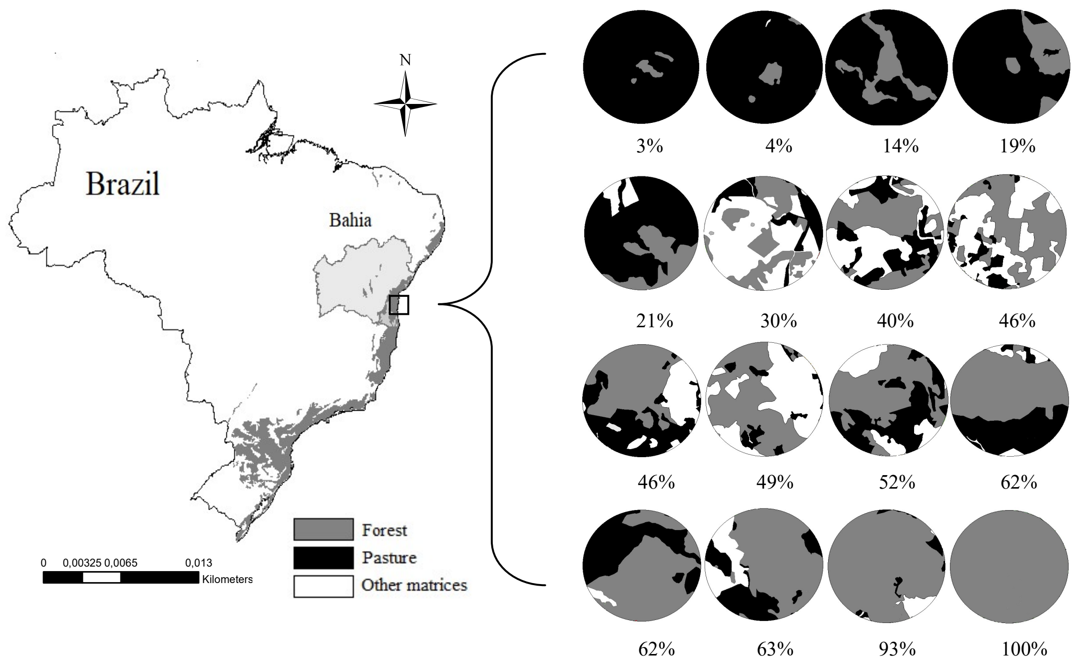

Figure 1. Map of the study area showing the spatial distribution of native forest fragments (gray color) and pasture in the matrix (black color) within the 16 landscapes where the plots were installed in Atlantic Forest in southern Bahia, Brazil. In detail, each landscape is followed by the respective forest cover percentage in a 1 km radius.

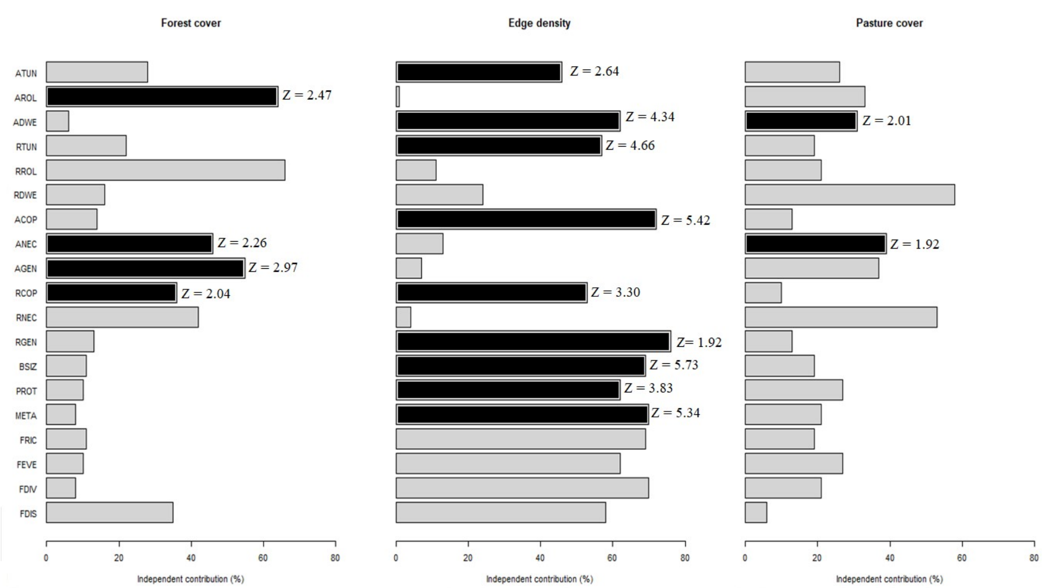

Figure 2. Gray bars represents independent contribution of each explanatory variable (relative importance) on dung beetle traits in Atlantic Forest – Bahia, Brazil. Black bars represents significant effects (α=0.05) as determined by the randomization test. Z-scores for the generated distribution of randomized and statistical significance is based on the upper 0.95 confident limit (Z ≥1.65). Legend: ABTUN-abundance tunnelers, ABROL-abundance rollers; ABDWE-abundance dwellers; RTUN-richness tunnelers; RROL-richness rollers; RDWE-richness dwellers; ABCOP-abundance coprophagous; ABNEC-abundance necrophagous; ABGEN-abundance generalists; RCOP-richness coprophagous; RNEC-richness necrophagous; RGEN-richness generalists; BSIZ-body size; PROT-protibia area; META-metatibia lenght; FRIC – functional richness; FEVE – functional evenness; FDIV – functional divergence; FDIS – functional dispersion.

Table 1.
AICc-based model selection for (i) resource-relocation behavior, (ii) diet preference, and (iii) morphological traits and (iv) functional diversity. Multimodel inference based on a model with all explanatory candidate variables followed by model selection (FC: forest cover, ED: edge density, PC: pasture cover in the matrix). We show results of all models within ΔAICc <4.

Dung beetle response metrics	Model ranks	Model	AICc	ΔAICc	ω	Cumulative ω
Resource-relocation behavior						
Tunnelers abundance	1	PC	43.11	0.00	0.46	0.46
	2	ED	45.00	1.89	0.18	0.64
Rollers abundance	1	ED + PC	44.68	0.00	0.49	0.49
	2	FC	46.30	1.62	0.22	0.71
Dwellers abundance	1	ED	39.03	0.00	0.87	0.87
	2	PC	42.81	3.78	0.13	1.00
Tunnelers richness	1	ED	34.21	0.00	0.72	0.72
	2	PC	36.06	1.85	0.28	1.00
Rollers richness	1	Null	49.30	0.00	0.40	0.40
Dwellers richness	1	Null	49.14	0.00	0.29	0.29
Diet preference						
Coprophagous abundance	1	ED	37.31	0.00	0.68	0.68
	2	PC	40.78	3.46	0.12	0.80
Necrophagous abundance	1	FC	45.09	0.00	0.40	0.40
Generalists abundance	1	FC	42.64	0.00	0.61	0.61
Coprophagous richness	1	ED	40.37	0.00	0.64	0.64
	2	FC	43.60	3.23	0.13	0.77
Necrophagous richness	1	PC	45.64	0.00	0.46	0.46
Generalists richness	1	Null	48.85	0.00	0.33	0.33
Morphological traits						
Body size	1	ED	32.43	0.00	0.32	0.32
	2	ED + PC	32.64	0.21	0.29	0.61
Protibia area	1	ED	38.14	0.00	0.42	0.42
	2	ED + FC	38.63	0.49	0.33	0.75
	3	ED + PC	41.76	3.63	0.07	0.82
Metatibia length	1	ED	38.14	0.00	0.32	0.32
Functional diversity indices						
FRIC - richness	1	Null	49.30	0.00	0.39	0.39
FEVE - evenness	1	Null	49.30	0.00	0.52	0.52
FDIS - dispersion	1	Null	49.30	0.00	0.54	0.54
FDIV - divergence	1	Null	49.30	0.00	0.37	0.37

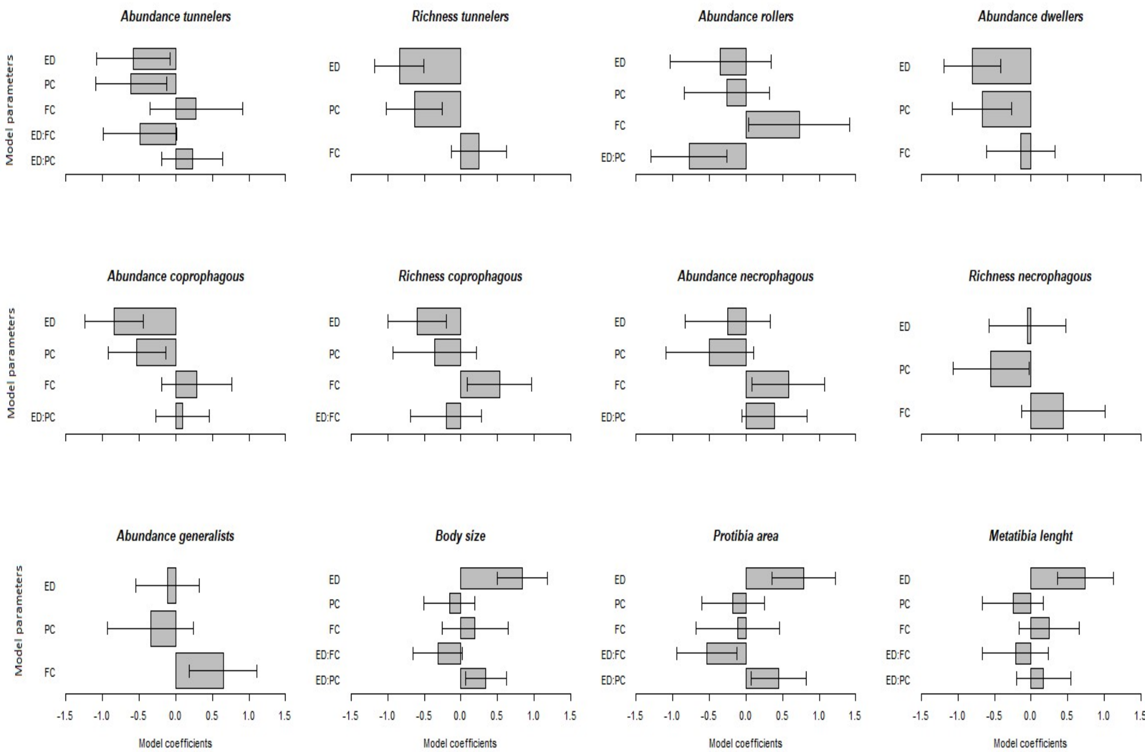

Figure 3. Model averaging of candidate models within ΔAICc < 4 for resource relocation behavior (tunnelers, rollers and dwellers), diet preference (coprophagous, necrophagous, generalists) and morphological traits (body size, protibia area, metatibia length) on effects of ED - edge density, PC - pasture cover, FC - forest cover, ED + FC - interaction edge density and forest cover, ED + PC - interaction edge density and pasture cover.

Supplementary material

Table S1. List of dung beetle species, as well as resource-relocation behavior, diet preference and total abundance, sampled in landscapes in the Atlantic forest, northeastern Brazil.

Species	Relocation behavior	Diet preference	Abundance
Anomiopus sp.1	Tunneler	Undefined	1
Anomiopus sp.2	Tunneler	Undefined	1
Aphengium curtum Silva & Vaz-de-Mello 2015	Tunneler	Generalist	8
Ateuchus oblongum (Harold, 1883)	Tunneler	Generalist	205
Ateuchus vigilans (Van Lansberge, 1874)	Tunneler	Coprophagous	19
Ateuchus volxemi(Borre, 1886)	Tunneler	Undefined	3
*Canthidium flavipes*Harold, 1867	Tunneler	Generalist	78
Canthidium sp.1	Tunneler	Generalist	14
Canthidium sp.2	Tunneler	Undefined	1
Canthidium sp.3	Tunneler	Coprophagous	98
Canthidium sp.4	Tunneler	Coprophagous	101
Canthidium sp.5	Tunneler	Coprophagous	56
Canthidium sp.6	Tunneler	Coprophagous	10
Canthidium sp.7	Tunneler	Undefined	2
Canthidium sp.8	Tunneler	Undefined	1
Canthidium sp.9	Tunneler	Undefined	1
Canthon nigripennis Van Lansberge, 1874	Roller	Necrophagous	10
*Canthon prasinus*Klug, 1833	Roller	Necrophagous	9
Canthon sp.1	Roller	Undefined	2
Canthon staigi (Pereira, 1953)	Roller	Necrophagous	38
Canthonella silphoides Harold, 1867	Roller	Generalist	1470
Coprophanaeus bellicosus (Olivier, 1789)	Tunneler	Necrophagous	43
Coprophanaeus dardanus (MacLeay, 1819)	Tunneler	Necrophagous	147
Deltochilum brasiliense (Castelnau, 1840)	Roller	Necrophagous	16
Deltochilum próx. *Calcaratum* Bates, 1870	Roller	Necrophagous	40
Deltochilum sp.1	Roller	Undefined	1
Dichotomius depressicollis (Harold, 1867)	Tunneler	Undefined	1
Dichotomius iannuzziae Valois, Vaz-de-Mello & Silva 2017	Tunneler	Generalist	914
Dichotomius irrinus (Harold, 1867)	Tunneler	Generalist	303
Dichotomius mormon Ljungh, 1799	Tunneler	Undefined	2
Eurysternus nanus Génier, 2009	Dweller	Generalist	10
Eutrichillum hirsutum (Boucomont, 1928)	Dweller	Necrophagous	24
Holocephalus sculptus (Gillet, 1907)	Tunneler	Undefined	3
Onthophagus haematopus Harold, 1875	Tunneler	Coprophagous	300
Paracanthon sp.1	Roller	Undefined	2
Phanaeus splendidulus (Fabricius, 1781)	Tunneler	Undefined	5
Uroxys sp.1	Tunneler	Undefined	5

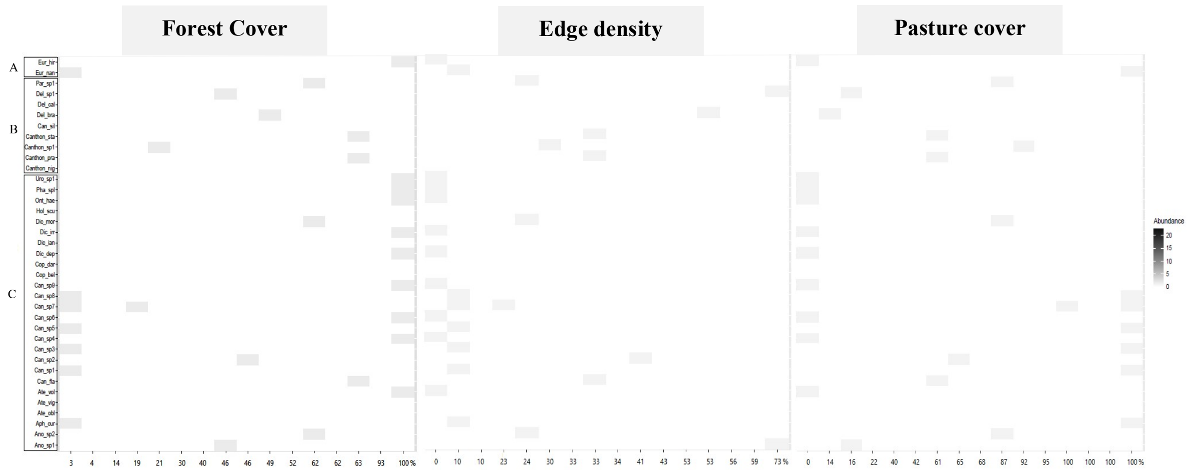

Figure S1. Heatmap of abundance normalized of dung beetle species in the 16 landscapes based on forest cover, edge density and pasture cover in the Atlantic Forest - Bahia, Brazil. A - dwellers, B - rollers, C - tunnelers.

Capítulo III

Dung beetles as indicators of human-modified habitats in the tropical forests: a review

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Dung beetles as indicators of human-modified habitats in the tropical forests: a review

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ABSTRACT

The selection of response variables of communities encompasses a crucial step to assess the effects of human-modified habitat on biodiversity. Nevertheless, little attention has been given to the process of variable selection, and the evaluation of trustworthy patterns on studies using inappropriate response variables. Here, we summarize the current knowledge about response variables of dung beetle on studies conducted in tropical forests. Specifically, we outline research history from a comprehensive literature review, examined response variables, and compared their contribution to studies on habitat changes and its effects on biodiversity. Moreover, we highlighted main results and gave suggestions in order to improve the quality of data for further researches. We recorded 194 studies from 1975 to 2018, developed in tropical forest of 31 different countries, with researchers mostly concentrated in Brazil, United Kingdom and Mexico. Our results highlight that the response variables that were mostly used to assess habitat changes were "abundance", followed by "species richness/diversity" and "body mass/size". On the other hand, "movement" and "genetic parameters" were the least used response variables. We suggest more attention during the process of obtaining and choosing of the best method for data treatment. The inappropriate use of response variables can generate bias towards the data analysis, undermining our confidence in the results of ecological studies with dung beetles.

Keywords: conservation, deforestation, habitat changes, insects, land use, Scarabaeinae.

1. Introduction

Natural ecosystems have been modified over centuries, leading to a cascade of species extinctions (Larsen et al., 2005; Wright, 2010), and habitat loss is classified as the most pervasive threats to biodiversity worldwide (Pimm and Raven, 2000; Cardinale et al., 2012). Thereby, in order to maximize and qualify studies (e.g. time, money, taxonomic reliability) of impacts in natural ecosystems, researchers led to discuss on the use of bioindicators (McGeoch, 1998). The development of bioindicators in terrestrial ecosystems gained strength from the 1980s (McGeoch, 1998) and since then, several criteria have been proposed for selection of appropriate bioindicators to terrestrial systems (Brown, 1991; McGeoch et al., 2002; Rainio and Niemelä, 2003).

Dung beetles of the subfamily Scarabaeinae (taxonomy follows Hanski and Cambefort, 1991) have been proposed as effective indicators of environmental change in tropical forest (Halffter and Favila, 1993; Spector, 2006; Gardner et al., 2008). Some characteristics of this group can be listed as favorable to use dung beetles as indicators: their sensibility to habitat alteration (Larsen et al., 2005; Nichols et al., 2007); well-understood ecological roles (Hanski and Cambefort, 1991); relatively stable taxonomy (Philips et al., 2004; Vaz-de-Mello et al., 2011); and can be sampled more cost-effectively than many other taxa (Larsen and Forsyth, 2005; Gardner et al., 2008). Furthermore, dung beetles are abundant in tropical forest (Nummelin and Hanski, 1989; Gill, 1991; Davis et al., 2001), favoring studies in such ecosystems.

Dung beetles provide several ecosystem functions, such as secondary seed dispersal, nutrient recycling, soil aeration and parasites control (Nichols et al., 2008). Previous studies with dung beetles have empirically proven the negative effects of human-modified habitat on dung beetle communities in tropical forests (e.g. Nichols et al., 2007; Sánchez-de-Jesús et al., 2016; Salomão et al., 2018a), impoverishing beetle diversity in more disturbed environments. The decrease on their abundance and diversity may result in cascading effects on ecosystem functioning, with important implications for forest regeneration and conservation (Andresen and Feer, 2005; Nichols et al., 2008; Lawson et al., 2012).

The selection of response variables encompasses a crucial step to assess the effects of habitat changes on biodiversity (Guisan and Zimmermann, 2000; Vaughan and Ormerod, 2003; Mac Nally, 2005). Ecological studies have directed little attention in the variable selection processes, and studies with focus on inappropriate response variables may fail to find trustworthy patterns (SU et al., 2004; Barlow et al., 2007). This alert already has been observed in dung beetles, with disparities between researcher's opinion and their choice of variables in published studies (Oliveira et al., 2017). With the persistence of such practices, a biased understanding on effects of human-modified habitat on biodiversity may reflect on doubtful results (Oliveira et al., 2017). Therefore, the use of inappropriate response variables may lead to a misconception on the interpretation of ecological patterns.

To better understand what dung beetle response variables are used in studies of habitat changes and in order to improve the quality of data, we summarize our current knowledge about response variables of dung beetles in tropical forests. With such results we can provide the outset of discussion on the importance of choice and improvement of response variables used. First, we outline research history of dung beetles as indicators of human-modified habitat in the tropical forests, evidencing timeline, main scientific journals and sites where researchers and fieldworks are mostly concentrated. Second, we explored the methods used to evaluate response variables and the percentage of contribution to analyses of different explanatory variable (e.g. fragment size, edge effects). Third, we highlight important research findings, included recommendations for obtainment of the variables and point out gaps for future researches.

2. Methods

We carried out a literature search on Web of Knowledge (accessed on August 2018) using the following search terms: [*dung beetle* OR *scarab* OR *scarab beetle* OR *scarabaeinae* OR *coprophagous beetles*] AND [*primary forest* OR *mature forest* OR *intact forest* OR *old growth forest* OR *virgin forest* OR *pristine forest*] AND [*fragmentation* OR *degradation* OR *forest loss* OR *deforestation OR habitat loss* OR *human* OR *modification* OR *land use* OR *logging* OR *stress* OR *matrix composition* OR *road* OR *human impacts* OR *fire* OR *edge]*. We used the method of qualitative and quantitative literature review based on individual studies to summarize response variables on dung beetles to habitat changes in tropical forests (Nichols et al., 2007; 2008).

The search allowed us to gather a total of 790 studies. Each study was carefully revised for the identification and categorization of the response variables presented. We limited results to studies that were published in scientific journals, tropical forests, encompassing dung beetles of Scarabaeidae: Scarabaeinae, in English language and disregarded studies of reviews or that did not use comparison with a conserved forest in the same system. The main focus of this review was the Scarabaeinae beetles, since they are the most representative family of dung beetles in the tropics (Schoolmeesters, 2018).

Aiming to build the database, we first outlined research history in tropical forests: year of publication; journal of publication; country of researchers and country of fieldwork. Response variables were grouped in a way that there were different categories:

abundance; richness/diversity; body mass/size; resource relocation behavior; diel activity, ecological functions, food preference, functional diversity, wing loading/area, physiological condition, body shape, movement and genetic parameters. To understand the contribution of different explanatory variables to ecological analyses, such variables were selected based Oliveira et al. (2007) and grouped in different categories related to direct and indirect effects of human-modified habitat. The following explanatory variables were used: edge density, forest structure and composition, fragment size, landscape connectivity, mammal diversity and biomass, and matrix composition. In addition, for each type of response variables we explored methods of preparing data for analyses (e.g. absolute value, estimators), main results - patterns and exceptions - on effects human-modified habitat, beyond suggestions for improvements and further studies. Finally, to better interpret our results we constructed maps with the distribution of ecological studies encompassing dung beetle in tropical forests using ArcGIS10.2 software (ESRI, 2011).

3. Overview

We recorded 194 studies from 1975 to 2018 that used dung beetles as indicators to understand the effects of habitat changes in tropical forests. Researchers from 47 countries were recorded, and the largest number of publications was associated with researchers from Brazil (n=67, and on 56 of them Brazilians were the first authors), United Kingdom (n=51, and on 25 of them British were first authors) and Mexico (n=47, and on of 31 of them Mexicans were first authors) (Fig. 1). In addition, fieldworks were conducted in 31 distinct countries, with the highest number of studies in tropical forests from Brazil (n=75), Mexico (n=31), Malaysia (n=20) and South Africa (n=15) (Fig. 1).

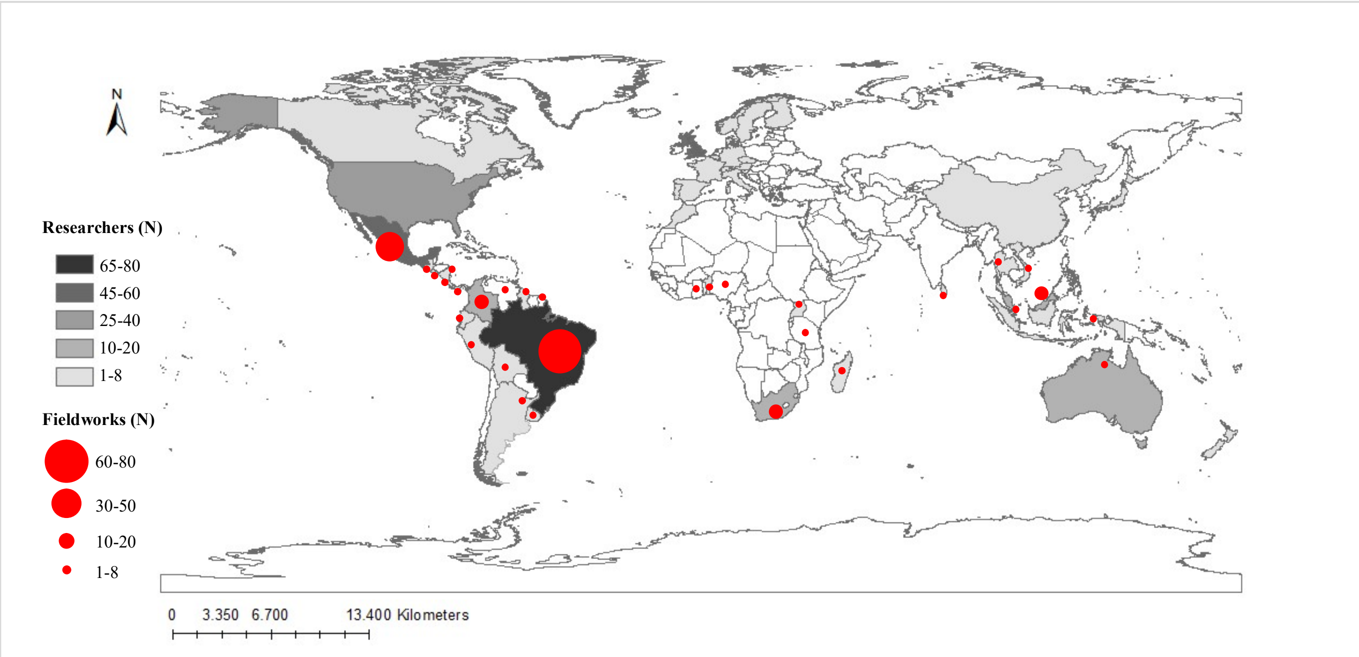

Fig.1. Map showing the spatial distribution of studies encompassing the effects of human-modified habitat on dung beetle communities in tropical forests from 1975 to 2018. Gradient of gray colors correspond to number of researchers by country and red circles represent the number of fieldworks developed by country.

The studies regarding effects habitat changes over dung beetle communities were recorded from 66 different scientific journals and had increase from 2005, one year after the review of Davis et al. (2004) on dung beetles as bioindicators (Fig. 2A). However, 50% of publications belonged to only eight journals: *Journal of Insect Conservation* (IF= 1.6), *Biotropica* (IF=2.3), *Biodiversity and Conservation* (IF=2.8), *Biological Conservation* (IF=4.0), *Ecological Indicators* (IF=3.4), *Plos one* (8; IF=2.8), *Environmental Entomology* (IF=1.7) and *Journal of Applied Ecology* (IF=5.2) (Fig. 2B). The response variables that were mostly used in the studies on habitat changes were “abundance” (96% of the studies), followed by “species richness/diversity” (92%) and “body mass/size” (42%). “Movement” and “genetic parameters” were the least used response variables (0.5%, only one study) (Fig. 2C). Details on the use of response variables for each type of explanatory variables can be visualized in figure 3.

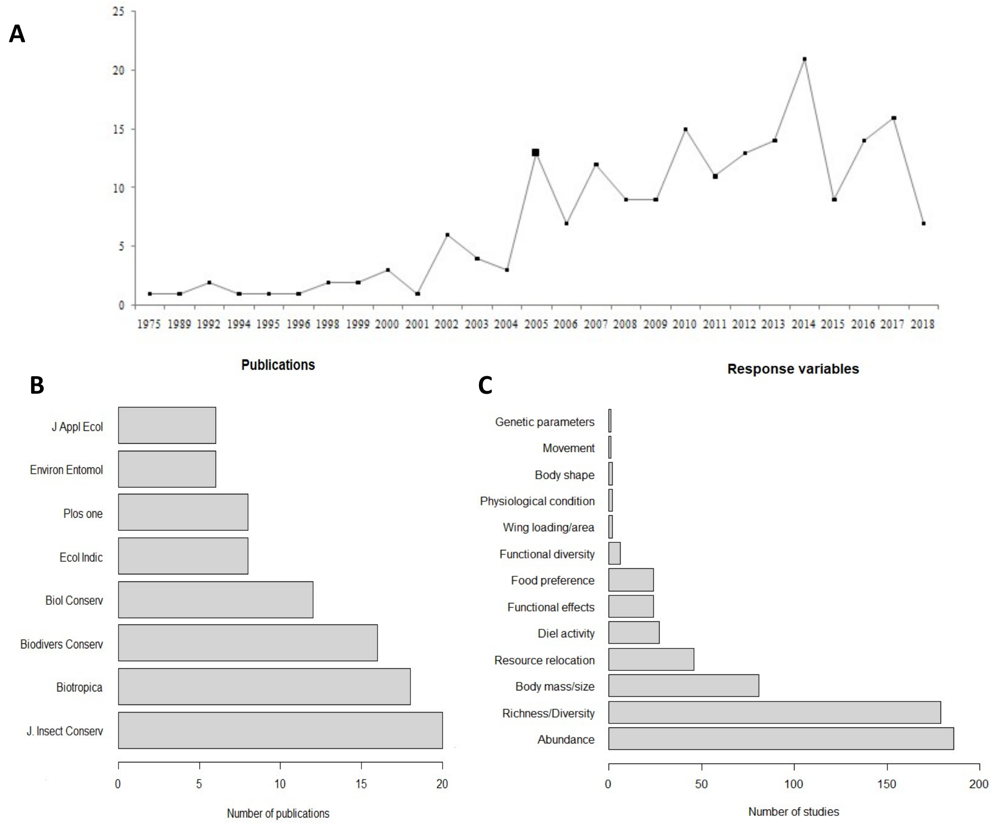

Fig.2. Number of publications using dung beetles to evaluated human-modified habitat effects in tropical forests throughout the years (A), through scientific journals (B) and number of occurrences of each response variable in the studies (C).

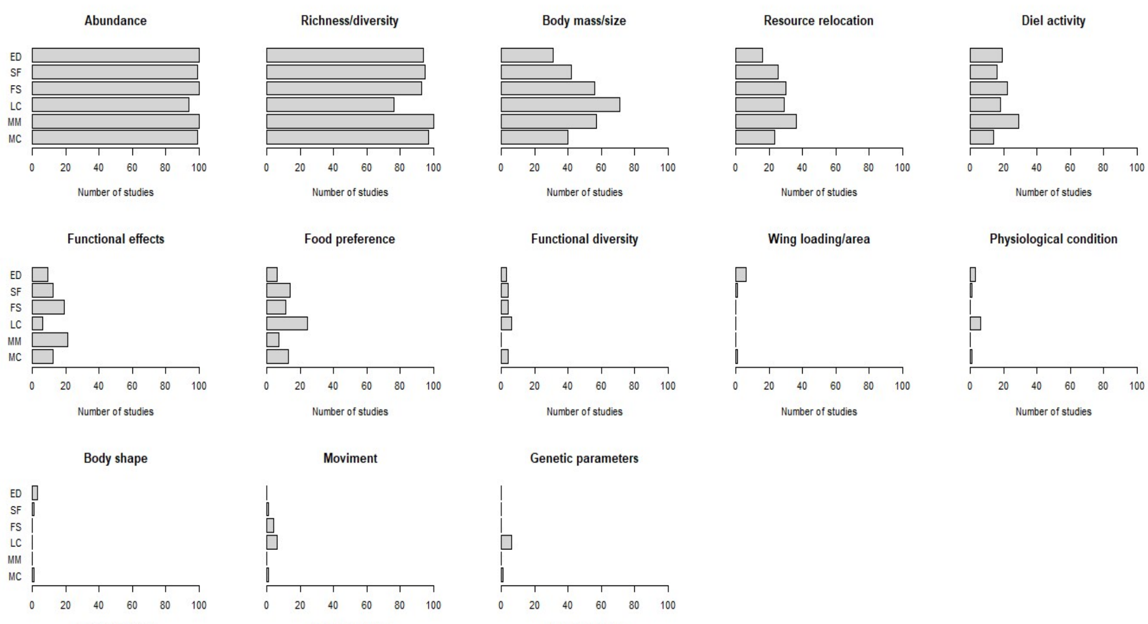

Fig. 3. Number of occurrences of each response variable by each explanatory variable type (ED – Edge density, FS – Forest structure and composition, SF – Fragment size, LC – Landscape connectivity, MM – Mammal diversity and biomass and MC – Matrix composition) with dung beetles in tropical forests.

ABUNDANCE

Overall result: We recorded a total of 186 studies evaluating abundance of dung beetles. Beetle abundance was the most used variable in studies on human-modified habitat. All studies used absolute abundances, and 16% used an approach of rank-abundance plots to identify abundance patterns of species, also known as Whittaker curves (see description of Whittaker, 1972). IndVal indices (see Dufrene and Legendre, 1997), which measures the statistical fidelity of a species to specific land-uses, based on absolute and relative abundances, were used on 11% of the studies. Beetle abundance was used on all studies that comprised edge effect, fragment size and mammal's diversity; besides of being used on most of the studies (>90%) comprising forest structure, forest composition, matrix composition, and landscape connectivity (Fig. 3).

Highlights: The decline of dung beetle abundance was observed with increase habitat loss and fragmentation (e.g. Filgueiras et al., 2015; Martelo et al., 2016; Alvarado et al., 2017). Reduction of fragment size and increase of mammalian defaunation negatively affected abundance of dung beetles, especially the forest specialists (Andresen and Laurence, 2007; Amézquita and Favila, 2011; Culot et al., 2013). On the other hand, we also found species with high abundance in degraded environments, which are matrix or even edge-specialists (Peyras et al., 2013; Filgueiras et al., 2015).

Suggestions: Dung beetle species abundance in tropical forests is thought to increase during the rainy season (Gill, 1991, but see Filgueiras et al., 2009; Iannuzzi et al., 2016), which is the reproductive period for many species (Halffter and Matthews, 1966; Andresen, 2008b). However, rainy days should be avoided for installation of traps (Estrada et al., 1999; Filgueiras et al., 2005), due to the strong decrease in the activity of such insects, what may bias the data collection. Loss of pitfall traps can occur during fieldwork (e.g. animals that remove the trap from the installation site due attractiveness of bait), however studies not report the number of traps lost and future studies are highly recommended to evaluate the importance, and bias these results. In addition, studies should be careful about influences of temporal variability on abundance of tropical dung beetles (Andresen, 2008a).

Species abundance patterns, based in the log normal distribution, are being used as an indicator of tropical forests disturbance (Hill et al., 1995b). We found species with high abundance in degraded environments, but dominance of few species (Scheffler, 2005; Nichols et al., 2007; Filgueiras et al., 2015). Nummelin (1998) reinforces attention on generalizations and argues that the fit to log normal distribution of dung beetle species abundances cannot be used as a straightforward universal. Geometric series models or the use of indicator species could be viable alternatives to the use of species abundance patterns) (Gray, 1987; Tokeshi, 1993).

Besides abundance per se, indicators of habitat specificity (e.g. IndVal) feature as important tools to suggest potential taxa that may be related to determined environmental characteristics. Furthermore, Anne Chao developed the software CLAM, which may also be successfully used as an indicator of habitat specificity on biodiversity studies (Chao and Lin, 2011; Chazdon et al., 2011). Although such indices work based on the absolute and relative abundance of the species, the results that may differ among each method. Thus, we suggest that careful comparisons may be performed to compare the responses of each indicator method.

SPECIES RICHNESS/DIVERSITY

Overall result: We recorded a total of 179 studies using species richness and diversity species of dung beetles. Species richness and diversity were the second most used variable in studies on human-modified habitat. Species richness and diversity were always used as absolute values, and 55% of studies mentioned the use estimators of richness and diversity, where 43% used Shannon-Weiner index, 32% Chao 1, 24% Jackknife 1, 19% Chao 2, 18% Simpson's index, 11% incidence-based coverage estimator ICE and 10% Bootstrap. Less than 10% of the studies used Jackknife 2, Mao Tau estimated, Fisher's alpha, Abundance-based coverage estimator ACE, Michaelis-Menten MM, Bergen-Parker and Clench method (see descriptions Colwell and Coddington, 1994; Brose, 2002; Chao, 2004; Magurran, 2004). The number of species richness estimators used per study ranged from one to nine. This variable was used in all studies comprising on mammal's diversity; in most of the studies (>90%) encompassing matrix composition, forest structure and composition, edge effect, and fragment size; and 76% of the studies comprising landscape connectivity (Fig. 3).

Highlights: Species richness and diversity tend to decrease as a result of habitat loss and fragmentation and are strongly related with landscape structure and mammalian fauna (Almeida et al., 2011; Barragán et al., 2011; Bogoni et al., 2016; Alvarado et al., 2017). Environmental conditions related to disturbed habitat (e.g. small fragments, loss of forest cover, open area habitats, edges forest and decreasing overall mammal biomass) causes a negative impact on richness and diversity of dung beetles (Andresen, 2008b; Amézquita and Favila, 2011; Culot et al., 2013; Barnes et al., 2014b; Sánchez-de-Jesús et al., 2015). It is noted that in studies on ecosystem functions provided by dung beetles tend to be more dependent of functional properties (e.g. resource relocation behavior) and combinations of species than species richness alone (Slade et al., 2007).

Suggestions: Currently, novel methods to evaluate dung beetle diversity are receiving much attention on ecological studies (Hernández et al., 2014; Silva et al., 2018a; Tonelli et al., 2018), and has the potential to be widely applied on Tropical ecosystems. For example, Hill numbers consist on a derivation of the classical diversity metrics, as Shannon and Simpson diversities (Hill, 1973; Jost, 2006). Another example is the partition of beta diversity, which may be analyzed through the components of nestedness and species turnover (Ferreira et al., 2018; Silva et al., 2018b). Such current tools are commonly used by mathematical formulas and R packages, as iNEXT, Vegan and betapart (Baselga et al., 2018; Hsieh et al., 2018; Oksanen et al., 2018), gives novel responses to classical ecological studies. Future studies encompassing dung beetle biodiversity should focus their attention on modern tools that may give new insights of the consequences of habitat changes. For example, Maturo and Batista (2018) has developed a new method that embraces diversity metrics under a wide scenario, the "biodiversity surface", which gives cues to the diversity changes over different scales.

BODY MASS/SIZE

Overall result: We recorded a total of 81 studies using body size/mass of dung beetles. This was the third variable most used in studies on human-modified habitat. Most of these studies (93%) obtained their data in field collections, and 7% of them were obtained from literature review. Body mass was used as absolute value (89%) or categorical (11%). For estimating body mass, the number of individuals weighed per species ranged from 10 (28% of studies) to all individuals (24%); others studies used between 15 and 50 individuals, however represented a low percentage. From categorical method that separated beetle body mass, all studies separated dung beetle species as small <0.1g and large >0.1g, based in Nichols et al. (2013). Notwithstanding, body size classes were also separated on different range intervals (see Halffter and Arellano, 2002; Navarrete and Halffter, 2008; Culot et al., 2013). Body size was used as absolute value (64%) or categorical (36%). The number of individuals measured per species ranged from 5 to all individuals collected, but the highest percentages were for all individuals (56%). From categorical method, beetles were grouped in blocks of small <10mm and large >10mm based in Hanski and Halffter (1991). The studies that obtained data by literature used references from Doube (1990), Davis (1996), Vulinec (2002) and Jankielsohn et al. (2001). In addition 71% of occurrence in published papers on landscape connectivity, 57% mammals diversity, 56% fragment size, 42% forest structure and composition, 40% on matrix composition and 31% edge effect (Fig. 3).

Highlights: The mean size and mass of beetles were significantly higher in continuous and primary forest sites than disturbed areas (e.g. forest fragments, pastures and forest edges) (Andresen, 2003; Spector and Ayzama, 2003; Alvarado et al., 2008). In addition, the presence of herbivorous and omnivorous mammals was an important driver that explained dung beetle body size (Bogoni, 2016), with large-bodied forest-specialist species mainly associated with mid and large-sized wild mammals (Klein, 1989; Halffter and Arellano, 2002; Sánchez-de-Jesús et al., 2016). On the other hand, dung beetle communities in pasture are characterized by the hyper-dominance of small-bodied species (Spector and Ayzama, 2003; Schelffer, 2005; Nichols et al., 2007). However, large species can also dominate in pastures (Andresen, 2008b; Díaz et al., 2010), and link between body size and extinction risk may not be universal (see Larsen et al., 2005).

Suggestions: When categorical method is chosen, it is important to also provide raw data in order to facilitate comparisons between studies, as well as to allow further analysis (e.g. meta-analysis). Body length and mass are traits correlated used to evaluate size of individuals (Lobo, 1993; Radtke and Williamson, 2005). To an accurate estimation of intraspecific variability in trait-based values, Griffiths et al. (2016) recommend measuring between 30 and 60 individuals. However, would be ideal to carry out more studies on this subject with different dung beetle communities. As proved previously, dung beetle morphometry may change according to habitat (Alves and Hernández, 2017). Therefore, we suggest to use equal number of individuals from each environment studied in future studies.

Body size is related to ecological services (Barnes et al., 2014a; Beynon et al., 2015). However, depending on the resource relocation behavior, dung beetle species may present different dynamics regarding resource utilization (Halffter and Edmonds, 1982; Scholtz et al., 2009), what may affect the ecological services that they provide. Therefore, future studies should consider the importance of each resource relocation behavior related to body size when analyzing ecosystem services of dung beetles, as resource removal rates and seed dispersal.

RESOURCE RELOCATION BEHAVIOR

Overall result: We recorded a total of 46 studies using resource relocation behavior of dung beetles. All studies used resource relocation behavior as variable categorical and beetle species were clustered as rollers (i.e. telecoprids), tunnelers (i.e. paracoprids) or dwellers (i.e. endocoprids). This classification was 67% based in literature by Halffter and Matthews (1966), Halffter and Edmonds (1982) and Hanski and Cambeffort (1991), and within these, 15% add new data based on specify behaviors (see Bornemissza, 1969; Hammond, 1976; Klemperer and Boulton, 1976). On the other hand, 33% of studies not mentioned the reference used. Resource relocation behavior was used 36% of occurrence in published papers on mammals diversity, 30% fragment size, 29% landscape connectivity, 25% forest structure and composition, 23% on matrix composition and 16% edge effect (Fig. 3).

Highlights: Studies show a decline of roller species in edge forest, pastures and environments with higher abundance of caviomorph rodents (Nichols et al., 2013; Hosaka et al., 2014; Kenyon et al., 2016). In habitats where there is a reduction of canopy cover and increase of open matrices, however, rollers exhibit a higher relative abundance when compared to tunnelers and dwellers (Navarette and Halffter, 2008; Beiroz et al., 2017; Gómez-Cifuentes et al., 2017). Tunnelers were negatively affected by reduction of percentage of canopy cover, increase of edge effect and open matrix (Audino et al., 2017;

Beiroz et al., 2017; Edwards et al., 2017). Furthermore, the presence of herbivore mammals was positively related to the diversity of tunneler species (Bogoni et al., 2016).
Suggestions: The little biological information and generalizations used on resource relocation behavior can be dangerous and exclude information of the functionality of the species. So, future studies that analyze this behavior for each species (in natural or laboratory conditions) are highly recommended. As also, studies linking a group of morphological characteristics with functionality may solve this problem (see Raine et al., 2018).

Although rollers and tunnelers response to human-modified habitats are relatively well-known, this is not the case for dweller species. This may be related to the relatively poor species richness of dwellers when compared to rollers and tunnelers. For example, in the neotropics dweller species are mostly composed by the genus *Eurysternus* Dalman (e.g. Horgan, 2008; Amézquita and Favila, 2010; Campos and Hernández, 2013). Due to the importance of dwellers for the ecosystem services provided by tropical dung beetles of America (Génier, 2009), and scarce precision on ecological response of dwellers to human-modified habitats, future studies should focus on understanding the patterns of such dung beetles.

DIEL ACTIVITY

Overall result: We recorded a total of 27 studies using diel activity of dung beetles. All studies used diel activity as variable categorical and beetles were clustered as diurnal, crepuscular (only by Boonrotpong et al., 2012; Nino et al., 2014) and nocturnal. Most of these studies obtained their data from literature (54% of studies used references based in Halffter and Matthews (1966); Doube (1990); Gill (1991), Hanski and Cambefort (1991); Halffter et al. (1992); Halffter and Favila (1993); Montes-de-Oca and Halffter (1995); Favila and Díaz (1997); Favila and Halffter (1997); Davis (1999); Hernández (2002); Vulinec (2002); Favila (2005); Krikken and Huijbregts (2007); Slade et al. (2007); Edmond and Zideck (2010); Nichols et al. (2008); Campos et al. (2011); Lopes et al. (2011); Qie et al. (2011); Slade et al. (2011); Schultze and Hernandez (2012); Nichols et al. (2013); Audino et al. (2014); Medina and Lopes (2014). Other studies used classification based from indicator value analysis (4% e.g. IndVal, Beiroz et al., 2018); or proportion based on abundances in each period (30%, e.g. Beiroz et al., 2017) and 3); and 12% not detail the method.

On most of these studies, the period from trap or bait replacement was between 11-12h (78%), and only two studies used between 3-4h (i.e. Boonrotpong et al., 2012; Nino et al., 2014). In addition, when mentioned in the methods (90%), schedules to bait installation were all at morning (6-8h) and night (18-20h). This variable was used in 36% of published papers on mammals diversity, 30% fragment size, 29% landscape connectivity, 25% forest structure and composition, 23% on matrix composition and 16% edge effect (Fig. 3).

Highlights: Diel activity was associated with body size and treated in terms of functional groups (i.e. small diurnal and large nocturnal, see Doube et al., 1990 for the classification). Large nocturnal beetles were mostly found in primary forest and large fragments, while small diurnal species were abundant in large and small fragments (Escobar, 2004; Amézquita and Favila, 2011). Nocturnal beetles were often defined as more tolerant than diurnal beetles to the forest disturbance (Vulinec, 2002; Beiroz et al., 2017), and nocturnal beetles were also more abundant than diurnal in forest edges (Halffter et al., 1992; Díaz et al., 2010). In addition, some studies shown that none of predictor variables related to habitat change (e.g. landscape connectivity and mammal abundance) were able to explain the variance of diurnal and nocturnal species (Andresen and Laurence, 2007; Audino et al., 2017).

Suggestions: Further studies are required to understand of duration of bait attractiveness on different quantity and environmental conditions (see Peck and Howden, 1984; Gittings and Giller, 1998; Verdú and Galante, 2004), since the dryness of the bait may be more accelerated during the day or open matrices and the power of attractiveness therefore reduced when compared to night or conserved forest. Also, there are cues that dial activity may change between populations of the same species (Lopes et al., 2011; Iannuzzi et al., 2016), but this has not been widely studied. Environmental conditions related to habitat disturbance could be affecting dial activity of plastic species, which could adapt to different environmental conditions, shifting their dial and seasonal activity period.

ECOLOGICAL FUNCTIONS

Overall result: We recorded a total of 24 studies using ecological functions of dung beetles. Ecological functions had been assessed by experimentations in field based on dung removal, seed burial, soil removal and carrion removal (71, 37, 12 and 8%, respectively). Most studies (68%) used cow, human or mix human:pig dung to experimentations of dung removal. However, others used dung of others vertebrates (e.g. monkey, pig, domestic dog and macropod). Results of dung removal were obtained mainly 24h after installation of experiment (76% of studies), but other time-intervals were also recorded (24%, e.g. after 30min, 48h, 72h, 18 days). There was no pattern on volume of dung used in the experiments, which ranged from 10g to 780g. A total of 65% of the researchers mentioned the use of a control experiment to avoid the confounding factor related to humidity (see Barnes et al., 2014b; Gray et al., 2014).

To assess seed burial process by dung beetles, most studies (78%) used cow or monkey dung, while others used a mix human:pig or only human dung. Similar to dung removal, there was no pattern on volume of dung used in the experiments, ranging from 10g to 780g. The number of studies using mimics (e.g. Nichols et al., 2013) and natural seeds (e.g. Andresen, 2003) was similar (n= 6 for each). Results of seed burial were obtained mainly 24h after installation of experiment (67% of studies), but also were registered 72h latter (33%). To quantify the amount of seed burial by dung beetles, the number of seed buried *vs* seed on the surface was evaluated.

Few studies have assessed soil removal process (only Braga et al., 2013; França et al., 2017; 2018), and experiments were developed in the same condition of dung removal. To quantify the amount of soil excavated by dung beetles, loose soil on the ground surface was collected with spoons or spatulas and weighed after drying at 60°C (67%) or 100°C (33%). Lastly, two studies focused on carrion removal highlighting functions associated with necrophagous beetles (i.e. Amézquita and Favila, 2011; Batilani-Filho and Hernández, 2017). Amézquita and Favila used 200g of fish carrion for 24h, while Batilani-Filho and Hernández used 50g of pig carrion for 48h. Ecological functions was used in 21% of published papers on mammal diversity, 19% fragment size, 12% on matrix composition and forest structure and composition 9% edge effect and 6% landscape connectivity (Fig. 3).

Highlights: A higher amount of ecosystem services were provided in continuous and primary forest than in small fragments and agriculture or pasture matrix (e.g. Andresen, 2003; Braga et al., 2013; Barnes et al., 2014b). Logging intensity, reduction of percentage of canopy cover and edge habitats had negatively effects on dung removal, carrion removal, soil removal and seed burial (Amézquita and Favila, 2011; Slade et al., 2011; Hosaka et al., 2014a; Batilani-Filho and Hernandez, 2017; França et al., 2017). On the other hand, some studies did not find significant differences on dung removal rates among land uses (Gray et al., 2014). However, is interesting to note that different patterns of responses can be obtained according to the scale used in the study (França et al., 2017).

Suggestions: There is no consensus about methodologies to standardize the evaluation of ecological functions of dung beetles. Nonetheless, some studies have already information about the optimum time-intervals used between experiments to evaluate ecological functions. Furthermore, future studies should focus on quantifying how sampling effort (i.e. number of traps and time interval to keep traps in the field) may affect the depletion effects on beetle communities, which could result in confounding effects over ecological functions.

Studies would be clearer on justifying the volume of dung or carrion used in the experiments. For example, if the amount was based in representative dung-pile size of several Neotropical frugivores (e.g. 10g, Andresen, 2003) or because was the smallest amount that could be used without total removal within 24h (e.g. 780g, Slade et al., 2011). Whereas, larger amounts of dung attract more species and individuals of dung beetles, and in some cases also larger beetles (Peck and Howden, 1984; Andresen, 2002a). The use of seeds mimics has the great advantage of not being removed by predators (Slade et al., 2007) and the burial rates between seeds or seed mimics was similar in a study from temperate forest (Koike et al., 2012). However, Culot et al. (2011) highlights that spherical seeds are more likely to be buried than the others shape and Andresen and Levey (2004) found differences in the process of burial according to seed size. Therefore, future studies should consider the importance of seed morphological features on seed burial process.

FOOD PREFERENCE

Overall result: We recorded a total of 24 studies using food preference of dung beetles. Most studies (96%) used food preference as a categorical variable, being beetle species clustered as coprophagous, necrophagous or generalists. This classification was obtained through of five different methods: 1) proportion based in abundance on determined bait type (56% of studies; e.g. Andresen 2008); 2) indicator value analysis as Levin's standardized or IndVal (11%; e.g. Campos et al., 2013; Beiroz et al., 2018); 3) literature review (7%; references from Halffter and Favila, 1993; Favila and Halffter, 1997); 4) presence–absence data to estimate the diet breadth (7%; Larsen et al., 2008); and 5) multinomial model (4%; Bourg et al., 2016). On the other hand, Horgan (2008) decided to use value of mean and standard error of individuals by each bait type using univariate general linear models (GLM) and removing the effect of blocks.

All studies used dung and carrion to examine food preference of dung beetles and 28% of studies added bait of fruit and 8% of fungus. The specific bait types for each category are: 1) *dung*: 68% human and 32% used others vertebrate dung (e.g. cow, mix human:pig, mix sheep:horse, wallaby and domestic dog); 2) *carrion rotten*: 33% bovine, 29% squid, 19% fish, 14% pig and 5% shrimp; 3) *fruit decomposition*: 83% banana and 17% mix papaya:tomato:banana:anona; 4) *fungus*: all mushrooms. All studies used pitfall trap and the most used exposure time was 48h (60%), followed by 24h (12%), other studies (28%) used 12h, 36h or 7 days. This variable was used in 24% of published papers on landscape connectivity, 14% forest structure and composition, 13% on matrix composition, 11% fragment size, 7% mammal diversity and 6% edge effect (Fig. 3).

Highlights: Diet breadth of dung beetles in the open matrices is lower when compared to forests (Horgan, 2008) and subsets of forest species may be driven to local extinction irrespective of their dietary breadth or specialization (Edwards et al., 2014a). Coprophagous beetles are negatively affected by canopy openness in undisturbed forests (Beiroz et al., 2017); however, there is also a dominance of coprophagous species in open matrices (Díaz et al., 2010). Necrophagous presented contrasting responses, with communities that were sensitive to environmental disturbance (Batilani-Filho and Hernandez, 2017), as well as other apparently tolerant to disturbance (Halffter et al., 2007; Navarrete and Hallfter, 2008; Beiroz et al., 2017). Generalist species were more abundant than other groups in forest edges (Halffter et al., 1992), and tended to change their selection of bait type depending on the habitat (Bourg, 2016). Finally, fungus-specialized species were associated with preserved forest (Hill, 1996).

Suggestions: According to the vast literature, human dung remains the most effective bait for the attraction of dung beetles in tropical forest (e.g. Filgueiras et al., 2009; Puker et al., 2013), and mix human-pig dung is a promising alternative for sampling of group due similar attractiveness (Marsh et al., 2013). However, few studies have explored attractiveness of different carrion types (but see Stavert et al., 2015; Ueda et al., 2015b). Further studies are required to understand of duration of bait attractiveness on different types, quantities and environmental conditions (12h, suggested by Barnes et al., 2014b; and 24h by Howden and Nealis, 2015), because of volatile profile bait used could be important in initiating food searching behaviour and determining dung beetle attraction to food resources (Stavert et al., 2015). In addition, cost-benefit assessment of distinct trap types according sampling times (e.g. see NTP-80, Morón and Terrón, 1984; pitfall trap, Montes-de-Oca and Halffter, 1995).

Dung beetles may change the proportion of food-specialist species according to disturbance in tropical forests. For example, Bourg et al. (2016) observed that tropical forest fragments had a lower number of carrion specialists than in pastures. Notwithstanding, it is still poorly known what factors may trigger a diet-specialist species to consume other resource than the preferred one. For a better comprehension of the niche-plasticity of each species when facing habitat disturbance, individual characteristics (e.g. sexual maturity, gender, health condition) deserved better care.

FUNCTIONAL DIVERSITY

Overall result: We recorded a total of six studies using functional diversity on dung beetles (Barragán et al., 2011; Audino et al., 2014; Barnes et al., 2014b; Edwards et al., 2014a; Silva and Hernandez, 2015a; Gómez-Cifuentes et al., 2017). Functional diversity had been accessed by four indices: functional evenness - FEVE, functional dispersion - FDIS, functional richness - FRIC and functional divergence - FDIV (86, 86, 72 and 43%, respectively) (see Villéger et al. (2008) and Laliberté and Legendre (2010) for description of each of these indices). All studies considered body mass during the calculation, while 55-75% included resource-relocation behaviour, diet preference and diel activity; and

<15% considered pronotum width, body shape or wing loading/area. There was no pattern on number of individuals measured for estimating mean trait values of species, which ranged from 5 (e.g. Gómez-Cifuentes et al., 2017) to all individuals sampled (e.g. Silva and Hernandez, 2015a). On the other hand, one study used data from literature (e.g. Barragán et al., 2011). This variable was used in 6% of studies comprising landscape connectivity; 4% fragment size, forest structure and composition and matrix composition; and 3% edge effect (Fig. 3).

Highlights: The highest FRIC values were recorded for dung beetle communities in primary and secondary forest, while in pastures, agriculture and restoration areas the loss of functional richness was evident. Likewise, indices of FEVE, FDIS and FDIV were lower in either pastures or agriculture matrix than in the native forest.

Suggestions: The intraspecific variability and co-related traits are important factors to functional diversity analyses (see Naeem and Wright, 2003; Cadotte et al., 2011). Thus, to dung beetles is recommend measuring of 30–60 individuals for an accurate estimation of species mean trait values, and traits can be adjust to avoid correlation (Griffths et al., 2015; 2016). To data that did not follow a normal curve is preferable to use trait's medians rather than means (Griffths et al., 2015). In addition, data should be taken from specimens collected from the site of study for greater reliability of analyses (Griffths et al., 2016).

WING LOADING/AREA

Overall result: We recorded two studies using wing loading or area of dung beetles (Larsen et al., 2008; Barnes et al., 2014a). All studies used absolute values of wing loading or area; however, the studies presented differences in the methods for obtaining the attributes related to wing. For example, wing loading was measured as the ratio of body mass to total wing area (Larsen et al., 2008; Barnes et al., 2014a), while wing area was measured as the total area of the left hind wing (mm^2), multiplied by two for total wing area (Barnes et al., 2014a). The number of individuals measured for each species varied according to individuals collected in the study (from 1 to 25 individuals). This variable was used in 6% of studies comprising edge effect and 1% forest structure and composition and matrix composition (Fig. 3).

Highlights: Results show that species with high wing loading tended to fly rapidly and continuously, while species with low wing loading tended to fly short distances. Thus, high wing loading may make forest-adapted species more sensitive to habitat loss and fragmentation by increasing their area requirements and species with lower wing loading were beneficed by matrix restoration, especially due their low dispersal ability.

Suggestions: The integration of studies on wing characteristics with physiology, behavior, and evolution may to increase the knowledge on interactions between species and environment, facilitating the understanding of differences on flight patterns and use of space by dung beetles in human-modified habitats. Similar to functional diversity, is preferable measuring of 30–60 individuals for an accurate estimation of species mean trait values due intraspecific variability (Griffths et al., 2016). Furthermore, flight activity is related to thermoregulation in dung beetles (Verdú and Lobo, 2008), and may be affected by wing load of beetle species. Thus, future studies could analyze potential synergetic effects that wing load and maintenance of corporal temperatures have over the spatial distribution of dung beetles over disturbed and conserved landscapes on tropical forests.

PHYSIOLOGICAL CONDITION

Overall result: We recorded a total of two studies using physiological condition of dung beetles (França et al., 2016b; Salomão et al., 2018a). Absolute values of physiological condition were used, being estimated through analysis of body size, body dry mass, fat mass, and muscle mass. However, the studies presented differences in the methods for obtaining the attributes related to physiological condition. For example, the extraction of lipid mass using 200 ml of n-hexane heated under reflux for 4 hr (18–22 cycles/hr) at 63–65°C was performed by França et al. (2016b), while using chloroform for 24 h was performed by Salomão et al. (2018a). This variable was used in 6% of studies comprising landscape connectivity, 3% edge effect and 1% forest structure and composition and matrix composition (Fig. 3).

Highlights: Most of the dung beetle species (83%) which are occupying disturbed environments exhibit increases in the fat storage, but there are a few species (17%) which physiologically are unaffected by environmental variables. In addition, environmental parameters that affect beetle abundances are not the same that affects physiological condition. Thus, this tool gives new insights regarding forest fragmentation and habitat loss, which may complement the traditional dung beetle studies that encompasses community structure. However, there are still scarce studies regarding these parameters.

Suggestions: Future studies should focus on understanding whether there are synergistic effects between habitat structure and ecological community parameters (e.g. species richness, abundance, diversity) over physiological condition of dung beetle species. For example, based on the density-dependence theories (Svensson and Sinervo, 2000; Rodenhouse et al., 2003; Sillet et al., 2004), abundant populations may be related to physiologically challenged individuals, which could present reduced condition when compared to populations with low abundances. In addition, studies analyzing the physiological condition of dung beetles according to sex may present cues regarding to what is the more sensible sex to the pressures of habitat transformation. Although it is known that physiological conditions of dung beetles are affected by landscape transformation, there is no data regarding the consequences of such effects. Future studies regarding the consequences of physiological condition over ecosystem services (e.g. excrement removal, seed dispersal) and fitness of dung beetle species may shed light on the effects of shifts in the health condition of such insects.

BODY SHAPE

Overall result: We recorded two studies using the body shape of dung beetles (Barnes et al., 2014a; Alves and Hernández, 2017). The studies presented differences in the methods for obtaining the attributes related to body shape. For example, the extraction of shape using the ratio of body mass to pronotum width and defining of body shape index (BSI) was performed by Barnes et al. (2014a), while using the tool of morphometric geometric through the placement of 15 anatomical landmarks in anteroposterior and ventral dorsal axis was performed by Alves and Hernandez (2017). This variable was used in 3% of studies comprising edge effects and 1% on forest structure and composition and matrix composition (Fig. 3).

Highlights: The results reported that dung beetles had a significant increase of BSI from the forest into the matrix habitats (Barnes et al., 2014a) and body shape in matrix of transgenic maize is different of conserved forest (Alves and Hernandez, 2017).

Suggestions: Body shape is an important variable to be incorporated into future studies on the structure of dung beetle assemblages, because the linking between body shape and size can elucidate questions about co-occurring species and their associated ecosystem processes (Hernandez et al., 2011; Barnes et al., 2014a). In addition, changes in shape already are used to detect environmental stress in other insects (see Hoffmann et al., 2002).

MOVEMENT

Overall result: We recorded one study using movement of dung beetles (Arellano et al., 2008a). This study was assessed by mark-release-recapture of individuals and was used the distance of 25m between traps. Beetles were marked with a unique combination of dots on the elytra and/or pronotum using silver pens and covered with a fine layer of glue with cyanocrilate (Arellano et al., 2008). This study focused on landscape connectivity, fragment size, forest structure and composition and matrix composition (Fig. 3).

Highlights: The movement rate was higher within forests than within open matrix and males dominate the long-distance movements when compared with females.

Suggestions: Protocols suggest of use of 50m distance between traps (Larsen and Forsyth, 2005) or 100m (Silva and Hernandez, 2015b) to eliminate interference (or dependence) between traps, because independence among samples is a basic premise in statistics analyses (Zuur et al., 2009). However, as distance may vary between species due gender, age categories, body size, food relocation behavior, and diel activity period (Arellano et al., 2008a; Silva and Hernández, 2015b), future efforts are required to improve this variable. Age categories may be determinate using characters-based body cuticle, spur's leg and the clypeus (see Martínez and Montes-de-Oca, 1994).

GENETIC PARAMETERS

Overall result: Until the present review, only the study of Ferreira-Neto et al. (2017) approached genetic parameters of dung beetles to evaluate effects of habitat fragmentation. To understand the effects of fragmentation at the genetic level, populations of dung beetles were studied using inter-simple sequence repeat (ISSR) markers to analyze the genetic diversity based on the number of loci, percentage of polymorphic loci and expected heterozygosity. This study focused on landscape connectivity and matrix composition (Fig. 3).

Highlights: Ferreira-Neto et al. (2017) found that the genetic traits suggesting that the populations are genetically divided in preserved and disturbed forest and beetles from preserved areas presented higher levels of genetic diversity compared to disturbed areas.

Suggestions: In face of the huge diversity of dung beetles in tropical forests compared with other groups, it is surprising that so few data are available regarding the effects of human-modification habitat on the population genetic diversity of species in this group. Such data could contribute enormously on the understanding of the genetic health and structure of populations and would be important to precisely correlate human-perturbations with the risk of local extinctions (see Templeton, 2013). Using SSR data (also known as microsatellite DNA) obtained through genomic approaches through Next Generation Sequencing, however, has shown more efficiency than previous gel-based analyses (Qin et al., 2017).

Conclusions

Based on our results, we can conclude that taxonomic diversity, which encompasses abundance, species richness and diversity, are the most used tools to analyze the effects of habitat modification in tropical forests. As dung beetles have a standardized sampling methodology (Halffter and Favila, 1993; Spector, 2006; Nishiwaki et al., 2017), we suggest that less-used approaches of dung beetle responses to habitat disturbance, as ecological functions and food preference, deserves better care and standardization regarding data surveys. By evaluating the response variables herein, we presented gaps of knowledge which deserved more intensive studies, for a broader comprehension of the effects of habitat disturbance over biodiversity.

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References

Aguilar-Amuchastegui, N.A., Henebry, G.M., 2007. Assessing sustainability indicators for tropical forests: Spatio-temporal heterogeneity, logging intensity, and dung beetle communities. Forest Ecol. Manag. 253, 56-67.

Almeida, S., Louzada, J., Sperber, C., Barlow, J., 2011. Subtle land-use change and tropical biodiversity: dung beetle communities in Cerrado grasslands and exotic pastures. Biotropica 43, 704-710.

Alvarado, F., Escobar., Williams, D.R., Arroyo-Rodríguez,V., Escobar-Hernández, F., 2018. The role of livestock intensification and landscape structure in maintaining tropical biodiversity. J. Appl. Ecol. 55, 185-194.

Amézquita, S., Fávila, M.E., 2010. Removal rates of native and exotic dung by dung beetles (Scarabaeidae: Scarabaeinae) in a fragmented tropical rain forest community and ecosystem ecology. Environ. Entomol. 39, 328-336.

Amézquita, S., Fávila, M.E., 2011. Carrion removal rates and diel activity of necrophagous beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rain forest. Environ. Entomol. 40, 239-246.

Andrade, R.B., Barlow, J. Louzada, J., Vaz-de-Mello, F.Z., Silveira, J.M., Cochrane, M.A., 2014. Tropical forest fires and biodiversity: dung beetle community and biomass responses in a northern Brazilian Amazon forest. J Insect Conserv. 18, 1097-1104.

Andrade, R.B., Barlow, J., Louzada,, J., Mestre, L., Silveira, J., Vaz-de-Mello, F.Z., Cochrane, M.A., 2014. Biotic congruence in humid tropical forests: A multi-taxa examination of spatial distribution and responses to forest disturbance. Ecol. Indic. 36, 572-581.

Andresen, E., 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. Ecography 26, 87-97.

Andresen, E., Levey, D.J., 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia 139, 45-54.

Andresen, E., 2005. Effects of season and vegetation type on community organization of dung beetles in a Tropical Dry Forest. Biotropica 37, 291-300.

Andresen, E., Feer, F., 2005. The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In P.-M. Forget, J. E. Lambert, P. E. Hulme, & S. B. Vander Wall (Eds.), Seed fate (pp. 331–349). Wallingford: CABI Publishing.

Andresen, E., 2008a. Short-term temporal variability in the abundance of tropical dung beetles. Insect Conserv. Divers. 1, 120-124.

Andresen, E., 2008b. Dung beetle assemblages in primary forest and disturbed habitats in a tropical dry forest landscape in western Mexico. J Insect Conserv. 12, 639-650.

Andresen, E., Laurence, S.G.W., 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica 39, 141-146.

Andresen, E., 2008. Short-term temporal variability in the abundance of tropical dung beetles. Insect Conserv. Divers. 1, 120-124.

Arellano, L., Hallfter, G., 2003. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. Acta Zool. Mex. 90, 27-76.

Arellano, L., Favila, M.E., Huerta, C., 2005. Diversity of dung and carrion beetles in a disturbed Mexican tropical montane cloud forest and on shade coffee plantations. Biodivers. Conserv. 14, 601-615.

Arellano, L., León-Cortés, J.L., Ovaskainen, O., 2008a. Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. Landscape Ecol. 23, 69-78.

Arellano, L., León-Cortés, J.L., Ovaskainen, O., 2008b. Response of dung beetle assemblages to landscape structure in remnant natural and modified habitats in southern Mexico. Insect Conserv. Divers. 1, 253-262.

Arroyo-Rodríguez, V., Ros, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M. Chazdon, R., 2013. Plant b-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. J. Ecol. 6, 1449-1458.

Audino, L.D., Louzada, J., Comita, L., 2014. Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity?. Biol. Conserv. 169, 248-257.

Audino, L.D., Murphy, S.J., Zambaldi, L., Louzada, J., Comita, L.S., 2017. Drivers of community assembly in tropical forest restoration sites: role of local environment, landscape, and space. Ecol. Appl. 27, 1731-1745.

Avendaño-Mendonza, C., Morón-Ríos, A., Cano, E.B., Léon-Cortés, J., 2005. Dung beetle community (Coleoptera: Scarabaeidae: Scarabaeinae) in a tropical landscape at the Lachua Region, Guatemala. Biodivers. Conserv. 14, 801-822.

Barlow, J., Gardner, T.A., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B. Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, 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-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres., C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. PNAS 47, 18555-18560.

Barlow, J., Louzada, J., Parry, L., Hernández, M.I.M., Hawes, J., Peres, C.A., Vaz-de-Mello, F.Z., Gardner, T.A., 2010. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. J. Appl. Ecol. 47, 779-788.

Barlow, J. Silveira, J.M., Mestre, L.A.M, Andrade, R.B., D'Andrea, G.C., Louzada, J., Vaz-de-Mello, F.Z., Numata, I., Lacau, S., Cochrane, M.A., 2012. Wildfires in bamboo-dominated Amazonian forest: impacts on above-ground biomass and biodiversity. B. PLoS One 7, e33373.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., MacN Nally, R., Thomson, J.R., Ferraz, S.F.B., Louzada, J., Oliveira, V.H.F., Parry, L., Solar, R.R.C., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.B., Cardoso, T.M., Oliveira, R.C.J., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535, 144-147.

Barnes, A.D., Emberson, R.M., Krell, F-T., Didham, R.K., 2014a. The role of species traits in mediating functional recovery during matrix restoration. PLoS One 9, e115385.

Barnes, A.D., Emberson, R.M., Chapman, H.M., Krell, F-T., Didham, R.K., 2014b. Matrix habitat restoration alters dung beetle species responses across tropical forest edges. Biol. Conserv. 170, 28-37.

Barragán, F., Moreno, C.E., Escobar, F., Hallfter, G., Navarrete, D., 2011. Negative impacts of human land use on dung beetle functional diversity. PLoS One 6, e17976.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Eco. Biogeogr. 19, 134-143.

Batilani-Filho, M., Hernandez, M.I.M., 2017. Decline of ecological functions performed by dung beetles in areas of Atlantic Forest and contribution of rollers and tunnelers in organic matter removal. Environ. Entomol. 46, 784-793.

Beiroz, W., Slade, E.M., Barlow, J., Silveira, J.M., Louzada, J., Sayer, E., 2017. Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change. Insect Conserv. Divers. 10, 94-106.

Beiroz, W., Sayer, E., Slade, E.M., Audino, L., Braga, R.F., Louzada, J., Barlow, J., 2018. Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape. Ecol. Indic. 95, 518-526.

Bett, J.Z., Farias, P.M., Silva, P.G., Hernández, M.I.M., 2014. Dung beetle communities in coal mining areas in the process of recovery. Biotemas 27, 197-200.

Beynon, S.A., Wainwright, W.A., Christie, M., 2015. The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry. Ecol. Entomol. 40, 124-135.

Bicknell, J.E., Phelps, S.P., Davies, R.G., Mann, D.J., Struebig, M.J., Davies, Z.G., 2014. Dung beetles as indicators for rapid impact assessments: evaluating best practice forestry in the neotropics. Ecol. Indic. 43, 154-161.

Bitencourt, B.S., Silva, P.G., 2016. Forest regeneration affects dung beetle assemblages (Coleoptera: Scarabaeinae) in the southern Brazilian Atlantic Forest. J. Insect Conserv. 20, 855-866.

Blaum, N. Seymour, C., Rossmanith, E., Schwager, M., Jeltsch, F., 2009. Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. Biodivers. Conserv. 18, 1187-1199.

Bogoni, J.A., Graipel, M.E., Castilho, P.V., Fantacini, F.M., Kuhnen, V.V., Luiz, M.R., Maccarini, T.B., Marcon, C.B., Texeira, C.S.P., Tortato, M.A., Vaz-de-Mello, F.Z., Hernández, M.I.M., 2016. Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodivers. Conserv. 25, 1661-1675.

Bogoni, J.A., Hernández, M.IM., 2014. Attractiveness of native mammal's feces of different trophic guilds to dung beetles (Coleoptera: Scarabaeinae). J. Insect Sci. 14, pii 299.

Boonrotpong, S., Sotthibandhu, S., Pholpunthin, C. 2004. Species composition of dung beetles in the primary and secondary forests at Ton Nga Chan Wildlife Sanctuary. ScienceAsia 30, 59-65.

Boonrotpong S., Sotthibandhu, S., Satasookc, C., 2012. Species turnover and diel flight activity of species of dung beetles, *Onthophagus*, in the tropical lowland forest of peninsular Thailand. J. Insect Sci. 12, pii 77.

Bornemissza, G.F., 1969. A new type of brood care observed in the dung beetle *Oniticellus cinctus* (Scarabaeidae). Pedobiologia, 9, 223-225.

Botes, A., McGeochb, M.A., van Rensburg, J., 2006. Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. Biol. Conserv. 30, 573-583.

Bourg, A., Escobar, F., MacGregor-Fors, I., Moreno, C.E., 2016. Got dung? Resource selection by dung beetles in neotropical forest fragments and cattle pastures. Neotrop. Entomol. 45, 490-498.

Braga, R.F., Korasaki, V., Audino, L.D., Louzada, J., 2012. Are dung beetles driving dung-fly abundance in traditional agricultural areas in the amazon?. Ecosys. 15, 1173-1181.

Braga, R.F., Korasaki, V., Andresen, E.L., Louzada, J., 2013. Dung beetle community and functions along a habitat- disturbance gradient in the amazon: a rapid assessment of ecological functions associated to biodiversity. PLoS One 8, e57786.

Brose, U., 2002. Estimating species richness of pitfall catches by non-parametric estimators. Pedobiologia 46, 101-107.

Brown Jr., K.S. Conservation of neotropical environments: Insects as Indicators. In Collins, N.M. & Thomas, J.A. (Eds.). The conservation of insects and their habitats. London, Academic Press, 1991. 349-404 p.

Caballero, U., León-Cortés, J.L., 2012. High diversity beetle assemblages attracted to carrion and dung in threatened tropical oak forests in Southern Mexico. J. Insect Conserv. 16, 537-547.

Cajaiba, R.L., Périco, E. Dalzochio, M.S., Silva, W.B., Bastos, R., Cabral, J.A., Santos, M., 2017a. Does the composition of Scarabaeidae (Coleoptera) communities reflect the extent of land use changes in the Brazilian Amazon?. Ecol. Indic. 74, 285-294.

Cajaiba, R.L., Périco, E., Silva, W.B., Santos, M., 2017b. Can dung beetles (Scarabaeinae) indicate the status of Amazonia's ecosystems? Insights integrating anthropogenic disturbance with seasonal patterns. Animal Biol. 67, 301-318.

Campos, R.C., Hernández, M.I.M., 2013. Dung beetle assemblages (Coleoptera, Scarabaeinae) in Atlantic forest fragments in southern Brazil. Rev. Bras. Entomol. 57, 47-54.

Campos, R.C., Hernández, M.I.M., 2015a. The importance of maize management on dung beetle communities in Atlantic Forest fragments. PLoS One 10, e0145000.

Campos, R.C., Hernández, M.I.M., 2015b. Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. Ecol. Indic. 49, 216-227.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59-67.

Carpio, C., Danoso, D.D., Ramón, G., Dangles, O., 2009. Short term response of dung beetle communities to disturbance by road construction in the Ecuadorian Amazon Ann. Soc. Entomol. Fr. 45, 455-469.

Chao, A., 2004. Species richness estimation. In: Balakrishnan N, Read CBand Vidakovic B (eds) Encyclopedia of statistical sciences. Wiley, New York.

Chao, A., Lin, S., 2011. User's Guide for Program CLAM (Classification Method). http://chao.stat.nthu.edu.tw/wordpress/wpcontent/uploads/software/CLAM%20User%20 Guide.pdf, accessed in February 11st 2019.

Chapman, C., Chapman, L.J., 2003. Fragmentation and alteration of seed dispersal processes: an initial evaluation of dung beetles, seed fate, and seedling diversity. Biotropica 35, 382-393.

Chazdon, R.L., Chao, A., Colwell, R.K., Lin, S.K., Norden, N., Letcher, S.G., Clark, D.B., Finegan, B., Arroyo, J.P., 2011. A novel statistical method for classifying habitat generalists and specialists. Ecol. 92, 1332-1343.

Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond B Biol Sci. 345, 101-118.

Correa, C.M.A., Puker, A., Korasaki, V., Ferreira, K.R. Abot, A.R., 2016. Attractiveness of baits to dung beetles in Brazilian savanna and exotic pasturelands. Entomol. Sci. 19, 112-123.

Costa, F., Pessoa, K.K., Liberal, C.N., Filgueiras, B.K.C., Salomão, R.P., Iannuzzi, L., 2013. What is the importance of open habitat in a predominantly closed forest area to the dung beetle (Coleoptera, Scarabaeinae) assemblage?. Rev. Bras. Entomol. 57, 329-334.

Costa, C.M.Q., Barreto, J.W., Moura, R.C., 2014. Changes in the dung beetle community in response to restinga forest degradation. J. Insect Conserv. 18, 895-902.

Costa, C., Oliveira, V.H.F., Maciel, R., Beiroz, W., Korasaki, V., Louzada, J., 2017. Variegated tropical landscapes conserve diverse dung beetle communities. PeerJ 5, e3125.

Culot, L., Mann, D.J., Muñoz-Lazo, F.J.J., Huynen, M-C., Huymann,, E.W., 2011. Tamarins and dung beetles: an efficient diplochorous dispersal system in the Peruvian Amazonia. Biotropica. 43, 84-92.

Culot, L., Bovy, E., Vaz-de-Mello, F.Z., Guevara, R., Galetti, M., 2013. Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biol. Conserv. 163, 79-89.

Cultid-Medina, C.A., Escobar, F., 2016. Assessing the ecological response of dung beetles in an agricultural landscape using number of individuals and biomass in diversity measures. Environ. Entomol. 45, 310-319.

Davis, A.L.V., 1994. Habitat fragmentation in southern Africa and distributional response patterns in specialist or generalist dung beetle families (Coleoptera). Afr. J. Ecol. 32, 192-207.

Davis, A.J., Sutton, S.L., 1998. The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical. Ecosystems. Divers. Distrib.4, 167-173.

Davis, A.J., Huijbregts, H., Krikken, J., 2000. The role of local and regional processes in shaping dung beetle communities in tropical forest plantations in Borneo. Glob. Ecol. Biogeogr. 9, 281-292.

Davis, A.J., 2000. Does reduced-impact logging help preserve biodiversity in tropical rainforests? A case study from Borneo using dung beetles (Coleoptera; Scarabaeoidea) as indicators. Environ. Entom. 29, 467-475.

Davis, A.J., Holloway, J.D., Huijbregt, H., Krikken, J., Kirk-Spriggs, A.H., Sutton, S.L., 2001. Dung beetles as indicators of change in the forests of northern Borneo. J. Appl. Ecol. 38, 593-616.

Davis, A.L.V., Van Aarde, R.J., Scholtz, C.H., Delport, J.H., 2002. Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. Glob. Ecol. Biogeogr. 11, 191-209.

Davis, A.L.V., Van Aarde, R.J., Scholtz, C.H., Delport, J.H., 2003. Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and unmined dune forest. Restoration Ecol. 11, 29-42.

Davis, A.L.V., Philips, T.K., 2005. Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation area. Community. Environm. Entomol. 34, 1081-1088.

Davis, A.L.V., Philips, T.K., 2009. Regional fragmentation of rain forest in west Africa and its effect on local dung beetle assemblage structure. Biotropica 41, 215-220.

Davis, A.L.V., Scholtz, C.H., Swemmer, A.M., 2012. Effects of land usage on dung beetle assemblage structure: Kruger National Park versus adjacent farmland in South Africa. J. Insect Conserv. 16, 399-411.

Davis, A.L.V., Swemmer, A.M. Scholtz, C.H., Deschodt, C.M., Tshikae, B.P., 2013. Roles of environmental variables and land usage as drivers of dung beetle assemblage structure in mopane woodland. Austral Ecol. 39, 313-327.

Díaz, A., Galatte, E., Favila, M.E., 2010. The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest. J. Insect Sci. 10, pii 81.

Doube, B.M., 1990. A functional classification for analysis of the structure of dung beetle assemblages. Ecol. Entomol., 15, 371-83.

Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhé, M.A., Hamer, K.C., Wilcove, D.S., 2010. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Proc. R. Soc. B. 278, 82-90.

Edwards, D. P., 2012. Reduced-impact logging and biodiversity conservation: a case study from Borneo. Ecol. Appl. 22, 561-71.

Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen, C., Wilcove, D.S., Hamer, K.C., 2014a. Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot?. Animal Conserv. 17, 163-173.

Edwards, D.P. Gilroy, J.J., Woodcock, P. Edwards, F.A., Larsen, T.H., Andrews, D.J.R., Derhé, M.A., Docherty, T.D.S., Hsu, W.W., Mitchell, S.L., Ota, T., Williams, L.J., Laurance, W.F., Hamer, K.C., Wilcove, D.S., 2014b. Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. Glob. Change Biol. 20, 183-191.

Edwards, F.A., Finan, j., Graham, L.K., Larsen, T.H., Wilcove, D., Hsu, W.W., Chey, V.K., Hamer, K.C., 2017. The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve. Biol. Conserv. 205, 85-92.

Escobar, F., 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. Trop. Zool. 17, 123-136.

Escobar, F., Halffter, G., Arellano, L., 2007. From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. Ecography 30, 193-208.

Estrada, A., Coates-Estrada, R., Dadda, A.A., Cammarano, P., 1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. J. Tropical Ecol. 14, 577-593.

Estrada, A., Anzures, A.D., Coates-Estrada, R., 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. Am. J. Primat. 48, 253-262.

Estrada, A., Coates-Estrada, R., 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. Biodivers. Conserv. 11, 1903-1918.

Farias, P.M., Arellano, L., Hernández, M.I.M., Ortiz, S.L., 2015. Response of the copro-necrophagous beetle (Coleoptera: Scarabaeinae) assemblage to a range of soil characteristics and livestock management in a tropical landscape. J. Insect Conserv. 19, 947-960.

Feer, F., Hingrat, Y., 2005. Effects of forest fragmentation on a Dung Beetle community in French Guiana. Conserv. Biol. 1103-1112.

Feer, F., 2008. Responses of dung beetle assemblages to characteristics of rain forest edges. Ecotropica 14, 49-62.

Feer, F., 2013. Variations in dung beetles assemblages (Coleoptera: Scarabaeidae) within two rain forest habitats in French Guiana. Rev. Biol. Tropical. 61, 753-768.

Ferreira, S.C., Silva, P.G., Paladini, A., Di Mare, R.A., 2018. Climatic variables drive temporal patterns of α and β diversities of dung Beetles. Bull. Entomol. Res. 4, 1-8.

Ferreira-Neto, C.A., Cruz, G.A.S., Amorim, I.C., Balbino, V.Q., Moura, R.C., 2017. Effects of fragmentation and anthropic pressure on the genetic structure of *Canthon* (Peltecanthon) *staigi* (Coleoptera: Scarabaeidae) populations in the Atlantic Forest domain. J. Insect Conserv. 21, 267-276.

Filgueiras, B.K. C., Liberal, C.N., Aguiar, C.D.M., Hernández, M.I.M., Iannuzzi, L., 2009. Attractivity of omnivore, carnivore and herbivore mammalian dung to Scarabaeinae (Coleoptera, Scarabaeidae) in a tropical Atlantic rainforest remnant. Rev. Bras. Entomol. 53, 422-427.

Filgueiras, B., Iannuzzi, L., Leal, I.R., 2011. Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biol. Conserv. 144, 362-369.

Filgueiras, B.K.C, Tabarelli, M., Leal, I.R., Vaz-de-Mello, F., Iannuzzi, L., 2015. Dung beetle persistence in human-modified landscapes: Combining indicator species with anthropogenic land use and fragmentation-related effects. Ecol. Indic. 55, 65-73.

Filgueiras B.K.C, Tabarelli, M., Leal, I.R., Vaz-de-Mello, F., Peres, C.A., Iannuzzi, L., 2016. Spatial replacement of dung beetles in edge-affected habitats: biotic homogenization or divergence in fragmented tropical forest landscapes? Divers. Distrib. 22, 400-409.

França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J.M., Barlow, J., 2016a. Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. J. Appl. Ecol. 53, 1-8.

França, F., Barlow, J., Araújo, B., Louzada, J., 2016b. Does selective logging stress tropical forest invertebrates? Using fat stores to examine sublethal responses in dung beetles. Ecol. Evol. 1-8.

França, F.M., Frazão, F.S., Korasaki, V., Louzada, J., Barlow, J., 2017. Identifying thresholds of logging intensity on dung beetle communities to improve the sustainable management of Amazonian tropical forests. Biol. Conserv. 216, 115-122.

França, F., Louzada, J., Barlow, J., 2018. Selective logging effects on `brown world' faecal-detritus pathway in tropical forests: A case study from Amazonia using dung beetles. Forest Ecol. Managem. 410, 136-143.

Gardner, T.A., Hernández, M.I.M., Barlow, J., Peres, C.A., 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. J. Appl. Ecol. 45, 883-893.

Génier, F., 2009. Le genre Eurysternus Dalman, 1824 (Scarabaeidae: Scarabaeinae: Oniticellini), révision taxonomique et clés de détermination illustrées. Pensoft, Sofia.

Gill, B.D., 1991. Dung beetles in tropical American forest. In I. Hanski and Y. Cambefort (eds.), Dung beetle ecology. Princeton University Press, Princeton, NJ.

Gilroy, J.J., Edwards, F.A., Uribe, C.A.M., Haugaasen, T., Edwards, D.P., 2014a. Minimizing the biodiversity impact of Neotropical oil palm development. Glob. Change Biol. 21, 1531-1540.

Gilroy, J.J., Prescott, G.W., Cardenas, J.S., Castañeda, P.G.P., Sánchez, A., 2014. Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. J. Appl. Ecol. 51, 1337-1346.

Gittings, T., Giller, P.S., 1998. Resource quality and the colonization and sucession of coprophagous dung beetles. Ecography 21, 581-592.

Gómez-Cifuentes, A.G., Munevar, A., Gimenez, V.C., Gatti, M.G., Zurita, G.A., 2017. Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina. J. Insect Conserv. 21, 147-156.

Gonzáles-Vainer, P., Morelli, E., Defeo, O., 2012. Differences in coprophilous beetle communities structure in Sierra de Minas (Uruguay): a mosaic landscape. Neotrop. Entomol. 41, 366-374.

Gray, C.L., Slade, E.M., Mann, D.J., Lewis, O.T., 2014. Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm- dominated tropical landscapes?. Ecol. Evol. 4, 1049-1060.

Gray, C.L., Simmons, Fayle, T.M., Mann, D.J., Slade, E.M., 2016. Are riparian forest reserves sources of invertebrate biodiversity spillover and associated ecosystem functions in oil palm landscapes? Biol. Conserv. 194, 176-183.

Gray, J.S., 1987. Species–abundance patterns. Organization of Communities, Past and Present (eds J.H.R. Gee & P.S. Giller), pp. 53 67. Blackwell Scientific, Oxford.

Gries, R., Louzada, J., Almeida, S., Macedo, R., Barlow, J., 2011. Evaluating the impacts and conservation value of exotic and native tree afforestation in Cerrado grasslands using dung beetles. Insect Conserv. Divers. 5, 175-185.

Grimbacher, P., Catterall, C.P., Kitching, R.L., 2006. Beetle species' responses suggest that microclimate mediates fragmentation effects in tropical Australian rainforest. Austral Ecol. 31, 458-470.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147-186.

Halffter, G., Matthews, E.G., 1966. The natural history of dung beetles of the subfamily Scarabaeinae. Fol. Entom. Mex. 12-14: 1-312.

Halffter, G., Edmonds, W.D., 1982. The nesting behaviour of dung beetles (Scarabaeinae): an ecological and evolutive approach. Instituto de Ecologia, Mexico City, Mexico.

Halffter, G., Favila, M., Halffter, V., 1992. A comparative study of the structure of the scarab guild in MexicanTropical rain forests and derived ecosystems. Fol. Entom. Mex. 84, 131-156.

Halffter, G, Favila, M.E., 1993. The Scarabaeinae (Insecta: Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. Biol. Intern. 27, 15-21.

Halffter, G., Arellano, L., 2002. Response of dung beetle diversity to human–induced changes in a tropical landscape. Biotropica 34, 144-154.

Halffter, G., Pineda, E., Arellano, L., Escobar, F., 2007. Instability of copronecrophagous beetle assemblages (Coleoptera: Scarabaeinae) in a Mountainous tropical landscape of Mexico. Environ. Entomol. 36, 1397-1407.

Hammond, P.M., 1976. Kleptoparasitic behavior of *Onthophagus suturalis* Peringuey (Coleoptera: Scarabaeidae) and other dung beetles. Coleopt. Bull. 30, 235-249.

Hanski, I., Cambefort, Y., 1991. Dung beetle ecology. I.Hanski and Y. Cambefort, editors. Princeton UniversityPress, Princeton, New Jersey, USA.

Hanski, I., Koivulehto, H., Cameron, A., Rahagala, P., 2007. Deforestation and apparent extinctions of endemic forest beetles in Madagascar. Biol. Lett. 3, 344-347.

Harvey, C.A., Gonzalez, J., Riba, E.S., 2006. Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. Biodivers. Conserv. 15, 555-585.

Hayes, L., Mann, D.J., MonastyrskII, A.L., Lewis, O.T., 2009. Rapid assessments of tropical dung beetle and butterfly assemblages: Contrasting trends along a forest disturbance gradient. Insect Conserv. Divers. 2, 194-203.

Hernandez, M.I.M, Vaz-de-Mello, F.Z., 2009. Seasonal and spatial species richness variation of dung beetle (Coleoptera, Scarabaeidae s. str.) in the Atlantic Forest of southeastern Brazil. Rev. Bras. Entomol. 53, 1-9.

Hernandez, M.I.M, Barreto, P.S.C.S., Costa, V.H., Creão-Duarte, A.J., Favila, M.E., 2014. Response of a dung beetle assemblage along a reforestation gradient in Restinga forest. J. Insect Conserv. 18, 539-546.

Hernandez, M.I.M., Monteiro, L.R., Favila, M.E., 2011. The role of body size and shape in understanding competitive interactions within a community of neotropical dung beetles. J. Insect Sci. 11, pii 13.

Heusi-Silveira, M., Lopes, B.C., Ide, S., Castellani, T.T., Hernández, M.I.M., 2012. Beetle (Insecta, Coleoptera) assemblage in a Southern Brazilian: effects of anthropogenic disturbance and vegetation complexity. Stud. Neotrop. Fauna Environ. 47, 203-214.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecol. 54, 427-431.

Hill, C.J., 1995. Linear strips of rain forest vegetation as potential dispersal corridors for rain forest insects. Conserv. Biol. 9, 1559-1566.

Hill, J.K., Hamer, K.C., Lace, L.A., Banham. W.M.T., 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. J. Appl. Ecol. 32, 754 760.

Hill, C.J. 1996. Habitat specificity and food preferences of an assemblage of tropical Australina dung beetles. J.Tropical Ecol. 12, 449-460.

Holloway, J.D., Spriggs, A.H., Khen, C.V., 1992. The response of some rain forest insect groups to logging and conversion to plantation. Phil. TransR. Soc. Lond. B. 335, 425-436.

Horgan, F.G., 2005. Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slope of the Peruvian Andes. Forest Ecol. Manag. 216, 117-133.

Horgan, F.G., 2006. Aggregation and coexistence of dung beetles in montane rain forest and deforested sites in Central Peru. J. Tropical Ecol. 22, 359-370.

Horgan, F.G., 2007. Dung beetles in pasture landscapes of Central America: proliferation of synanthropogenic species and decline of forest specialists. Biodivers. Conserv. 16, 2149-2165.

Horgan, F.G., 2008. Dung beetle assemblages in forests and pastures of El Salvador: a functional comparison. Biodivers. Conserv. 17, 2961-2978.

Horgan, F.G., 2009. Invasion and retreat: shifting assemblages of dung beetles amidst changing agricultural landscapes in central Peru. Biodivers. Conserv. 18, 3519-3541.

Hosaka, T., Ninno, M., Kon, M., Ochi, T., Yamada, T., Fletcher, C.D., Okuda, T., 2014a. Impacts of small-scale clearings due to selective logging on dung beetle communities. Biotropica 46, 720-731.

Hosaka T., Ninno, M., Kon, M., Ochi, T., Yamada, T, Fletcher, C., Okuda, T., 2014b. Effects of logging road networks on the ecological functions of dung beetles in peninsular Malaysia. Forest Ecol. Manag. 326, 18-24.

Hsieh, T.C., Ma, K.H., Chao, A. Package 'iNEXT' - https://cran.r-project.org/web/packages/iNEXT/iNEXT.pdf

Howdan, H.F., Nealis, V.G., 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). Biotropica 7, 77-83.

Iannuzzi, L., Salomão, R.P., Costa, F.C., Liberal, C.L., 2016. Environmental patterns and daily activity of dung beetles (Coleoptera: Scarabaeidae) in the Atlantic Rainforest of Brazil. Entomotropica 31, 196-207.

Jacobs, C.T., Scholtz, C.H., Escobar, F., Davis, A.L.V., 2010. How might intensification of farming influence dung beetle diversity (Coleoptera: Scarabaeidae) in Maputo Special Reserve (Mozambique)?. J. Insect Conserv. 14, 389-399.

Jost, L., 2006. Entropy and Diversity. Oikos 113, 363-375.

Kenyon, T.M., Mayfield, M.M., Monteith, G.B. Menéndez, R., 2016. The effects of land use change on native dung beetle diversity and function in Australia's Wet Tropics. Austral Ecol. 41, 797-808.

Kessler, M., Abrahamczyk, S., Bos, M., Buchori, D. Putra, D.D., 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. Ecol. Appl. 19, 2142-2156.

Kishimoto-Yamada, K., Hyodo, F., Matsuoka, M., Hashimoto, Y., Kon, M., Ochi, T., Yamane, S., Ishii, R., Itioka, T., 2013. Effects of remnant primary forests on ant and dung beetle species diversity in a secondary forest in Sarawak, Malaysia. J. Insect Conserv. 17, 591-605.

Klein, B.C., 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. Ecol. 70, 1715-1725.

Klemperer, H.G., Boulton, R., 1976. Brood burrow construction and brood care by *Heliocopris japetus* (Klug) and *Heliocopris hamadryus* Fabricius (Coleoptera: Scarabaeidae). Ecol. Entomol. 1, 19-29.

Koike, S., Morimoto, H., Kozakai, C., Arimoto, I., Soga, M., Yamazaki, K., Koganezawa, M., 2012. The role of dung beetles as a secondary seed disperser after dispersal by frugivore mammals in a temperate deciduous forest. Acta Oecol. 41, 74–81.

Korasaki, V., Lopes, J., Brown, G.G., Louzada, J., 2012. Using dung beetles to evaluate the effects of urbanization on Atlantic Forest biodiversity. Insect Sci. 20, 393-406.

Korasaki, V., Braga, R.F., Zanetti, R., Moreira, F.M.S., Vaz-de-Mello, F.Z., Louzada, J., 2013. Conservation value of alternative land-use systems for dung beetles in Amazon: valuing traditional farming practices. Biodivers. Conserv. 22, 1485-1499.

Kotze, D.J., Lawes, M.J., 2007. Viability of ecological processes in small Afromontane forest patches in South Africa Austral. Ecol. 32, 294-304.

Kudavidanage, E.P., Quie, L., Lee, J.S.H., 2012. Linking biodiversity and ecosystem functioning of dung beetles in South and Southeast Asian tropical rainforests. Raffles B. Zool. 25, 141-154.

Lachat, T.U., Attignon, S., Djego, J., Goergen, G., Nagel, P., Sinsin, B., Peveling, R., 2006. Arthropod diversity in Lama Forest reserve (South Benin), a mosaic of natural, degraded and plantation forests. Biodivers. Conserv. 15, 3-23.

Lam, T.Y., Fletcher, C., Ramag, B.S., Doll, H.M., Joann, C.L., Nur-Zati, A.M., Butod, E., Kassim, A.R., Harrison, R.D., Potts, M.D., 2014. Using habitat characteristics to predict faunal diversity in tropical production forests. Biotropica 46, 50-57.

Larsen, T.H., Forsyth, A., 2005. Trap spacing and transect design for dung beetle biodiversity studies. Biotropica 37, 322–325.

Larsen, T.H., Williams, N.M., Kremer, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8, 538-547.

Larsen, T.H., Lopera, A., Forysth, A., 2008. Understand trait dependent community disassembly: dung beetles, density functions and forest fragmentation. Conserv. Biol. 22, 1288-1298.

Larsen, T.H., 2012. Upslope range shifts of Andean dung beetles in response to deforestation: compounding and confounding effects of microclimatic change. Biotropica 44, 82-89.

LaScaleia, M.C., Reynolds, C., Magagula, C., Roets, F., MCCleery, R.A., 2018. Dung beetle richness decreases with increasing landscape structural heterogeneity in an African savanna-agricultural mosaic. Insect Conserv. Divers. 11, 396-406.

Lawson, C.R., Mann D.J., Lewis, O.T., 2012. Dung beetles reduce clustering of tropical tree seedling. Biotropica 44, 271-275.

Liberal, C.N., Farias, A.M.I., Meiado, M.V., Filgueiras, B.K.C., Iannuzzi, L., 2011. How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. J. Insect Sci. 11, pii 114.

Lobo, J.M., 1993. Estimation of dung beetle biomass (Coleoptera: Scarabaeoidea). Eur. J. Entomol. 90, 235-238.

Lopes, J., Korasaki, V., Catelli, L.L., Marçal, V.V.M., Nunes, M.P.B.P., 2011. A comparison of dung beetle assemblage structure (Coleoptera: Scarabaeidae: Scarabaeinae) between an Atlantic forest fragment and adjacent abandoned pasture in Paraná, Brazil. Zool. 28, 72-79.

Louzada, J., Lima, A.P., Matavelli, R., Zambaldi, L., Barlow, J., 2010a. Community structure of dung beetles in Amazonian savannas: role of fire disturbance, vegetation and landscape structure. Landscape Ecol. 25, 631-641.

Louzada, J., Gardner, T., Peres, C., Barlow, J., 2010. A multi-taxa assessment of nestedness patterns across a multiple-use Amazonian forest landscape. Biol. Conserv. 143, 1102-1109.

Mac Nally, R., 2005. Scale and an organism-centric focus for studying interspecific interactions in landscapes. In W. J. A. and M. R. Moss (Eds.) Issues and perspectives in landscape ecology. pp. 52–69, Cambridge University Press, Cambridge, UK.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell Publishing.

Marsh, C.J., Feitosa, R., Louzada, J., Ewers, R.M., 2018. Is β-diversity of Amazonian ant and dung beetles communities elevated at rainforest edges?. J. Biogeogr. 45, 1966-1979.

Marsh, C.J., Louzada, J., Beiroz, W., Ewers, R.M., 2013. Optimising bait for pitfall trapping of Amazonian dung beetles (Coleptera: Scarabaeinae). PLoS One 8, e73147.

Martello, F., Andriolli, F., Souza, T.B., Dodonov., Ribeiro, M.C., 2016. Edge and land use effects on dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in Brazilian cerrado vegetation. J. Insect Conserv. 20, 957-970.

Maturo, F., Tonio Di Battista., 2018. A functional approach to Hill's numbers for assessing changes in species variety of ecological communities over time. Ecol. Indic. 84, 70-81.

Mcgeoch, M., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biol. Reviews 73: 181-201.

Mcgeoch, M.A., Van Rensburg, B.J, Botes, A., 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. J. Appl. Ecol. 39, 661-672.

Medina, C.A., Escobar, F., Kattan, G.H., 2002. Diversity and habitat use of dung beetles in a restored Andean landscape. Biotropica 34, 181-187.

Moctezuma, V., Halffter, G., Escobar, F., 2016. Response of copronecrophagous beetle communities to habitat disturbance in two mountains of the Mexican Transition Zone: influence of historical and ecological factors. J. Insect Conserv. 13, e0196839.

Molina, S.I., Valladares, G.R., Gardner, S., Cabido, M.R., 1999. The effects of logging and grazing on the insect community associated with a semi-arid chaco forest in central Argentina. J. Arid Environ. 42, 29-42.

Montoya-Molina, S., Giraldo-Echeverri, C.G., Montoya-Lerma, J., Chará, J., Escobar, F., Calle, Z., 2016. Land sharing vs. land sparing in the dry Caribbean lowlands: A dung beetles' perspective. Appl. Soil Ecol. 98, 204-212.

Navarrete, D., Halffter, G., 2008. 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. Biodivers. Conserv. 17, 2869-2898.

Neita, J.C., Escobar, F., 2012. The potential value of agroforestry to dung beetle diversity in the wet tropical forests of the Pacific lowlands of Colombia. Agroforest. Syst. 85, 121-131.

Neves, F.S., Oliveira, V.H.F., Espirito-Santo, M.M., Vaz-de-Mello, F.Z., Louzada, J., Sanchez-Azofeifa, A., Fernandes, G.W., 2010. Successional and seasonal changes in a community of dung beetles (Coleoptera: Scarabaeinae) in a Brazilian tropical dry forest. Nature Conserv. 8, 160-164.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M., Vulinec, K., 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biol. Conserv. 137, 1-19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E., Network, T.S.R., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biol. Conserv. 141, 1461-1474.

Nichols, E., Uriarte, M., Peres, C.A., Louzada, J., Braga, R.F., 2013. Human-induced trophic cascades along the fecal detritus pathway. PLoS One 8, e75819.

Nielsen, S.T., 2007. Deforestation and biodiversity: effects of bushland cultivation on dung beetles in semi-arid Tanzania. Biodivers. Conserv. 16, 2753-2769.

Niino, M., Hosaka, T., Ochi, T., Yamada, T., Okuda, T., 2014. Diel flight activity and habitat preference of dung beetles (Coleoptera: Scarabaeidae) in Peninsular Malaysia. Raffles B. Zool. 62, 795-804.

Nishiwaki, A.P.M.; Pinheiros, S.M.G.; Gusmão, L.O.; Silva, E.C.; Santos, A.F.M.S.; El-Deir, S.G., 2017. Scarabaeidae family (Coleoptera) as potential environmental quality bioindicator. Revista Geama 3, 68-77.

Nummelin, M., Hanski, I., 1989. Dung beetles of the Kibale Forest, Uganda; comparison between virgin and managed forests. J. Tropical Ecol. 5, 349-352.

Nummelin, M., 1998. Log!normal distribution of species abundances is not a universal indicator of rain forest disturbance. J. Appl. Ecol. 35, 454-457.

Nyeko, P., 2009. Dung beetle assemblages and seasonality in primary forest and forest fragments on agricultural landscapes in Budongo, Uganda. Biotropica 41, 476-484.

Oldekop, J.A., Bebbington, A.J., Truelove, N.K., Tysklin, N., Villamarín, S., Preziosi, R., 2012. Co-occurrence patterns of common and rare leaf-litter frogs, epiphytic ferns and dung beetles across a gradient of human disturbance. PLoS One 7, e38922.

Oliveira, V-H. F., Barlow, J., Gardner, T., Louzada, J., 2017. Do we select the best metrics for assessing land use effects on biodiversity? Basic Appl. Ecol. 21, 85-93.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. https://cran.r-project.org/web/packages/vegan/vegan.pdf

Peck , S.B., Howden, H.F., 1984. Response of a dung beetle guild to different sizes of dung bait in a Panamanian rainforest. Biotropica 16, 235–238.

Peyras, M., Vespa, N.I., Bellocq, I., Zurita, G.A., 2013. Quantifying edge effects: t,he role of habitat contrast and species specialization. J. Insect Conserv. 17, 807-820.

Pimm, S.L., Raven, P., 2000. Extinction by numbers. Nature 403, 843-845.

Pineda, E., Moreno, C., Escobar, F., Halffter, G., 2005. Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. Conserv. Biol. 19, 400-410.

Philips, T. K., Pretorius, E., Scholtz, C.H., 2004. A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. Invertebrate System. 18, 53-88.

Pyrke, J.S., Roets, F., Samways, M.J., 2013. Importance of habitat heterogeneity in remnant patches for conserving dung beetles. Biodivers. Conserv. 22, 2857-2873.

Qie, L., Lee, T.M., Sodhi, N.S., Lim, S.H., 2010. Dung beetle assemblages on tropical land-bridge islands: small island effect and vulnerable species. J. Biogeogr. 38, 792-804.

Quintero, I. Roslin, T., 2005. Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. Ecol. 86, 3303-3311.

Quintero, I., Halffter, G., 2009. Temporal changes a community of dung beetles (Insecta: Coleoptera: Scarabaeinae) resulting from the modification and fragmentation of tropical rain forest. Acta Zool. Mex. 25, 625-649.

Qin, H., Yang, G. Provan J., Liu, J., Gao. L., 2017. Using MiddRAD-seq data to develop polymorphic microsatellite markers for an endangered yew species. Plant Divers. 39, 294-299.

Radtke, M.G., Williamson, G.B., 2005. Volume and linear measurements as predictors of dung beetle (Coleoptera: Scarabaeidae) biomass. An. Entomol. Soc. Am. 98, 548-551.

Raine, E.H., Gray, C.L., Mann, D.J., Slade, E.M., 2018. Tropical dung beetle morphological traits predict functional traits and show intraspecific differences across land uses. Ecol. Evol. 8, 8686-8696.

Rainio, J., Niemelä, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers. Conserv. 12, 487-506.

Reyes-Novelo,E., Delfin-González, H., Móron, M.A., 2007. Copro-necrophagous beetle (Coleoptera: Scarabaeidae) diversity in an agroecosystem in Yucatan, Mexico. R. Biol. Trop. 55, 83-99.

Rodenhouse, N.L., Sillett, T.S., Doran, P.J., Holmes, R.T., 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. Proc. Biol. Sci. 270, 2105-2110.

Rodrigues, M.M., Uchôa, M.A., Ide, S., 2013. Dung beetles (Coleoptera: Scarabaeoidea) in three landscapes in Mato Grosso do Sul, Brazil . Braz. J. Biol. 73, 211-220.

Roque, F.O., Corrêa, E.C., Valente-Neto, F., Stefan, G., Schulz, G., Souza, P.R.B., Motta, C.M., Bavutti, L.L.O., Colzani, E., Demétrio, M.F., Escarpinati, S.C., Silvestre, R., Vaz-de-Mello, F.Z., Siqueira, T., Quintero, J.M.O., 2017. Idiosyncratic responses of aquatic and terrestrial insects to different levels of environmental integrity in riparian zones in a karst tropical dry forest region. Austral Entomol. 56, 459-465.

Ros, M., Escobar, F., Halffter, G., 2011. How dung beetles respond to a human-modified variegated landscape in Mexican cloud forest: A study of biodiversity integrating ecological and biogeographical perspectives. Diversity Distrib. 18, 377-389.

Salomão, R.P., Iannuzzi, L., 2015. Dung beetle (Coleoptera, Scarabaeidae) assemblage of a highly fragmented landscape of Atlantic forest: from small to the largest fragments of northeastern Brazilian region. Rev. Bras. Entomol. 59, 126-131.

Salomão, R.P., Iannuzzi, L., 2017. How do regeneration stages of Caatinga forests influence the structure of dung beetle (Coleoptera: Scarabaeidae) Assemblage?. Coleopterists Bull. 71, 578-588.

Salomão, R.P., González-Tokman, D., Dátillo, W., López-Acosta, C., Favila, M.E., 2018a. Landscape structure and composition define the body condition of dung beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rainforest. Ecol. Indic. 88, 144-151.

Salomão, R.P., Pordeus, L.M.M., Lira, A.F.A., Iannuzzi, L., 2018. Edaphic beetle (Insecta: Coleoptera) diversity over a forest-matrix gradient in a tropical rainforest. J. Insect Conserv. 22, 511-519.

Sánchez-de-Jesús, H.A., Arroyo-Rodríguez, Andresen, E., Escobar, F., 2015. Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. Landscape Ecol. 31, 843-854.

Santos-Heredia, C., Andresen, E., Stevenson, P., 2011. Secondary seed dispersal by dung beetles in an Amazonian forest fragment of Colombia: Influence of dung type and edge effect. Integr. Ecol. 6, 399-408.

Santos-Heredia, C., Andresen, E., Zárate, D.A., Escobar, F., 2018. Dung beetles and their ecological functions in three agroforestry systems in the Lacandona rainforest of Mexico. Biodivers. Conserv. 27, 2379-2394.

Scheffler, P.Y., 2005. Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. J. Tropical Ecol. 21, 9-19.

Scholtz, C.H., Davis, A.L.V., Kryger, U., 2009. Evolutionary biology and conservation of dung beetles. Pensoft Publishers, Sofia-Moscow.

Schoolmeesters, P., 2018. Scarabs: World Scarabaeidae Database (version dec 2018). In: Species 2000 & ITIS Catalogue of Life, 2018 Annual Checklist (Roskov, Y., Abucay, L., Orrell, T., Nicolson, D., Bailly, N., Kirk, P.M., Bourgoin, T., DeWalt, R.E., Decock, W., De Wever A., Nieukerken, E. van, Zarucchi, J., Penev, L., eds.). Digital resource at www.catalogueoflife.org/annual-checklist/2018. Species 2000: Naturalis, Leiden, the Netherlands. ISSN 2405-884X.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Veddeler, D., Muhlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I., Tscharntke, T., 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. Ecol. Appl. 14, 1321-1333.

Shahabuddin., Schulze, C.H., Tscharntke, T., 2005. Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). Biodivers. Conserv. 14, 863-877.

Shahabuddin., 2010. Diversity and community structure of dung beetles (Coleoptera: Scarabaeidae) across a habitat disturbance gradient in Lore Lindu National Park, Central Sulawesi. Biodiversitas 11, 29-33.

Shahabuddin., Hidayat, P., Manuwoto, S., Noerdjito, W.A., Tscharntk, T., Schulze, C.H., 2010. Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. J. Tropical Ecol.26, 53-65.

Shahabuddin., 2011. Effect of land use change on ecosystem function of dung beetles: experimental evidence from Wallacea Region in Sulawesi, Indonesia. Biodiversitas 12, 177-181.

Shahabuddin, S., Hasanah, U., Elijonnahdi, E., 2014. Effectiveness of dung beetles as bioindicators of environmental changes in land-use gradient in Sulawesi, Indonesia. Biotropica 21, 48-58.

Sillet, T.S., Rodenhouse, N.L., Holmes, R.T., 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. Ecol. 85, 2467-2477.

Silva F.A.B., Costa, C.M.Q., Moura, R.C., Farias, A.I., 2010. Study of the dung beetle (Coleoptera: Scarabaeidae) community at two sites: Atlantic Forest and clear-cut, Pernambuco, Brazil. Environ. Entomol. 39, 359-367.

Silva, P.G., Vaz-de-Meloo, F.Z., DiMare, R.A., 2013. Diversity and seasonality of Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in Santa Maria, Rio Grande do Sul, Brazil. An. Acad. Bras. Cienc. 85, 679-697.

Silva, R., Coletti, F., Costa, D.A., Vaz-de-Mello, F.Z., 2014. Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) of forests and pastures of southwestern Brazilian Amazon: Survey of species and feeding guilds. Acta Amaz. 44, 345-352.

Silva, P.G., Hernández, M.I.M., 2015a. Scale-dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches. PLoS One 10, e0123030.

Silva, P.G., Hernández, M.I.M., 2015b. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. PLoS One 10, e0126112

Silva, P.G., Hernández, M.I.M., 2016. Spatial variation of dung beetle assemblages associated with forest structure in remnants of southern Brazilian Atlantic Forest. Rev. Bras. Entomol. 60, 73-81.

Silva, R., Pelissari, T.D., Krinski, D., Canale, G.,Vaz-de-Mello, F.Z., 2017. Abrupt species loss of the Amazonian dung beetle in pastures adjacent to species-rich forests. J. Insect Conserv. 21, 487-494.

Silva, PG., Lobo, J.M. Hensen, M.C., Vaz-de-Mello, F.Z., Hernández, M.I.M., 2018a. Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. Divers. Distrib. 24, 1277–129.

Silva, P.G. Hernández, M.I.M., Heino, J., 2018b. Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. Divers. Distrib. 24, 1674-1686.

Silveira, J.M., Louzada, J., Barlow, J., Andrade, R., Mestre, L., Solar, R., Lacau, S., Cochrane, M.A., 2015. A Multi-Taxa assessment of biodiversity change after single and recurrent wildfires in a Brazilian Amazon Forest. Biotropica 48, 170-180.

Simelane, T.S., 2010. Impacts of traditional land uses on biodiversity outside conservation areas: effects on dung beetle communities of Vaalbos National Park. Afr. J. Ecol. 48, 490-501.

Slade, E.M, Mann, D.J., Villanueva, J.F., Lewis, O.T., 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. J. Animal Ecol. 76, 1094-1104.

Slade, E.M., Mann, D.J., Villanueva, J.F., Lewis, O.T., 2011. Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. Biol. Conserv. 144, 166-174.

Smith, R.J., 2017. Solutions for loss of information in high-beta-diversity community data. Methods Ecol. Evol. 8, 68-74

Spector, S., 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation.Coleopterists Bull. 60, 71-83.

SU, J. C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conserv. Biol. 18, 167-173.

Svensson, E., Sinvervo, B., 2000. Experimental excursions on adaptive landscapes: density-dependent selection on egg size. Evol. 54, 1396-1403.

Templeton, A.R., 2013. Genética de populações e teoria microevolutiva. Sociedade Brasileira de Genética. 706pp.

Tonelli, M., Verdú, J.R., Zunino, M., 2018. Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. Biodivers. Conserv. 27, 189-204.

Tokeshi, M., 1993. Species abundance patterns and community structure. Adv. Ecol. Research, 24, 111-186.

Tregidgo, D., J. Qie, L., Barlow, Sodhi, N.S., Lee-Hong, S.L., 2010. Vertical stratification responses of an arboreal dung beetle species to tropical forest fragmentation in Malaysia. Biotropica 42, 521-525.

Ueda, A., Dwidadra, D., Noerdjito, W.A., Kon, M., Ochia, T., Takahashi, M., Fukuyama, K., 2015. Effect of habitat transformation from grassland to *Acacia mangium* plantation on dung beetle assemblage in East Kalimantan, Indonesia. J. Insect Conserv. 19, 765-780.

Vaughan, I.P., Ormerod, S.J., 2003. Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. Conserv. Biol. 17, 1601-1611.

Vaz-de-Mello, F.Z., Edmonds, W.D., Ocampo, F.C., Schoolmeesters, P., 2011. A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). Zootaxa 2854, 73p.

Verdú, J.R., Moreno, C.E., Sánchez-Rojas, G., Numa, C., Galante, E., Halffter, G., 2007. Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. Biol. Conserv. 40, 308-317.

Verdú, J.R., Galante, E., 2004. Behavioral and morphological adaptations for a low-quality resource in semi-arid environments: dung beetles (Coleoptera, Scarabaeoidea) associated with the European rabbit (*Oryctolagu cuniculus* L.). J. Nat. Hist. 38, 705-715.

Verdú, J.R., Lobo, J.M., 2008. Ecophysiology of thermoregulation in endothermic dung beetles: Ecological and geographical implications. Insect Ecol. Conserv. 2008, 1-28.

Viegas, G., Stenert, C., Schulz, U.H., Maltchik, L., 2014. Dung beetle communities as biological indicators of riparian forest widths in southern Brazil. Ecol. Indic. 36, 703-710.

Vieira, L., Louzada, J., Spector, S., 2008. Effects of degradation and replacement of southern Brazilian coastal sandy vegetation on the dung beetles (Coleoptera: Scarabaeidae). Biotropica 40, 719-727.

Villada-Bedoya, S., Cultid-Medina, C.A., Escobar, F., Guevara, R., Zurita, G., 2017. Edge effects on dung beetle assemblages in an Andean mosaic of forest and coffee plantations. Biotropica 49, 195-205.

Vulinec, K., 2000. Dung beetles (Coleoptera: Scarabaeidae), monkeys, and conservation in Amazonia. Flor. Entomol. 83, 229-241.

Vulinec. K., 2002. Dung Beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. Biotropica 34, 297-309.

Vulinec, K., Lambert, J.E., Mellow, D.J., 2006. Primate and dung beetle communities in secondary growth rain forests: implications for conservation of seed dispersal systems. Int. J. Primat. 27, 855-879.

Vulinec, K., Lima, A.P. Carvalho-Jr. E.A.R., Mellow, D.J., 2008. Dung beetles and long-term habitat fragmentation in Alter do Chão, Amazônia, Brazil. Tropical Conserv. Sci. 1, 111-121.

Wassenaar, T.D., Van aarde, R.J., Pimm, S.L., Ferreira, S.M., 2005. Community convergence in disturbed subtropical dune forests. Ecol. 86, 655-666.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251

Williams, D.R., Alvarado, F., Green, R.E., Manica, A., Phalan, B. *et al*. 2017. Land-use strategies to balance livestock production, biodiversity conservation and carbon storage in Yucatan, Mexico. Glob. Change Biol. 23, 5260-5272.

Wright, S.J., 2010. The future of tropical forests. Ann. N. Y. Acad. Sci. 1195, 1-27.

Supplementary material

Table S1. Response variables of dung beetles used in studies on human-modification habitats in tropical forests.

	Abundance	Richness/Diversity	Body mass/size	Resource relocation	Diel activity	Ecological functions	Food preference	Functional diversity	Wing loading/area	Stress physiological	Body shape	Movement	Genetic parameters
Aguilar-Amuchastegui and Henebry 2007	+	+											
Almeida et al. 2011	+	+	+	+									
Alvarado et al. 2017	+	+	+										
Alves and Hernandez 2017											+		
Amézquita and Fávila 2010	+		+	+		+							
Amézquita and Fávila 2011	+	+	+	+	+	+							
Andrade et al. 2014	+	+	+	+									
Andrade et al.2014	+	+											
Andresen and Laurence 2007	+	+			+								
Andresen 2003	+	+	+			+							
Andresen 2007	+	+	+				+						
Arellano and Hallfter 2003	+	+											
Arellano et al. 2005	+	+	+	+			+						
Arellano et al. 2008	+											+	
Arellano et al. 2008	+	+											
Audino et al. 2014	+	+	+	+	+		+	+					
Audino et al. 2017	+	+	+	+	+		+						
Avendano-Mendonza et al. 2005	+	+	+	+									
Barlow et al. 2007	+	+											
Barlow et al. 2010	+	+											
Barlow et al. 2012	+	+											
Barlow et al. 2016	+	+											
Barnes et al. 2014a	+		+			+		+	+		+		
Barnes et al. 2014b	+	+											
Barragán et al. 2011	+	+	+	+	+		+	+					
Batilani-Filho and Hernandez 2017	+	+	+	+		+	+						
Beiroz et al. 2017	+	+	+	+	+		+						
Beiroz et al. 2018	+	+	+	+	+		+						
Bett et al. 2014	+	+	+										

	Abundance	Richness/Diversity	Body mass/size	Resource relocation	Diel activity	Ecological functions	Food preference	Functional diversity	Wing loading/area	Stress physiological	Body shape	Movement	Genetic parameters
Bicknell et al. 2014	+	+											
Bitencourt et al. 2016	+	+											
Blaum et al. 2009	+	+											
Bogoni et al. 2016	+	+	+	+			+						
Boonrotpong et al. 2004	+	+											
Boonrotpong et al. 2012	+	+			+								
Botes et al. 2006	+	+											
Bourg et al. 2016	+	+					+						
Braga et al. 2012	+	+	+			+							
Braga et al. 2013	+	+	+			+							
Caballero and León-Cortés 2012	+	+											
Cajaiba et al. 2017a	+	+											
Cajaiba et al. 2017b	+	+											
Campos & Hernandez 2013	+	+	+	+			+						
Campos & Hernandez 2015a	+	+	+										
Campos & Hernandez. 2015b	+	+											
Carpio et al. 2009	+	+	+										
Chapman & Chapman 2003	+	+	+	+	+								
Costa et al. 2013	+	+											
Costa et al. 2014	+	+											
Costa et al. 2017	+	+	+										
Culot et al. 2011	+	+				+							
Culot et al. 2013	+	+	+										
Cultid-Medina and Escobar 2016	+	+	+										
Davis and Philips 2005	+	+											
Davis and Philips 2009	+	+											
Davis and Sutton 1998	+	+											
Davis 1994	+	+											
Davis et al. 2000	+	+											
Davis 2000	+	+											
Davis et al. 2001	+	+											
Davis et al. 2002	+	+											
Davis et al. 2003	+	+											
Davis et al. 2012	+	+											

	Abundance	Richness/Diversity	Body mass/size	Resource relocation	Diel activity	Ecological functions	Food preference	Functional diversity	Wing loading/area	Stress physiological	Body shape	Movement	Genetic parameters
Davis et al. 2013	+	+	+										
Díaz et al. 2010	+	+	+	+	+		+						
Edwards et al. 2010	+	+											
Edwards et al. 2014a	+	+											
Edwards et al. 2014b	+	+	+	+	+		+	+					
Edwards et al. 2017	+	+	+	+	+								
Escobar 2004	+	+	+	+	+								
Escobar et al. 2007	+	+											
Estrada and Coates-Estrada 2002													
Estrada et al. 1998	+	+											
Estrada et al. 1999	+	+											
Farias et al. 2015	+	+	+										
Feer and Hingrat 2005	+	+	+										
Feer 2008	+	+											
Feer 2013	+	+	+										
Ferreira-Neto et al. 2017													+
Filgueiras et al. 2011	+	+	+	+			+						
Filgueiras et al. 2015	+	+	+										
Filgueiras et al. 2016	+	+											
França et al. 2016a	+	+	+										
França et al. 2016b	+									+			
França et al. 2017	+	+	+			+							
França et al. 2018	+	+	+			+							
Gardner et al. 2008a	+	+	+										
Gilroy et al. 2014a	+	+											
Gilroy et al. 2014b	+	+											
Gómez-Cifuentes et al. 2017	+	+	+	+				+					
Gonzáles-Vainer et al. 2012	+	+											
Gray et al. 2014	+	+	+	+	+	+							
Gray et al. 2016	+	+				+							
Gries et al. 2011	+	+											
Grimbacher et al. 2006	+	+											
Halffter and Arellano 2002	+	+	+		+		+						
Halffter at al. 2007	+	+	+				+						

	Abundance	Richness/Diversity	Body mass/size	Resource relocation	Diel activity	Ecological functions	Food preference	Functional diversity	Wing loading/area	Stress physiological	Body shape	Movement	Genetic parameters
Halffter et al. 1992	+	+	+	+	+		+						
Hanski et al. 2007	+												
Harvey et al. 2006	+	+											
Hayes et al. 2009	+	+											
Hernandez and Vaz de Mello 2009	+	+											
Hernandez et al. 2014	+	+											
Heusi-Silveira et al. 2012	+	+											
Hill 1995	+	+											
Hill 1996	+	+			+		+						
Holloway et al. 1992	+	+											
Horgan 2005	+	+	+			+							
Horgan 2006	+	+	+	+									
Horgan 2007	+	+	+										
Horgan 2008	+	+	+		+		+						
Horgan 2009	+	+	+										
Hosaka et al. 2014a	+	+											
Hosaka et al. 2014b	+	+	+	+		+							
Howdan and Nealis 1975	+	+											
Jacobs et al. 2010	+	+											
Kenyon et al. 2016	+	+	+	+		+							
Kessler et al. 2009	+	+											
Kishimoto-Yamada et al. 2013	+	+											
Klein 1989	+	+											
Korasaki et al. 2012	+	+		+									
Korasaki et al. 2013	+	+	+										
Kotze & Lawes. 2007	+	+											
Kudavidanage et al. 2012	+	+		+		+							
Lachat et al. 2004													
Lam et al. 2013	+	+											
Larsen 2012	+	+											
Larsen et al. 2005	+	+	+			+							
Larsen et al. 2008	+	+	+	+	+				+				
LaScaleia et al. 2018	+	+											
Liberal et al. 2011	+	+											

	Abundance	Richness/Diversity	Body mass/size	Resource relocation	Diel activity	Ecological functions	Food preference	Functional diversity	Wing loading/area	Stress physiological	Body shape	Movement	Genetic parameters
Lopes et al. 2011	+	+			+								
Louzada et al. 2010a	+	+		+									
Louzada et al. 2010b	+	+											
Marsh et al. 2018	+	+											
Martello et al. 2016	+	+		+									
McGeoch et al. 2002	+	+											
Medina et al. 2002	+	+											
Moctezuma et al. 2016	+	+											
Molina et al. 1999	+	+											
Montoya-Molina et al. 2016	+	+											
Navarrete and Halffter 2008	+	+	+	+	+		+						
Neita and Escobar 2012	+	+	+	+									
Neves et al. 2010	+	+											
Nichols et al. 2013	+	+	+	+		+							
Nielsen 2007	+	+	+										
Niino et al. 2014	+	+	+		+								
Nyeko 2009	+	+	+	+									
Oldekop et al. 2012	+	+											
Peyras et al. 2013	+	+											
Pineda et al. 2005	+	+	+				+						
Pyrke et al. 2013	+	+											
Qie et al. 2010	+	+	+		+		+						
Quintero and Halffter 2009	+	+	+	+	+								
Quintero and Roslin 2005	+	+											
Reyes-Novelo et al. 2007	+	+	+	+	+		+						
Rodrigues et al. 2013	+	+											
Roque et al. 2017	+	+											
Ros et al. 2011	+	+	+										
Salomão & Iannuzzi 2015	+	+											
Salomão& Iannuzzi 2017	+	+											
Salomão et al. 2018a	+		+							+			
Salomão et al. 2018b	+	+											
Sánchez-de-Jesús et al. 2015	+	+	+										
Santos-Heredia et al. 2011	+	+				+							

	Abundance	Richness/Diversity	Body mass/size	Resource relocation	Diel activity	Ecological functions	Food preference	Functional diversity	Wing loading/area	Stress physiological	Body shape	Movement	Genetic parameters
Santos-Heredia et al. 2018	+	+	+			+							
Scheffler 2005	+	+	+										
Schulze et al. 2004	+	+											
Shahabuddin 2010	+	+											
Shahabuddin et al. 2005	+	+	+										
Shahabuddin et al. 2010	+	+											
Shahabuddin 2011						+							
Shahabuddin et al. 2014	+	+											
Silva e Hernandez 2015	+		+	+	+		+	+					
Silva et al. 2010													
Silva et al. 2013	+	+		+									
Silva and Hernandez 2016	+	+	+										
Silva et al. 2017													
Silveira et al. 2015	+	+											
Simelane 2010	+	+		+									
Slade et al. 2011	+	+	+	+	+	+							
Steenkamp and Chown 2006	+	+	+	+									
Tregidgo et al. 2010	+	+											
Ueda et al. 2015a	+	+	+										
Verdú et al. 2007													
Viegas et al. 2014	+	+											
Vieira et al. 2008													
Villada-Bedoya et al. 2017	+	+											
Vulinec et al. 2008	+	+	+										
Vulinec 2000	+	+	+			+							
Vulinec 2002	+	+	+	+	+	+							
Vulinec et al. 2006	+	+	+	+	+	+							
Wassenaar et al. 2005	+	+											
Williams et al. 2017	+	+											

CONSIDERAÇÕES FINAIS

O objetivo geral desta tese foi fornecer uma melhor compreensão de como modificações feitas pelo homem na paisagem influenciam a biodiversidade em regiões de florestas tropicais. Utilizando os escarabeíneos como táxon focal, foram avaliadas as alterações que ocorrem no grupo (tais como abundância e riqueza de espécies, composição, grupos funcionais, características morfológicas) em paisagens com diferentes graus de cobertura florestal e densidade de borda e cobertura de pastagem. Para fazer isso, foram amostrados escarabeíneos em paisagens localizadas na Floresta Atlântica do sul da Bahia, Brasil. Além disso, foi realizada uma revisão completa da literatura sobre as variáveis respostas utilizadas para escarabeíneos em estudos de modificação de habitat, o que ajudou a elucidar o estado da arte do uso de besouros escarabeíneos como indicadores ambientais bem como a identificar as principais lacunas que poderão servir de base para futuros estudos.

Os resultados do primeiro estudo fornecem uma base sobre os efeitos da perda da cobertura florestal sobre a diversidade de besouros escarabeíneos na Floresta Atlântica, um dos principais *hotspots* globais de biodiversidade. Como conseqüência da redução de cobertura florestal, a perda de espécies de grupos funcionais distintos fornece sinais de que diferentes funções ecossistêmicas podem estar sendo negativamente afetadas. Além disso, foi encontrado, no segundo estudo, que a densidade de bordas foi a principal variável responsável pelas mudanças na comunidade de escarabeíneos. Entretanto, a porcentagem de cobertura de floresta e pastagem em escala de paisagem também influenciou significativamente várias respostas dos besouros. Estes resultados sugerem a necessidade de estratégias de conservação e manejo voltadas para a proteção da Floresta Atlântica, que visem a promoção da recuperação de cobertura florestal e redução na cobertura de pastagens e densidade de bordas em nível de paisagem.

A revisão de literatura realizada no terceiro estudo permitiu acessar um amplo nível de detalhamento acerca das variáveis respostas utilizadas em estudos sobre modificação de habitat, sendo abundância, riqueza de espécies e massa corporal as mais utilizadas, ao passo que outras variáveis como parâmetros genéticos e movimento ainda são pouco exploradas. Reconhecendo que a seleção das variáveis respostas é um passo crucial para avaliar os efeitos das alterações ambientais, além de indicar lacunas, foram propostas soluções para problemas enfrentados por diversos pesquisadores que utilizam besouros escarabeíneos para estudar os efeitos de mudanças ambientais.

Ao considerar estes trabalhos em conjunto, nota-se que o primeiro é completado pelo segundo e que o terceiro se destaca pelo detalhamento das variáveis respostas utilizadas em estudos sobre modificação de habitats em florestas tropicais. Tal estratégia no último capítulo foi utilizada como forma de entender como as variáveis respostas estão sendo utilizadas neste grupo de besouros. O cumprimento dos objetivos dos estudos realizados nesta tese será ainda mais satisfatório se as análises realizadas servirem como parâmetro para a utilização de ferramentas em estudos ulteriores acerca de modificação de habitat em paisagens tropicais e influenciarem discussões sobre estratégias para a conservação da biodiversidade, sobretudo com besouros escarabeíneos.