UNIVERSIDADE FEDERAL DE LAVRAS

LÍVIA DORNELES AUDINO

ESTRUTURAÇÃO DA COMUNIDADE DE SCARABAEINAE EM UM GRADIENTE DE RESTAURAÇÃO DE FLORESTA ATLÂNTICA

LAVRAS – MG
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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Entomologia, área de concentração em Entomologia, para a obtenção do título de Doutor.

Orientador
Dr. Júlio Neil Cassa Louzada

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Aos meus pais, Pérsio e Denise, por compreenderem minha constante ausência, e por terem sido os principais motivadores da busca por um futuro melhor

DEDICO

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“The next century will, I believe, be the era of restoration in ecology”

E. O. Wilson (1992)

RESUMO GERAL

A restauração ecológica tem sido considerada uma estratégia importante para reduzir a perda da biodiversidade e manter as funções ecossistêmicas. É necessário, portanto, conhecer sua real eficácia em relação à conservação e à manutenção dos diferentes componentes dos ecossistemas. Além disso, é preciso encontrar bases teóricas que fundamentem as práticas de restauração. A presente tese teve como objetivo geral estudar a estruturação da comunidade de besouros escarabeíneos em um gradiente de restauração de Floresta Atlântica, determinando se as trajetórias de estruturação convergem ou divergem de sistemas referência e degradados e analisando quais fatores são os principais determinantes desta estruturação. Para isso, os besouros foram amostrado em 15 áreas de restauração florestal de diferentes idades e em cinco áreas de floresta primária, secundária de estágio avançado (sistemas referência) e de pastagem (sistema degradado). A comunidade dos besouros foram caracterizadas de acordo com a diversidade e a composição de características funcionais. Todas as áreas de restauração foram mensuradas em relação às suas condições ambientais locais (estrutura da vegetação e solo), contexto de paisagem (porcentagem de floresta ao redor e distância de reservas ambientais) e padrões espaciais (PCNMs). O sucesso da restauração foi avaliado por meio de medidas da diversidade de espécies, composição e diversidade funcional. Os resultados mostram que as áreas de restauração conseguem abrigar espécies florestais e estão convergindo em direção ao sistema referência de acordo com a similaridade na composição de espécies. Contudo, a diversidade de espécies e funcional é extremamente baixa, contendo padrões similares aos das pastagens. Isso mostra que 18 anos não foram suficientes para recuperar uma comunidade diversa e estável. Também demonstrou-se a importância de se utilizar mais de uma métrica para caracterizar as comunidades encontradas nas áreas de restauração, a fim de obter uma melhor avaliação sobre o seu sucesso. A composição de espécies e características funcionais dos escarabeíneos foram predominantemente determinadas por processos baseados em nicho, principalmente por filtros ambientais locais. Os padrões espaciais e de paisagem tiveram pequena ou nenhuma contribuição independente, apresentando efeitos compartilhados um com o outro e com as variáveis ambientais. A dispersão dos escarabeíneos foi, principalmente, determinada por respostas específicas de cada espécie às variáveis ambientais. Também documentou-se como estas variáveis ambientais e de paisagem tornam as áreas de restauração mais similares à floresta primária em relação à composição de espécies e de características funcionais.

Palavras-chave: Sucesso de restauração. Características funcionais. Filtros ambientais. Limites de dispersão. Paisagem.

GENERAL ABSTRACT

Restoration ecology is being considered an important strategy to reduce biodiversity loss and maintain ecosystem functions. Thus, it is necessary to know the real efficacy of this strategy in relation to the conservation and maintenance of different ecosystem components. Besides, it is important to find theoretical basis to support restoration practices. The general objective of the present thesis was to study dung beetle community assembly in an Atlantic Forest restoration chronosequence, determining whether the assembly trajectories converge or diverge from the reference and degraded systems and analyzing which factors are the main determinants of this assembly. So, we sampled dung beetles in 15 forest restoration areas of different ages and in five areas of primary forest, old secondary forest (reference systems) and introduced pastures (degraded system). Dung beetle communities were categorized according to functional trait diversity and composition. All restoration areas were measured in relation to its local environmental conditions (vegetation structure and soil), landscape context (forest cover percentage surrounding and distance to environmental reserves) and spatial patterns (PCNM's). Restoration success was evaluated using measures of species diversity, composition and functional diversity. Our results show that restoration areas have the capacity to host forest-restricted species and are progressing towards the reference systems according to species composition similarity. However, species diversity and functional diversity was extremely low, presenting similar patterns to the ones found in pastures (starting point of the restoration). This demonstrates that 18 years was not enough to recover a diverse and stable dung beetle community. We also underscore the importance of utilizing more than one metric to characterize assemblages found in restored areas in order to better evaluate restoration success. Assembly of both species and functional trait composition were predominantly driven by niche-based processes, mainly by the influence of local environmental filters. Landscape and spatial descriptors had little or none independent contributions, presenting mostly shared effects with each other and local environment. Dung beetle dispersal is mostly determined by species specific environmental responses. However, the importance of stochastic factor cannot be completely rule out. We also document how these environment and landscape variables make the restoration areas more similar to the primary forest in relation to species and functional trait composition.

Keywords: Restoration success. Functional traits. Environmental filters. Dispersal limitation. Landscape.

SUMÁRIO

PRIMEIRA PARTE

PRIMEIRA PARTE

1 INTRODUÇÃO

Desde o seu reconhecimento como um campo da ciência, há cerca de 30 anos, a restauração ecológica tem sido considerada uma estratégia importante para reverter os danos causados pelos seres humanos no ambiente terrestre e aquático. Contudo, restaurar um ecossistema não é uma tarefa fácil. Pode-se, facilmente, comparar as práticas de restauração com a montagem de um difícil quebra-cabeça, em que é necessário encaixar milhares de peças altamente dinâmicas, que constituem os ecossistemas. Isso se torna ainda mais difícil em florestas tropicais, devido à sua alta complexidade e número de espécies envolvidas. Mesmo assim, a restauração ecológica tem sido cada vez mais empregada no mundo inteiro, principalmente para garantir a conservação da diversidade biológica e a manutenção das funções de um ambiente.

A ecologia da restauração é uma ciência recente e, apesar do seu grande crescimento teórico e prático, nos últimos anos, a escassez de informações é ainda uma realidade. Além disso, na maioria dos estudos existentes utilizaram-se plantas como táxon-foco, mostrando padrões que podem não se encaixar para outros grupos. Estes fatores podem interferir grandemente no sucesso dos esforços de restauração. Por este motivo, fica clara a importância da realização de estudos sobre esta temática, que envolvam tanto outros grupos taxonômicos como a utilização de diferentes abordagens, possibilitando o avanço desta importante área do conhecimento. Duas grandes questões que têm sido levantadas como essenciais para colaborar com o avanço da restauração ecológica são a avaliação do sucesso dos esforços de restauração existentes e a conexão entre teorias ecológicas e a prática da restauração.

A investigação do sucesso da restauração é difícil, pois é necessário encontrar sistemas referência de qualidade para fins de comparação, e investigar sua eficácia por meio de métricas que possam refletir diferentes aspectos das comunidades e ecossistemas. É com este tipo de avaliação que se pode saber se a restauração está sendo realmente eficaz, em termos de conservação da biodiversidade e fornecimento de funções e serviços ecológicos. Além disso, é possível identificar a presença de fatores que estejam limitando este sucesso. Portanto, conhecer o progresso da restauração é um ponto crítico e uma prioridade nos estudos sobre este ramo da ciência.

Outra questão que tem sido muito debatida, atualmente, é sobre a conexão entre teoria científica e prática, e o quanto esta abordagem é capaz de melhorar os métodos de restauração. Inicialmente, a restauração ecológica era uma ciência muito mais experimental do que teórica. Suas técnicas eram fundamentadas em estudos de caso, utilizando a abordagem de tentativa e erro, o que não permitia extrapolar os resultados de um sistema para outro e gerar avanços nesta área do conhecimento. Recentemente, reconheceu-se a importância de basear os projetos de restauração em teorias ecológicas, como, por exemplo, a de sucessão e estruturação de comunidades biológicas. Contudo, ainda existe uma grande necessidade em avançar nos estudos que conectem as bases teóricas da restauração com suas práticas. Avanços na interação destes dois campos irão, indubitavelmente, possibilitar o controle mais preciso da restauração e conservação de ecossistemas naturais, em relação ao que temos hoje.

A presente tese conta com dois capítulos, em formato de artigo, nos quais se abordam estes importantes temas dentro da restauração ecológica. No primeiro capítulo, o sucesso da restauração de uma floresta tropical (Floresta Atlântica) foi avaliado utilizando-se besouros escarabeíneos (Coleoptera: Scarabaeinae) como bioindicadores da qualidade ambiental. Para estimar esta eficácia, utilizaram-se diferentes métricas da comunidade, como diversidade de espécies, composição de espécies e diversidade funcional. Por meio destas métricas é possível identificar padrões de identidade e diversidade das comunidades que se encontram nas áreas de restauração, assim como do funcionamento destes ecossistemas. Nesse contexto, investigaram-se os padrões de estruturação da comunidade de Scarabaeinae ao longo de um gradiente de idades de restauração de Floresta Atlântica. Adicionalmente, compararam-se as áreas de restauração com sistemas referência (floresta primária e floresta secundária de estágio avançado) e sistema degradado (pastagem), para avaliar o sucesso de restauração.

No segundo capítulo avalia-se a importância da teoria da estruturação de comunidades (teoria neutra e de nicho) para guiar os esforços de restauração. Para isso, investigou-se a importância relativa de condições ambientais locais, contexto de paisagem e padrões espaciais para determinar a composição de espécies e de características funcionais dos escarabeíneos em um gradiente de 15 áreas de restauração de floresta Atlântica. Também se verificou como variáveis ambientais locais e de paisagem influenciam a similaridade das áreas de restauração com o sistema referência, em relação à composição de espécies e às características funcionais, indicando valores potenciais destas variáveis que garantam uma maior similaridade.

2 REFERENCIAL TEÓRICO

2.1 Florestas tropicais: estado atual e perspectivas futuras

As florestas tropicais ocupam menos que 10% da superfície da Terra e são consideradas um dos ecossistemas mais importantes, em âmbito mundial (MAYAUX et al., 2005; MYERS, 1992). Elas abrigam, no mínimo, metade de todas as espécie do planeta e fornecem serviços ecológicos significantes para a humanidade (DIRZO; RAVEN, 2003; GARDNER et al., 2009; MYERS, 1992). Estes serviços ecossistêmicos incluem captura e armazenamento de carbono, regulação do clima, regulação da qualidade do ar e da água, conservação da biodiversidade, provisão de bens como alimento, fibra, água e combustível e controle de pragas e doenças (BALA et al., 2007; BERENGUER et al., 2014; FAO, 2012; FEARNSIDE, 1997; FOLEY et al., 2005).

Apesar de sua reconhecida importância, as florestas tropicais estão sendo degradadas e desaparecendo rapidamente, à medida que a população humana e a economia aumentam (GARDNER et al., 2013; GEIST; LAMBIN, 2002; LEWIS, 2009; WRIGHT, 2005). A população das regiões tropicais está crescendo exponencialmente, saindo de 1,8 bilhão, em 1950, para 4,9 bilhões de habitantes, em 2000. Este cenário tende a ficar pior em um futuro próximo, quando a população e a economia deverão crescer ainda mais rápido (WRIGHT, 2005).

Para satisfazer às necessidades humanas econômicas, grandes áreas de floresta tropical têm sido alteradas ou removidas e convertidas em outros sistemas de uso da terra (FOLEY et al., 2005; HANSEN; STEHMAN; POTAPOV, 2010). Grande parte deste desmatamento e degradação é recente, apresentando um pico nas décadas de 1980 e 90 (WRIGHT, 2005). Esta situação está sendo impulsionada, principalmente, pela expansão agrícola e da silvicultura, a urbanização e a ampliação de infraestruturas (GEIST; LAMBIN, 2002). De acordo com as estimativas, entre 1990 e 1997, aproximadamente 5,8 milhões de hectares de floresta tropical úmida foram desmatados a cada ano e 2,3 milhões de hectares foram degradados (ACHARD et al., 2002). Entre os anos de 2000 e 2005, mais 274.615 km^2 foram perdidos, o que representa 1,4% das florestas tropicais úmidas do mundo (ASNER et al., 2009). No início do século XX, quase metade das florestas tropicais foi desmatada (WRIGHT, 2005). Este número está altamente associado com a expansão agrícola, sendo responsável por quase 96% de todos os casos de desmatamento (ACHARD et al., 2002; GEIST; LAMBIN, 2002; MAYAUX et al., 2005).

Estas mudanças têm alterado a identidade das paisagens tropicais e são consideradas uma das principais causas da perda da biodiversidade (FOLEY et al., 2005; TURNER; LAMBIN; REENBERG, 2007). Atualmente, estas paisagens representam mosaicos contendo remanescentes de floresta tropical imersos em uma matriz de sistemas antropizados, que variam desde florestas secundárias até sistemas de uso introduzidos sem cobertura de dossel (LEWIS, 2009; WRIGHT, 2005). Muitos autores sugerem que este novo cenário pode causar um número total de extinções similar àqueles encontrados nos eventos de extinção em massa da história geológica da Terra (e.g. DIRZO; RAVEN, 2003; LAURANCE, 2007). De acordo com Dirzo and Raven (2003), estas extinções podem atingir mais de um terço de todas as espécies do planeta. Além das consequências para a biodiversidade, o desmatamento das florestas tropicais pode também causar um aumento nos níveis de dióxido de carbono da atmosfera, contribuindo para acelerar as mudanças climáticas (SALA et al., 2000).

Existe um grande debate, na literatura, sobre qual a forma mais eficaz de conservar a biodiversidade e os processos ecossistêmicos das florestas tropicais (BARLOW et al., 2007; CHAZDON, 2008; DENT; WRIGHT, 2009; GIBSON et al., 2011). Muitos pesquisadores defendem que remanescentes de floresta primária são insubstituíveis para sustentar a biodiversidade tropical (e.g. BARLOW et al., 2007; GARDNER et al., 2007; GIBSON et al., 2011). Outros acreditam que é possível manter os serviços ecológicos e a conservação da biodiversidade por meio do aumento do número de áreas de floresta secundária (e.g. CHAZDON, 2008; DENT; WRIGHT, 2009; WRIGHT; MULLER-LANDAU, 2006).

É inegável que áreas de floresta primária são essenciais para espécies especialistas de floresta (BARLOW et al., 2007; GIBSON et al., 2011). No entanto, apenas 9,8% das florestas tropicais se encontram em áreas de proteção integral (GARDNER et al., 2009). Embora este número tenha aumentado nos últimos anos, muitas áreas protegidas de floresta tropical não estão sendo eficazes, a longo prazo, para conservar a diversidade biológica e funcional (LAURANCE et al., 2012). Isso vem acontecendo, principalmente, devido às intervenções humanas e à influência de sistemas modificados ao redor destas áreas (LAURANCE et al., 2012).

Diante desta realidade, é essencial conectar a proteção de áreas de floresta primária com o manejo dos diferentes sistemas de uso da terra que compõem as matrizes das paisagens tropicais (GARDNER et al., 2009; MELO et al., 2013; PERFECTO; VANDERMEER, 2008). Adicionalmente, a restauração de florestas tropicais também tem sido proposta como uma excelente alternativa para reverter os danos já causados (BANKS-LEITE et al., 2014; CHAZDON, 2008).

2.1.1 Floresta Atlântica

A Floresta Atlântica é uma das florestais tropicais mais ameaçadas do mundo, tendo sido identificada como um dos cinco mais importantes "hotspots" de biodiversidade (MYERS et al., 2000; SLOAN et al., 2014). Ela abriga cerca de 1% a 8% de todas as espécies do planeta, sendo muitas exclusivas deste bioma (MYERS et al., 2000). Até o momento, já foram registradas 20.000 espécies de plantas, 263 espécies de mamíferos, 963 de aves, 306 de répteis, 475 de anfíbios e 350 espécies de peixes de água doce (MITTERMEIER et al., 2005). Deste total, 8.732 espécies são endêmicas, o que representa cerca de 40% das espécies citadas acima (MITTERMEIER et al., 2005). Contudo, muitas das espécies da Floresta Atlântica têm sido extintas ou estão ameaçadas de extinção, devido ao longo histórico de exploração deste bioma (BROOKS; TOBIAS; BALMFORD, 1999; RODRIGUES et al., 2009; TABARELLI et al., 2010)

A Floresta Atlântica cobria, originalmente, cerca de 150 milhões de hectares no território brasileiro, parte da Argentina e do Paraguai (RIBEIRO et al., 2009; SOS MATA ATLÂNTICA, 2014). No Brasil, se estende do norte do Rio Grande do Sul ao sul do Rio Grande do Norte, abrangendo cerca de 17 estados brasileiros (17,4% do território brasileiro) (METZGER, 2009; RANTA et al., 1998; SOS MATA ATLÂNTICA, 2014). O desmatamento e a degradação da Floresta Atlântica começaram com a colonização europeia, há mais de 500 anos, sendo o primeiro bioma brasileiro a ser afetado (DEAN, 1997; RODRIGUES et al., 2009). Todo este processo esteve intimamente relacionado com a exploração econômica de produtos advindos da floresta, assim como pela transformação das áreas florestais em diferentes sistemas de uso da terra.

Tudo começou com a exploração do pau-brasil (*Caesalpinia echinata*), pelos portugueses, no início do século XVI. Logo, esta exploração seletiva deu lugar ao desmatamento das florestas para o cultivo da cana-de-açúcar e a implantação de pastagens. Durante os séculos XIX e XX, o desenvolvimento das plantações de café e de *Eucalyptus* e a expansão urbana foram também grandes responsáveis pelo desmatamento da Floresta Atlântica (DEAN, 1997; METZGER, 2009; MORELLATO; HADDAD, 2000; RANTA et al., 1998).

Apesar das restrições legais, este desmatamento continua até hoje, atingindo taxas de 350 km^2 por ano (METZGER, 2009).

A Floresta Atlântica era uma das maiores florestas tropicais da América. Hoje, ela representa um dos grandes exemplos de paisagens fragmentadas mundiais, estando distribuída em remanescentes florestais de pequeno tamanho (< 50 ha), imersos em uma matriz de ambientes modificados pelas atividades humanas (RANTA et al., 1998; RIBEIRO et al., 2009). Atualmente, o Brasil tem apenas 12% da sua cobertura florestal original de Mata Atlântica (RIBEIRO et al., 2009). Adicionalmente, de acordo com o recente estudo de Sloan et al. (2014), a Floresta Atlântica retém apenas 3,5% da sua vegetação primária. Apesar destes preocupantes números, apenas uma pequena parcela dos remanescentes florestais se encontra sob algum tipo de proteção (RIBEIRO et al., 2009). Áreas protegidas de qualquer categoria (categorias IUCN I-VI) cobrem apenas 4% de todo o bioma e áreas estritamente protegidas, apenas 1,7% (LAIRANA, 2003). Além disso, a maioria destas áreas é pequenas demais para garantir a persistência das espécies em longo prazo (MARSDEN et al., 2005).

2.2 Restauração ecológica

Apesar de ser um campo da ciência recente, a restauração ecológica tem sido praticada há milhares de anos (GALATOWITSCH, 2012; PALMER; FALK; ZEDLER, 2006). Atividades de reflorestamento tiveram início durante a Revolução Industrial, especialmente para remediar problemas e danos econômicos causados por colapsos ambientais. Estas ações visavam, principalmente, reduzir a erosão do solo e os danos gerados pelas práticas de mineração, a fim de atenuar os problemas de produção agrícola e pecuária, assim como de saúde pública. Isto motivou uma série de programas e políticas para a proteção da qualidade do ar, do solo e da água.

Na segunda metade do século XIX, a restauração começou a ser motivada pela nostalgia do contato com a natureza e por preocupações éticas sobre a extinção de espécies. Em 1870, o jardineiro e jornalista William Robinson publicou o primeiro livro popular sobre desenho e manejo de jardins naturais, chamado “The Wild Garden”. Em 1932, Aldo Leopold e seus colegas do Jardim Botânico da Universidade de Winconsin (Madison Arboretum) começaram a reconstruir ecossistemas naturais da região, criando réplicas de florestas, savanas e áreas alagadas (GALATOWITSCH, 2012). Inspirados nessas atividades, os cientistas William Jordan e John Aber, da mesma universidade, introduziram pela primeira vez o termo restauração ecológica (ABER; JORDAN, 1985; JORDAN, 1985). Estes autores acreditavam que a reconstrução de ecossistemas necessitava de um entendimento mais profundo sobre a ecologia das comunidades que eles almejavam recriar. A partir disso, a restauração ecológica começou a crescer como um importante ramo da ciência, havendo um aumento no número de livros escritos sobre o assunto, artigos científicos e, inclusive, o estabelecimento de revistas científicas específicas (BRUDVIG, 2011; SUDING, 2011).

A restauração ecológica está baseada em atividades que têm como função iniciar ou acelerar a recuperação de ecossistemas que foram degradados, danificados ou destruídos (JACKSON; LOPOUKHINE; HILLYARD, 1995; SER, 2004). Na literatura, geralmente, definem-se de forma diferente os termos “ecologia da restauração” e “restauração ecológica”. A ecologia da restauração se refere à exploração científica dos ecossistemas que estão sob reparo e a restauração ecológica, às próprias práticas de restauração (ARONSON et al., 2006; GALATOWITSCH, 2012). As atividades de restauração podem envolver simplesmente a remoção da perturbação, permitindo que o sistema se recupere sozinho por processos ecológicos naturais (GALATOWITSCH, 2012; PALMER; FALK; ZEDLER, 2006). Podem envolver também uma série de práticas e intervenções que visem acelerar o processo de recuperação, como, por exemplo, o plantio de espécies nativas por meio do uso de mudas ou sementes (GALATOWITSCH, 2012).

A habilidade de reconstruir ecossistemas nunca será suficiente para conter os danos da atual destruição de habitats naturais (BRUDVIG, 2011). A restauração ecológica deve ser um complemento da conservação biológica (YOUNG, 2000), já que a conservação de ecossistemas naturais preservados ainda é uma prioridade (BRUDVIG, 2011; HOBBS; HARRIS, 2001). Contudo, em muitas partes do mundo, não existem quantidades suficientes de habitats naturais para garantir a persistência de muitas espécies em longo prazo (BRUDVIG, 2011; RODRIGUES et al., 2009).

Diante da realidade atual, a restauração ecológica entra como uma estratégia importante para garantir a conservação da diversidade biológica e a manutenção das funções e serviços de um ambiente, satisfazendo também às demandas da sociedade (ARONSON; ALEXANDER, 2013; ARONSON et al., 2006; BULLOCK et al., 2011; HOBBS; HARRIS, 2001; MONTOYA; ROGERS; MEMMOTT, 2012).

2.2.1 O sucesso da restauração

Conhecer o sucesso da restauração é extremamente importante, pois traz informações sobre os benefícios desta estratégia, assim como de suas limitações (MATTHEWS; SPYREAS, 2010; RUIZ-JAEN; AIDE, 2005; SUDING, 2011). Contudo, pesquisadores ainda se deparam com uma série de dificuldades para avaliar a eficácia dos projetos de restauração. Tradicionalmente, estes estudos têm sido realizados por meio da comparação das áreas de restauração com sistemas referência (ARONSON; DHILLION; LE FLOC’H, 1995; BULLOCK et al., 2011; REY BENAYAS et al., 2009).

Sistemas referência são, geralmente, ecossistemas não degradados, um estado histórico ou uma extensão natural ou seminatural do ecossistema, representando o que se pretende alcançar com o resultado final da restauração (BULLOCK et al., 2011; REY BENAYAS et al., 2009). Contudo, o uso de sistemas referência tem sido bastante debatido ultimamente (CHOI et al., 2008; HOBBS; HIGGS; HARRIS, 2009; HOBBS et al., 2006, 2011; SUDING, 2011; THORPE; STANLEY, 2011) porque dificilmente os sistemas restaurados voltarão a ser o que eram antes, principalmente porque estarão submetidos às constantes mudanças ambientais dos dias atuais (e.g. climáticas, uso da terra) (CHOI et al., 2008; LOCKWOOD, 1997; SUDING, 2011).

Estas constantes mudanças ambientais podem mudar a trajetória de sucessão das áreas de restauração para estados alternativos e, até mesmo, dar origem a novos ecossistemas (HOBBS; HIGGS; HARRIS, 2009; HOBBS et al., 2006; SUDING; GROSS; HOUSEMAN, 2004). Outro fator importante é a dificuldade em encontrar sistemas referência de qualidade, principalmente em regiões extremamente fragmentadas e/ou degradadas (RODRIGUES et al., 2009). A escolha errada do sistema referência pode gerar resultados errôneos sobre a eficácia dos esforços de restauração (RODRIGUES et al., 2009; WHITE; WALKER, 1997).

Portanto, muito autores defendem a ideia de que a restauração deve focar em criar ecossistemas autossustentáveis e funcionais, capazes de conservar a biodiversidade local, não sendo, necessariamente, semelhantes ao sistema referência (e.g. HOBBS et al., 2011; SUDING, 2011). Apesar das críticas, o uso de sistemas referência é ainda um bom ponto de partida para saber quais são os benefícios das práticas de restauração (BULLOCK et al., 2011; REY BENAYAS et al., 2009; WHITE; WALKER, 1997).

Outra dificuldade nesta questão está em saber quais parâmetros das comunidades e ecossistemas devem ser mensurados para avaliar o sucesso de restauração (RUIZ-JAEN; AIDE, 2005; SUDING, 2011).

A Sociedade da Ecologia da Restauração criou um guia citando nove atributos que devem ser medidos para avaliar este sucesso. São eles: 1) diversidade e estrutura da comunidade similar ao sistema referência; 2) presença de espécies nativas; 3) presença de grupos funcionais necessários para garantir estabilidade a longo prazo; 4) capacidade do ambiente físico em sustentar populações reprodutivas; 5) funcionamento regular; 6) integração com a paisagem; 7) eliminação de ameaças potenciais; 8) resiliência a distúrbios naturais e 9) autossustentabilidade (SER, 2004). Apesar de estes atributos serem importantes para garantir uma boa avaliação da eficácia dos esforços de restauração, poucos projetos contam com tempo e recursos financeiros suficientes para monitorar todos estes parâmetros (RUIZ-JAEN; AIDE, 2005).

A maioria dos estudos que investigaram o sucesso de restauração utilizou um enfoque taxonômico e as plantas como ferramenta de avaliação (BRUDVIG, 2011; MAJER, 2009; RUIZ-JAEN; AIDE, 2005). Inicialmente, acredita-se que a fauna retornaria ao local restaurado, juntamente com o retorno da vegetação (BRUDVIG, 2011; MAJER, 2009). Contudo, os princípios básicos da restauração ecológica começaram a ser debatidos e remodelados. Hoje já se sabe que esta não é uma realidade, e que o retorno da fauna depende de uma série de outros fatores, como, por exemplo, contexto de paisagem, fatores bióticos, *pool* de espécies regionais (BRUDVIG, 2011; GRIMBACHER; CATTERALL, 2007). Já se reconhece também que o processo de restauração não pode se limitar a restaurar apenas solos e plantas (MAJER; BRENNAN; MOIR, 2007). É imprescindível restaurar também a fauna associada a estes ambientes, já que, para obter um ecossistema autossustentável, é preciso recuperar as funções e os serviços ecossistêmicos fornecidos pela diversidade de espécies e suas interações (MAJER; BRENNAN; MOIR, 2007; MONTOYA; ROGERS; MEMMOTT, 2012). Com isso, houve um aumento no número de estudos sobre a recuperação da fauna, sendo estas pesquisas muito mais voltadas aos vertebrados do que aos invertebrados (BRUDVIG, 2011; MAJER, 2009). Recentemente, a restauração ecológica tem começado a adotar uma perspectiva funcional em seus estudos (AERTS; HONNAY, 2011; BARNES; EMBERSON; KRELL, 2014; CADOTTE; CARSCADDEN; MIROTCHNICK, 2011; MONTOYA; ROGERS; MEMMOTT, 2012), o que tem sido feito por meio da avaliação da diversidade funcional ou das características funcionais das espécies presentes nas comunidades (AERTS; HONNAY, 2011; BRUDVIG, 2011).

Apesar do aumento no número de estudos, ainda faltam pesquisas abrangentes que investiguem a eficácia da restauração (SUDING, 2011). Um estudo relevante sobre o assunto é o de Rey Benayas et al. (2009), que realizaram uma meta-análise de 89 projetos de restauração em diferentes biomas e diferentes escalas de tempo (áreas de restauração que apresentavam de 5 a 300 anos). Eles mostraram que a restauração ecológica é capaz de aumentar a provisão de biodiversidade e serviços ecossistêmicos quando comparadas com sistemas degradados. Contudo, as áreas de restauração nunca se igualaram ao sistema referência em relação a diversidade de espécies e serviços ecossistêmicos.

2.2.2. Tempo de recuperação da fauna em florestas tropicais

O tempo de recuperação de um ecossistema pode depender de uma série de fatores, como tipo de ecossistema, magnitude da perturbação e variáveis da comunidade que foram medidas (JONES; SCHMITZ, 2009). A recuperação de ecossistemas severamente degradados é possível, mas pode levar de décadas a meio século. Além disso, este é um processo tipicamente mais lento em sistemas florestais, comparados com outros tipos de ecossistemas (JONES; SCHMITZ, 2009).

Duas importantes revisões abordaram a recuperação da comunidade faunística durante a regeneração de florestas tropicais após o abandono da terra (DENT; WRIGHT, 2009; DUNN, 2004). Dunn (2004) concluiu que a riqueza de espécies pode atingir níveis similares ao do sistema referência após 20-40 anos, mas a recuperação da composição de espécies é um processo mais lento. Em contrapartida, Dent e Wright (2009) relataram que, em décadas, é possível obter uma composição de espécies similar à de florestas preservadas. As atividades de restauração que envolvem o plantio de árvores nativas são usadas para acelerar o processo de regeneração e recuperação (CATTERALL et al., 2012), mas muito poucos estudos avaliaram a recuperação da fauna, especialmente de invertebrados, após a restauração ativa de uma floresta tropical (e.g. CATTERALL et al., 2012; DOMINGUEZ-HAYDAR; ARMBRECHT, 2011; GRIMBACHER; CATTERALL, 2007; JANSEN, 1997).

Estudos sobre restauração, principalmente em outros tipos de ecossistemas, mostram que o aumento na riqueza de espécies de invertebrados pode ser alcançada relativamente rápido (cerca de 10 anos), mas a recuperação da composição de espécies pode ser um processo muito mais lento (ANDERSEN; HOFFMANN; SOMES, 2003; JANSEN, 1997; NICHOLS; NICHOLS, 2003; WATTS; CLARKSON; DIDHAM, 2008).

2.2.3 Teoria da estruturação de comunidades e restauração ecológica

Inicialmente, a ecologia da restauração era uma ciência muito mais experimental do que teórica (YOUNG, 2000) e as suas técnicas eram geralmente fundamentadas em estudos de caso e técnicas de tentativa e erro (HOBBS; NORTON, 1996). Isso não permitia extrapolar os resultados de um sistema para outro e gerar avanços nesta área do conhecimento (HALLE; FATTORINI, 2004). A falta de bases teóricas por trás das atividades relacionadas à restauração ecológica era evidente, e este problema tinha e ainda tem sido extensivamente documentado na literatura (ABER; JORDAN, 1985; HOBBS; HARRIS, 2001b; HOBBS; NORTON, 1996; MONTOYA; ROGERS; MEMMOTT, 2012; PALMER; AMBROSE; POFF, 1997; TEMPERTON et al., 2004a; YOUNG, 2000). Apesar de existir um recente debate sobre a real utilidade da teoria científica para os esforços de restauração (CABIN, 2007a, 2007b; GIARDINA et al., 2007), já é praticamente unânime o reconhecimento de sua importância para aprimorar as técnicas de restauração.

Desde então, a ciência da ecologia da restauração tem avançado rapidamente e muitos projetos de restauração tem sido baseados em conceitos ecológicos e teorias que estão sendo colocados em teste (ARONSON; ALEXANDER, 2013; BRUDVIG, 2011; HOBBS; HARRIS, 2001b; RODRIGUES et al., 2009). Contudo, ainda existe uma grande necessidade em gerar avanços na ciência da restauração e diminuir ainda mais a distância entre a teoria e a prática (ARONSON; ALEXANDER, 2013; MONTOYA; ROGERS; MEMMOTT, 2012; RODRIGUES et al., 2009).

A teoria proveniente da ecologia de comunidades é relevante para a restauração ecológica porque os esforços de restauração frequentemente são voltados para as comunidades biológicas (PALMER; AMBROSE; POFF, 1997). Sendo assim, o entendimento sobre as regras que governam a organização de espécies em comunidades (processo conhecido como *assembly rules*) tem sido considerado uma das bases conceituais da ecologia da restauração (TEMPERTON et al., 2004b; YOUNG, 2000). Estas duas áreas da ciência são extremamente complementares, mas na prática apresentam pouca interação (MONTOYA; ROGERS; MEMMOTT, 2012; TEMPERTON et al., 2004b). Avanços na interação destes dois campos de pesquisa irão indubitavelmente possibilitar o controle mais preciso da restauração e conservação de ecossistemas naturais em relação ao que temos hoje (TEMPERTON et al., 2004b). Os estudos que usaram a teoria de estruturação de comunidades para guiar as práticas de restauração ainda são poucos em relação a totalidade de estudos que existem sobre restauração ecológica (e.g. BARNES; EMBERSON; KRELL, 2014; FUNK et al., 2008; HELSEN; HERMY; HONNAY, 2012; LAUGHLIN, 2014; MATTHEWS et al., 2009). Contudo, já demonstraram a importância desta teoria para guiar as práticas de restauração. Barnes et al. (2014) evidenciam que o retorno das funções ecológicas de áreas restauradas é influenciado tanto por fatores aleatórios como pelas características das espécies presentes. Funk et al. (2008) examinaram como o conhecimento sobre a estruturação da comunidade de plantas pode ser usado para fortalecer comunidades restauradas à resistência da invasão de espécies exóticas. Helsen, Hermy e Honney (2012) comprovam que em áreas restauradas os processos determinísticos atuam em nível de característica das espécies e fatores aleatórios em nível de espécie. Laughlin (2014) mostra como o conhecimento sobre estruturação de comunidades pode ser utilizado em modelos baseados nas características das espécies a fim de criar comunidades mais funcionais e estáveis. Matthews et al. (2009) demonstram que a estruturação da comunidade de plantas em áreas restauradas é determinada tanto por fatores ambientais como da paisagem.

A ideia de que existem regras que governam a estruturação de comunidades biológicas foi explorada primeiramente por Jared Diamond em 1975, em seu trabalho intitulado “assembly of species communities” (DIAMOND, 1975). Diamond pesquisou a distribuição de espécies de pássaros em um arquipélago localizado em Papua, Nova Guiné. Embora a origem desta ideia tenha sido atribuída ao trabalho de Diamond, o interesse em saber como as comunidades são estruturadas existe por muito tempo. Clements estudando florestas norte-americanas, realizou trabalho pioneiro nesta área de estruturação de comunidades, propondo a teoria de comunidades fechadas. De acordo com Clements (1916, 1936) a estrutura e o funcionamento das comunidades biológicas são regulados pelas interações entre as espécies e estas funcionam como um "superorganismo". As comunidades são portanto distinguíveis (fronteiras reconhecidas) e podem desenvolver um estado de clímax. Gleason (1917, 1939) formulou uma ideia oposta à de Clements ao estudar também florestas norte-americanas. Para Gleason, as comunidades eram agrupamentos aleatórios, onde as espécies se juntavam apenas devido as condições e recursos do local. Sua teoria, conhecida como comunidades abertas, defendia uma ausência de zonas de transição entre duas comunidades, havendo um continuum com substituição gradual de espécies em um gradiente de condições ecológicas.

Desde então, a busca pelas regras de estruturação de comunidades biológicas tem sido um dos principais desafios da ecologia nas últimas décadas (CHASE; MYERS, 2011b; DE BELLO et al., 2012; GÖTZENBERGER et al., 2012; MYERS et al., 2013; WEIHER et al., 2011). Procura-se compreender como as espécies que chegam a um ambiente se combinam para formar uma comunidade (BELYEA; LANCASTER, 1999), se realmente existem regras por trás desta organização ou se ela acontece basicamente por processos aleatórios (CHASE; MYERS, 2011a; WEIHER et al., 2011).

Desta forma, são conhecidos três principais modelos de estruturação de comunidades: o determinístico, o estocástico e os estados alternativos estáveis. O modelo determinístico tem como base a teoria de nichos e prediz que a estruturação de comunidades biológicas é vista como uma consequência da influência de fatores físicos e bióticos, sendo principalmente determinada pelas diferenças específicas de cada espécie (CHASE; LEIBOLD, 2003). No estocástico acredita-se que todas os indivíduos são equivalentes ecologicamente e que a estruturação acontece por processos aleatórios, dependendo da ordem de chegada dos organismos, extinção aleatória e deriva ecológica (HUBBELL, 2001). Já, o modelo de estados alternativos estáveis é atualmente o mais aceito, e relata que a estruturação de comunidades é definida tanto por processos determinísticos como pelos estocásticos (TEMPERTON et al., 2004b).

A teoria da estruturação de comunidades biológicas frequentemente prediz que comunidades locais são subconjuntos do pool de espécies da região delimitadas por uma série de filtros ecológicos (WEIHER et al., 2011). Desta forma, em um habitat específico, apenas algumas espécies do *pool* regional conseguirão se estabelecer, porque os filtros ecológicos existentes irão selecionar aquelas que conseguem sobreviver, e excluir as que não apresentam características adequadas para se estabelecer naquelas condições (KEDDY, 1992). Os filtros ecológicos podem ser caracterizados como abióticos, bióticos e limites de dispersão das espécies (modelo neutro) (BELYEA; LANCASTER, 1999; GÖTZENBERGER et al., 2012; WEIHER et al., 2011). Os filtros abióticos estão relacionados a fatores ambientais e os bióticos, à dinâmica interna das comunidades biológicas, como a interações entre as espécies (BELYEA; LANCASTER, 1999; GÖTZENBERGER et al., 2012; WEIHER et al., 2011). As pesquisas têm mostrado que a influência de filtros abióticos na estruturação de comunidades tende a causar uma maior similaridade nas características das espécies coexistentes (GRIME, 2006). Isso acontece porque as espécies devem apresentar requisitos e adaptações comuns para determinado tipo de condição ambiental (KEDDY, 1992). Se a estruturação é guiada por fatores bióticos, as espécies coexistentes podem ser mais dissimilares ou similares entre si. A dissimilaridade pode acontecer devido ao aumento da partição de recursos e a similaridade devido à exclusão competitiva (BELYEA; LANCASTER, 1999; WEIHER et al., 2011). A competição pode, entretanto aumentar a similaridade entre as espécies coexistentes através da exclusão das espécies que apresentam características associadas a baixa habilidade competitiva (CHESSON, 2000). Além da competição, a predação também pode influenciar os processos de estruturação de comunidades (CHASE et al., 2009). Predadores são capazes de determinar a importância relativa de fatores estocásticos e determinísticos sobre a estruturação da comunidade de presas, porque eles são capazes de mudar padrões de coexistência, abundância relativa e diversidade de presas (MCPEEK, 1998). Predadores podem aumentar a probabilidade de ocorrência de eventos estocásticos ao diminuir o número de indivíduos de uma comunidade. Isso é capaz de aumentar a extinção local de espécies por eventos aleatórios, gerando comunidades divergentes entre locais ambientalmente semelhantes. Predadores podem também aumentar a importância de processos determinísticos por diminuir o pool de espécies disponível para a colonização. Isso é capaz de gerar comunidades convergentes entre locais ambientalmente semelhantes (CHASE et al., 2009). Nesse sentido, a estruturação de comunidades pode ser influenciada simultaneamente pelos três tipos de filtros ecológicos citados acima (BELYEA; LANCASTER, 1999; WEIHER et al., 2011).

Os filtros abióticos que têm sido apontados como importantes na estruturação de comunidades em áreas de restauração são condições ambientais locais e contexto de paisagem (BRUDVIG, 2011; MATTHEWS et al., 2009). Contudo, a maioria dos estudos tem investigado os efeitos de variáveis ambientais locais para promover a diversidade em áreas de restauração. Poucos são os estudos que avaliaram como as métricas de paisagem podem influenciar a restauração (BRUDVIG, 2011).

2.3 Importância do uso de besouros rola-bostas nos estudos de restauração

Os besouros da subfamília Scarabaeinae (Coleoptera: Scarabaeidae), popularmente conhecidos como rola-bostas, podem servir como excelente ferramenta para os estudos sobre restauração ambiental. Apesar de serem poucos os estudos que utilizaram os escarabeíneos para avaliar o sucesso da restauração (e.g. BARNES; EMBERSON; KRELL, 2014; BETT et al., 2014; DAVIS et al., 2003, 2002; SILVA; HERNÁNDEZ, 2014), estes já evidenciam a eficácia destes besouros para monitorar a qualidade de ambientes restaurados.

Os escarabeíneos são considerados um excelente grupo modelo para a pesquisa de padrões em ecologia de comunidades, um táxon ideal para o monitoramento da biodiversidade, além de serem responsáveis por uma série de funções ecológicas importantes para os ecossistemas terrestres (NICHOLS et al., 2008; SPECTOR, 2006). Estes besouros têm sido amplamente utilizados para avaliar o valor de conservação de diferentes sistemas de uso da terra (e.g. ALMEIDA et al., 2011; BARLOW et al., 2007; BARRAGÁN et al., 2011; KORASAKI et al., 2013), já que são considerados bioindicadores de alto custo-benefício (GARDNER et al., 2008), sendo sensíveis e respondendo rapidamente a mudanças ambientais (HALFFTER; FAVILA, 1993). Apresentam também uma comunidade bem definida em termos taxonômicos e funcionais, o que auxilia grandemente a realização de qualquer tipo de estudo (HANSKI; CAMBEFORT, 1991). Eles também podem servir para o monitoramento da biodiversidade por depender de recursos provenientes de outros organismos, como aves, mamíferos, árvores (SPECTOR, 2006). Estes insetos são detritívoros, se alimentando principalmente de fezes, carcaça e frutos em decomposição (HALFFTER; MATTHEWS, 1966; HANSKI; CAMBEFORT, 1991).

Estudos já comprovaram que a caça de mamíferos pode afetar indiretamente a comunidade de escarabeíneos (CULOT et al., 2013; NICHOLS et al., 2009). Portanto, a comunidade de escarabeíneos pode ser altamente determinada pela presença de outros organismos. Devido aos seus hábitos alimentares e de nidificação, estes besouros fornecem uma série de funções ecológicas, auxiliando na manutenção e funcionamento dos ecossistemas onde estão inseridos. Os escarabeíneos costumam manejar o recurso de forma bastante peculiar, fazendo bolas e as enterrando em túneis escavados no solo (HANSKI; CAMBEFORT, 1991). Estas bolas de recurso irão servir tanto para a sua alimentação como para nidificação (HALFFTER; MATTHEWS, 1966).

Devido a este comportamento, eles podem ser responsáveis pela ciclagem de nutrientes, dispersão secundária de sementes, aeração do solo e controle de parasitas de vertebrados (HALFFTER; MATTHEWS, 1966; NICHOLS et al., 2008). Um estudo recente sugere inclusive que os escarabeíneos apresentam um efeito potencial na redução da emissão de gases metano proveniente das massas fecais de bovinos (PENTTILÄ et al., 2013). Assim, o sucesso da restauração pode ser profundamente influenciado pela presença ou ausência destes besouros.

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SEGUNDA PARTE - ARTIGOS

ARTIGO 1

Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity?

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ABSTRACT

Tropical forest restoration is becoming increasingly more applied to offset biodiversity loss and maintain ecosystem processes, but knowledge about its efficacy is still limited. We evaluated the success of tropical forest active restoration using dung beetles (Coleoptera: Scarabaeinae) as bioindicators and combining measures of species diversity, composition and functional diversity. We assessed patterns of dung beetles community assembly along a restoration chronosequence and also compared restoration areas with reference (primary and old secondary forest) and degraded (pasture) ecosystems. Species composition in the restoration areas was clearly progressing towards the preserved forests and deviating from the pasture with increasing restoration age. We also found a turnover of open environment specialists and habitat generalists to forest generalists and forest specialist species along the restoration chronosequence. However, the majority of individuals in the older restored habitats were typically forest generalists. Biomass was the only variable that increased with restoration age. Species richness, number of individuals, biomass and functional richness in the restored areas were similar to, or even smaller, than in pastures and substantially lower than forest reference sites. Rarefied richness, functional evenness and functional dispersion did not vary between the habitats. We found that while restored areas have the capacity to host forest-restricted species, 18 years since active restoration has not been long enough to recover a stable and diverse dung beetle assemblage. Our study also demonstrates that measures of composition, species diversity and functional diversity can complement each other and contribute to a better understanding of the efficacy of restoration practices.

Key-words: active restoration, Atlantic Forest, chronosequence, functional traits, pasture, Scarabaeinae.

1. Introduction

The maintenance of tropical forest biodiversity and ecosystem processes depends on the development of effective conservation efforts, which remains a great challenge to conservationists (Gardner et al., 2009; Rands et al., 2010). Ecological restoration has been considered one of the major strategies to mitigate the ongoing biodiversity crisis and is being increasingly applied worldwide (Bullock et al., 2011; Montoya et al., 2012; Rands et al., 2010). Restoration practices are based on intentional activities that aim to recover the physical structure, biodiversity and ecological functions of a degraded ecosystem (Galatowitsch, 2012). However, this is not an easy task, especially when it comes to restoring complex systems, such as tropical forests (Goosem and Tucker, 1995).

The assessment of restoration progress is a critical step in the application and refinement of restoration strategies, enabling the identification of constraints to success and the prediction of restoration outcomes (Matthews and Spyreas, 2010). The typical approach used is through comparisons of the restored sites with undisturbed reference systems and degraded systems (Matthews and Spyreas, 2010; Rey Benayas et al., 2009). However, most studies taking this approach have focused on plants, largely disregarding faunal recovery (Brudvig, 2011; Majer, 2009). This botanical bias arose because it was assumed that fauna would return with vegetation development (Majer, 2009). However, recent studies investigating faunal recovery have shown that other variables besides vegetation per se can influence its return (e.g. connectivity, composition of the surrounding landscape, regional species pool, biotic factors) (Brudvig, 2011; Grimbacher and Catterall, 2007; Majer, 2009). Even less is known about the recovery of ecological functions provided by biological diversity (Brudvig, 2011; Cadotte et al., 2011). Therefore, to truly determine restoration effectiveness and create self-sustainable functioning ecosystems it is critical to monitor not only plants, but also the return of fauna and functions associated with biodiversity (Cadotte et al., 2011; Majer, 2009).

Functional diversity is being increasingly advocated in the literature as a metric by which to evaluate the success of restoration programmes (e.g. Brudvig, 2011; Cadotte et al., 2011; Montoya et al., 2012), because it reflects aspects of the relationship between biological diversity, ecosystem functioning and environmental constraints (Díaz and Cabido, 2001; Mouchet et al., 2010). Indices of functional diversity are based on species traits found in a community and express the extent of functional differences among species in multidimensional space (Mouchet et al., 2010; Petchey and Gaston, 2006; Villéger et al., 2008). High functional diversity can result in greater resilience of the ecosystem to disturbance and higher levels of ecosystem functioning (Cadotte et al., 2011; Montoya et al., 2012). This type of information is not obtained when measuring only species diversity and composition, which are traditionally used to assess recovery in the restoration studies (Mayfield et al., 2010; Mouchet et al., 2010; Mouillot et al., 2013). Therefore, incorporating functional diversity metrics into restoration studies will aid in evaluations of restoration strategy effectiveness and decision-making (Cadotte et al., 2011; Montoya et al., 2012).

Monitoring the species and functional diversity of all fauna in restored areas is typically not logistically feasible, particularly in highly diverse systems like tropical forests. One approach is to select a group of organisms that serve as bioindicators, i.e. taxa that indicate environmental conditions (Gerlach et al., 2013). Dung beetles (Coleoptera: Scarabaeinae) have been widely proposed as cost-effective bioindicators because they are sensitive to ecosystem changes, easily sampled, broadly distributed, and their taxonomy and ecology are relatively well known (Gardner et al., 2008; Halffter and Favila, 1993; McGeoch et al., 2002; Nichols et al., 2007; Spector, 2006). They are also an ideal taxon for biodiversity monitoring because they rely on a large range of resources including rotten fruit, carcasses and feces of other animals (Spector, 2006). In addition, dung beetles are important components of terrestrial ecosystems, providing a set of ecological functions such as nutrient cycling, secondary seed dispersal, soil turbation, fertilization and biological control of vertebrate parasites (Nichols et al., 2008). Thus, dung beetle assemblages can both indicate and influence the success of restoration efforts.

Here we evaluate the efficacy of tropical forest restoration using dung beetles as bioindicators, combining measures of species diversity, composition and functional diversity. To assess restoration progress we evaluated patterns of dung beetle community assembly along a tropical forest restoration chronosequence. Additionally we compared restoration areas with reference (primary and old secondary forest) and degraded (pasture) ecosystems to assess restoration success. Specifically, we asked (1) Does dung beetle species composition shift with increasing time since restoration? (2) Do species richness, number of individuals, biomass and functional diversity increase with restored forest age? (3) Are restoration areas progressing towards the reference system and deviating from the degraded system based on these parameters?

2. Materials and Methods

2.1 Study area

The study was conducted in the south of Bahia state, Brazil, covering the municipalities of Eunápolis, Porto Seguro, Belmonte and Itagimirim. This region was originally dominated by tropical lowland rainforest and is in the Atlantic Forest domain (IBGE, 2012). Atlantic Forest is considered one of the five biodiversity hotspots, is internationally recognized for its high levels of biodiversity and endemism (Myers et al., 2000). Although the region south of Bahia still holds large remnants of Atlantic Forest (Ribeiro et al., 2009), most of the original forest was cleared during the 1960s and 70s mainly for timber exploitation, pastures and plantations of exotic tree monocultures (Carvalho et al., 1994; Nascimento et al., 2009; Oliveira et al., 1997). In 1990, <7% of the original Atlantic Forest remained (Carvalho et al., 1994).

According to the Köppen classification (Kottek et al., 2006), the regional climate is Af (tropical rainforest climate), without a dry season and with rains well distributed throughout the year. Mean annual temperature is 22.6 ºC and is fairly constant over the year, with a range of 18.9ºC to 27.9ºC. Average elevation of the region is 180 m, and mean annual precipitation is 1600 mm (Veracel, 2007).

2.2 Sampling sites

Since 1994, Veracel Cellulose S.A. company has been restoring Atlantic rainforest vegetation in areas of degraded pasture in the south of Bahia. This company has an enormous influence in the study region, owning ~210 000 hectares of land in 10 municipalities. Of this total, more than 105 000 ha is set aside for conservation and protection of native vegetation and 90 453 ha is planted with *Eucalyptus* sp. In 2004 the company started to restore a minimum of 400 ha per year, and at the end of 2011 it had replanted a total of 4300 hectares of Atlantic Forest (Veracel, 2011), offering an excellent opportunity to assess tropical rainforest restoration success.

The restoration techniques employed by Veracel consist of active planting of Atlantic rainforest tree species (1111 seedlings per hectare) mainly in valleys, riversides, steep slopes and other protected areas. Initially ants are controlled using formicide baits, and grasses and herbaceous weeds are controlled with herbicide if they occur in high densities (2 kg/ha). Manual mowing is implemented in areas with weeds ≥1 m tall and subsoiling is used to reduce soil compaction. The restored area is also fertilized before seedlings are planted. Monitoring of planting success is frequent in the first 3 years of the restoration process and after this period, it is conducted every 5 years.

Dung beetle sampling was conducted in 15 forest restoration areas of varying ages (with size of restored area in parentheses): 0 years (2 months since planting - 64 ha), 1 year (400 ha), 2 years (64 ha), 3 years (15 ha), 4 years (191 ha), 5 years (7 ha), 8 years (106 ha), 9 years (5 ha), 11 years (36 ha), 12 years (3 ha), 13 years (54 ha), 14 years (14 ha), 15 years (3 ha), 17 years (9 ha) and 18 years (11 ha). The restoration areas included in the study were typically separated by ≥500 m. We also sampled reference and degraded sites in order to quantify restoration success. We considered primary Atlantic Forest and old secondary forest (>40 years old) as the reference sites, representing the desired end point of restoration. Areas that have been converted by humans to pastures were considered degraded sites, representing the starting point of restoration. Collections were carried out in five areas of each of these systems (primary forest, old secondary forest and pasture). The sampled areas of primary and old secondary forest were located in the Veracel Station Private Reserve of Natural Heritage (RPPN Estação Veracel), one of the largest private reserves in the Atlantic Forest with an area of 6069 ha and a continuous mosaic of primary and secondary forest in advanced stages. Each of the reference and degraded sampled areas were ≥1 km from each other.

One sampled restoration area (15 years) was located inside RPPN at a distance of 5 m from the preserved rainforests, but >1 km from the sampled primary and secondary forest sites. The other studied restoration areas were situated between 20 km and 70 km from the RPPN Estação Veracel. We found a negative relationship between restoration age and distance to the RPPN (r^2 = -0.42, p = 0.004). However, we found no evidence for effects of distance to the reserve on the dung beetle assemblage (Table A.1 in Appendix A), Because the size of the restoration areas also varied widely (from 3 – 400 ha), we also tested effects of restoration area size on the dung beetle assemblage, and found no effects of this variable (Table A.1 in Appendix A). Therefore, we did not include distance to the RPPN or restoration area size in subsequent analyses.

2.3 Dung beetle sampling

Sampling was conducted during the rainy season, in May - June 2012. We used pitfall traps baited with ~25 g of human feces, carrion (bovine spleen) or rotten banana in order to attract the main feeding guilds of dung beetles. The traps consisted of a plastic container (19 cm diameter, 11 cm height), half-filled with a saline solution and detergent, a bait recipient (5 cm diameter, 5 cm height) suspended in the center of the trap and a plastic lid placed above ground to protect from rain and sun.

In each of the reference, degraded and restoration areas, we placed four sample points spaced 100 m apart along a linear transect. Each sample point contained three pitfall traps separated by 3 m, one with each bait type (feces, carrion, fruit), for a total of 12 pitfall traps per study area. Traps were placed at a minimum distance of 50 m from the edge whenever possible and left in the field for 48h prior to collection. All captures were processed in the laboratory, and dung beetles were identified to the species level by Dr. Fernando Z. Vaz-de-Mello. Vouchers were deposited in Laboratório de Ecologia e Conservação de Invertebrados, Universidade Federal de Lavras (Lavras, Minas Gerais, Brazil) and in Setor de Entomologia da Coleção Zoológica do Instituto de Biociências da Universidade Federal de Mato Grosso (Cuiabá, Mato Grosso, Brazil).

2.4 Dung beetle traits

Species were characterized in terms of five ecological attributes: habitat specificity (forest specialists = only found in primary or old secondary forest; open environment specialists = only found in pasture; forest generalists = found in *Eucalyptus* plantations, primary and old secondary forests, i.e. species that occur in natural and human-altered forested environments; or habitat generalists = found in multiple habitats, i.e. species that occur in natural and human-altered forested and open environments), food relocation habit (rollers, tunnellers or dwellers), diet (coprophages, necrophages, carpophages or generalists), diel activity (nocturnal or diurnal) and biomass (Table B.1 in Appendix B). Protocols for trait assignments are described in Appendix B. When necessary, we also obtained additional information on dung beetle traits from the literature and specialists.

2.5 Data analysis

2.5.1 Species composition and categories of habitat specificity

To determine whether species composition of dung beetle assemblage is progressing towards or deviating from the degraded and reference sites we performed a principal coordinates analysis (PCO) and a permutational multivariate analysis of variance (PERMANOVA), using the software Primer v.6 with PERMANOVA+ (Anderson et al., 2006; Clarke and Gorley, 2009). PCO was used to map the similarity between sites and PERMANOVA to test for significant differences in species composition between groups formed by PCO. These analyses were based on Bray-Curtis similarity, using standardized and square root transformed abundance data. To carry out this comparison the restoration areas were categorized as early-stage (0- 4 years), mid-stage (5- 12 years) and late-stage restoration (13- 18 years) (this categorization follows criteria defined by Brazilian law, see Conama, 1994).

Bray-Curtis similarity of the restoration areas to primary forest, secondary forest and pasture was used as a response variable to verify if there was a relationship with restoration age. We performed a regression analysis using generalized linear models (GLMs) with Gaussian errors in the R software (R Development Core Team, 2012).

We used GLMs to test for a relationship between restoration age and the proportion of species and individuals classified as forest specialists, forest generalists, open environment specialists and habitat generalists. We used binomial errors for the proportion of species richness of open environment specialists and binomial errors corrected for overdispersion (quasi-binomial) for the other variables.

2.5.2 Species richness, number of individuals and biomass

We tested for effects of restoration age on total species richness, rarefied species richness, number of individuals and biomass using GLMs. We used Poisson errors for species richness and Poisson errors corrected for overdispersion (quasi-Poisson) for the other variables. Because numbers of individuals varied among sites, we also rarefied species richness to six individuals, which was the minimum number of dung beetles sampled in an area. This analysis was implemented using the vegan package and rarefy function (Oksanen et al., 2013) in the R software package (R Development Core Team, 2012).

To test for differences among habitat types (early, mid, late-stage restoration, primary forest, secondary forest and pasture), we used GLM with Poisson errors for species richness and quasi-Poisson for rarefied richness, abundance and biomass. Subsequently, we performed a contrast analysis to verify which categories were distinct in relation to the response variables.

2.5.3 Functional diversity

To calculate functional diversity we used dung beetle traits that have particular importance in ecosystem functioning, specifically: food relocation habit, diet, dial activity and biomass (e.g. Barragán et al., 2011). We calculated three indices of functional diversity for each study area: functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis). FRic represents the amount of functional space occupied by the species present in a community and is measured as a convex hull volume. FEve corresponds to the distribution of species abundance in the functional space (Villéger et al., 2008). FDis is the mean distance of individual species to the centroid of all species in the multidimensional trait space (Laliberté and Legendre, 2010). Functional diversity calculations were implemented with the dbFD function in the FD package for R (Laliberté and Shipley, 2012).

We evaluated the influence of restoration age and habitat categories on FRic, FEve and FDis using GLMs with Gaussian errors. All GLMs were performed in the R software package (R Development Core Team, 2012), followed by residual analysis to check for the error distribution and adequacy of the model.

3. Results

We sampled 52 species in a total of 10 154 dung beetles across the habitat types, with 29 species and 4 467 individuals from primary forest, 31 species and 3941 individuals from old secondary forest, 20 species and 280 individuals from late-stage restoration, 17 species and 744 individuals from mid-stage restoration, 10 species and 171 individuals from early-stage restoration and 13 species and 551 individuals from pasture (Appendix C, Table C.1).

3.1 Species composition and categories of habitat specificity

According to PCO, species composition in the restoration areas are clearly progressing towards the reference sites (primary and old secondary forest) and deviating from the degraded site (pasture) with increasing restoration age (Fig. 1). Late-stage restoration areas are closer to primary and secondary forest compared with early and mid-stage restoration. The relationship of Bray-Curtis similarity with restoration age confirmed these patterns: similarity of the restoration areas to primary and secondary forest was positively influenced by restoration age (primary forest: $F = 14.33$, $p = 0.002$ – Fig. 2a; secondary forest: $F = 13.69$, $p = 0.002$ – Fig. 2b). In contrast, similarity to pasture was negatively influenced by restoration age ($F = 14.11$, $p = 0.002$ – Fig. 2c). However, PERMANOVA (Table D.1 in Appendix D) revealed that with the exception of primary forest and old secondary forest ($t = 1.04$; $p = 0.41$), all the categories in PCO were significantly different from each other based on species composition (pseudo-$F = 7.45$; $p = 0.0001$).

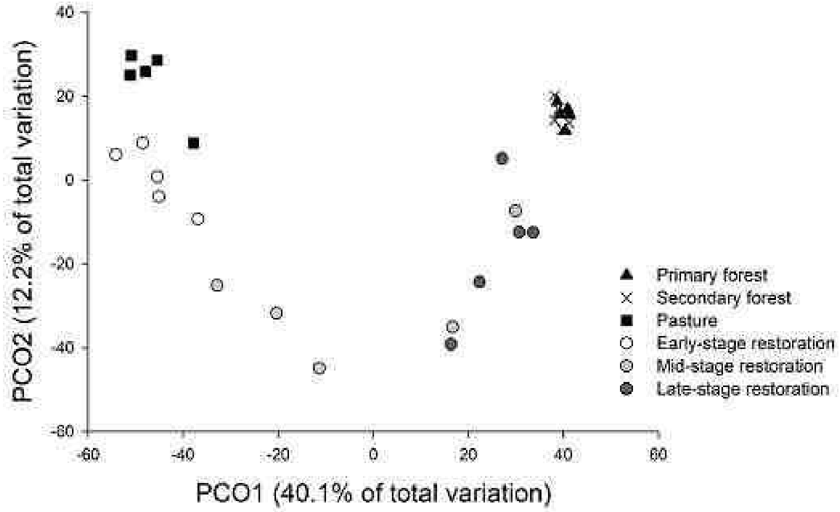

Fig. 1. Principal coordinates analysis (PCO) of dung beetle species composition based on Bray-Curtis similarity to compare forest restoration areas with the reference (primary forest and secondary forest) and degraded (pasture) sites. Early-stage restoration is represented by areas that have 0 - 4 years, mid-stage restoration: 5 - 12 years and late-stage restoration: 13 - 18 years.

Percentage of species that were forest specialists increased with restoration age (F = 7.56, p = 0.016 – Fig. 3a), but this pattern was not found for the percentage of individuals (F = 2.00, p = 0.1805 – Fig. 3b).. There was no relationship between the percentage of species that were forest generalists and restoration age (F = 2.19, p = 0.16 – Fig. 3c), however the percentage of forest generalist individuals increased with restoration age (F = 13.16, p = 0.003 – Fig. 3d). The percentage of species that were open environment specialists (χ^2 = 10.83; p = 0.01 – Fig. 3e) and percentage of individuals (F = 7.15, p = 0.01 – Fig. 3f) both declined with restoration age. The same pattern was found for habitat generalists (species richness (%): F = 9.13, p = 0.009 – Fig. 3g; number of individuals (%): F = 13.21, p = 0.003 – Fig. 3h).

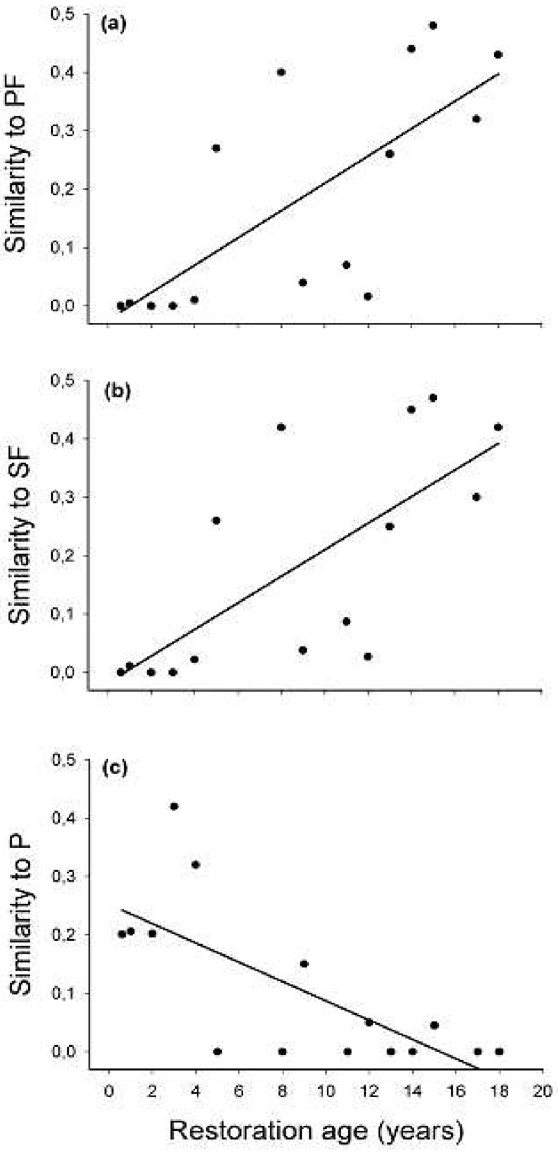

Fig. 2. Relationship between restoration age and dung beetle assemblage similarity (Bray-Curtis index) to primary forest (a), secondary forest (b) and pasture (c). PF = primary forest; SF = secondary forest; P = pasture.

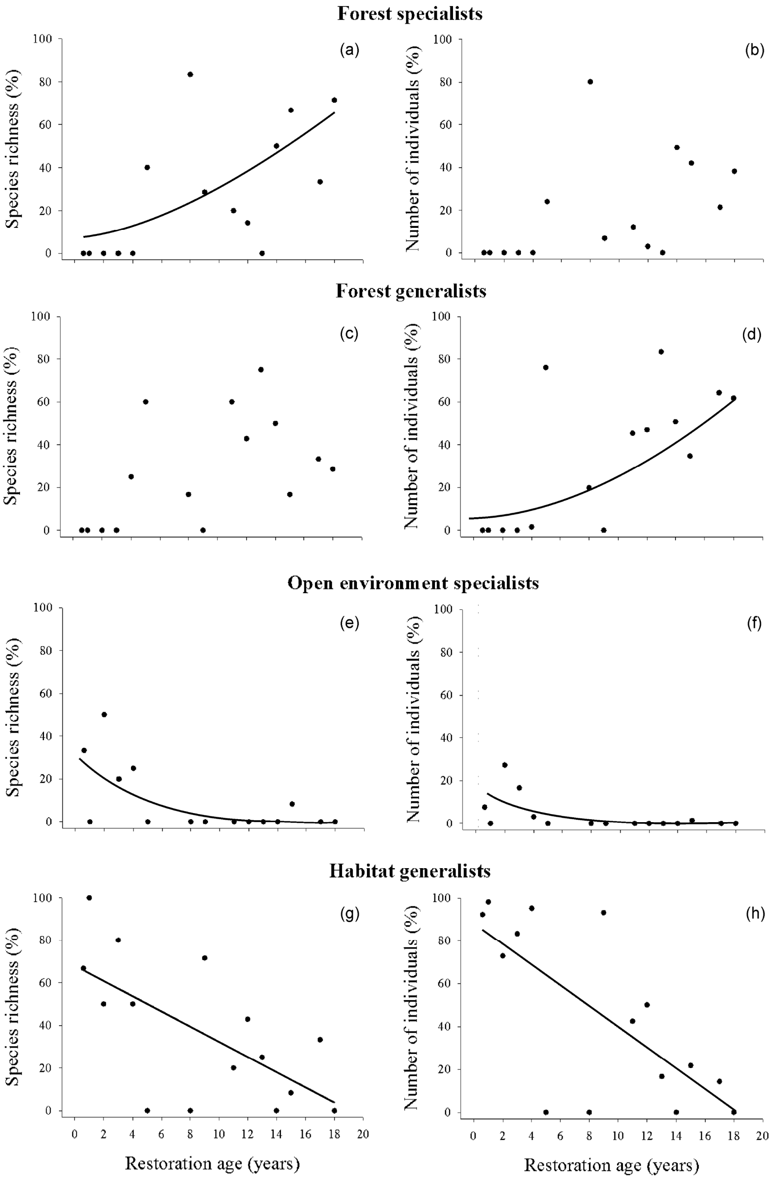

Fig. 3. Relationship between restoration age and the percentage of species (a) and individuals (b) classified as forest specialist, the percentage of species (c) and individuals (d) classified as forest generalists, the percentage of species (e) and individuals (f) classified as open environment specialists, and the percentage of species (g) and individuals (h) classified as habitat generalists.

3.2 Species richness, number of individuals and biomass

Species richness ($\chi^2 = 10.98$; $p = 0.17$ – Fig. 4a), rarified species richness ($F = 1.40$; $p = 0.26$ – Fig. 4b) and number of individuals ($F = 0.81$; $p = 0.38$ – Fig. 4c) did not have a significant relation with restoration age. Biomass was the only variable influenced by restoration age, increasing in older restoration areas ($F = 8.3108$, $p = 0.01282$ – Fig. 4d).

Mean species richness ($\chi^2 = 38.05$; $p < 0.001$ – Fig. 4e) differed among habitat types, while rarefied species richness was similar ($F = 0.48$; $p = 0.8162$ – Fig. 4f). Species richness was highest in primary and secondary forest and lowest in early-stage restoration areas, while pasture, mid-stage and late-stage restoration had intermediate levels of species richness and were not significantly different from each other. Species accumulation curves for each habitat type are shown in Appendix C, Figure C.1. Number of individuals ($F = 25.77$; $p < 0.001$ – Fig. 4g) and biomass ($F = 45.71$; $p < 0.001$ – Fig. 4h) also differed among habitat types. Primary forest and secondary forest were similar to each other and had the highest number of individuals compared with the other systems. There were no significant differences in mean number of individuals found in pasture, early-stage, mid-stage and late-stage restoration. Biomass showed the same pattern found for species richness (Fig. 4h).

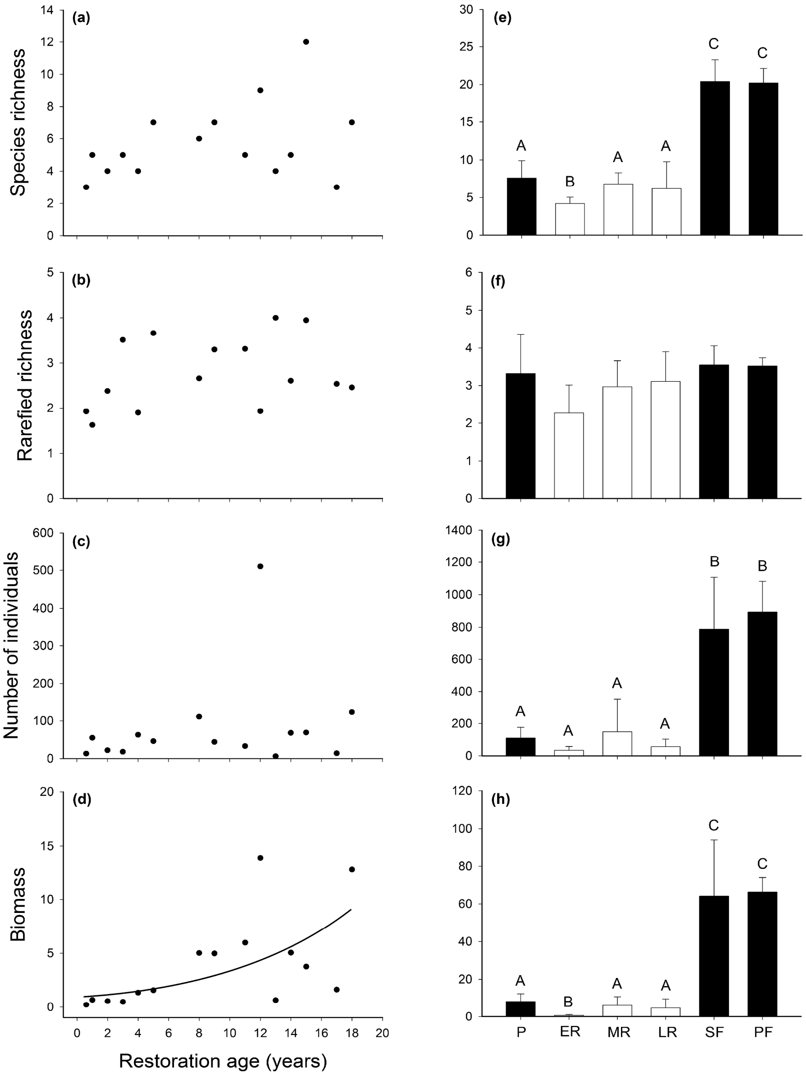

Fig. 4. a – d. Relationship between restoration age and species richness, species richness rarefied to 6 individuals, abundance and biomass. **e – h.** Mean ± SD species richness, rarefied richness, abundance and biomass recorded in the different habitat types (P = pasture; ER = early-stage restoration; MR = mid-stage restoration; LR = late-stage restoration; SF = secondary forest; PF = primary forest). Unlike letters indicate significant differences ($P < 0.05$). Black

bars represent the reference and degraded sites and white bars the forest restoration areas.

3.3 Functional diversity

Restoration age did not influence FRic (F = 0.0982; p = 0.759 – Fig. 5a), FEve (F = 0.475; p = 0.5028 – Fig. 5b) or FDis (F = 0.9125; p = 0.3569 – Fig. 5c). However, there was significant variation in mean FRic (F = 16.476; $p < 0.001$ – Fig. 5d) among habitat types. Lowest mean FRic was found in the restoration areas, and was similar among early-stage, mid-stage and late-stage restoration. This index was higher in the pasture compared with restored forest, but secondary and primary forest recorded the highest values. FEve (F = 1.5455; p = 0.2001 – Fig. 5e) and FDis (F = 2.143; p = 0.07964 – Fig. 5f) were not statistically different among the habitat types.

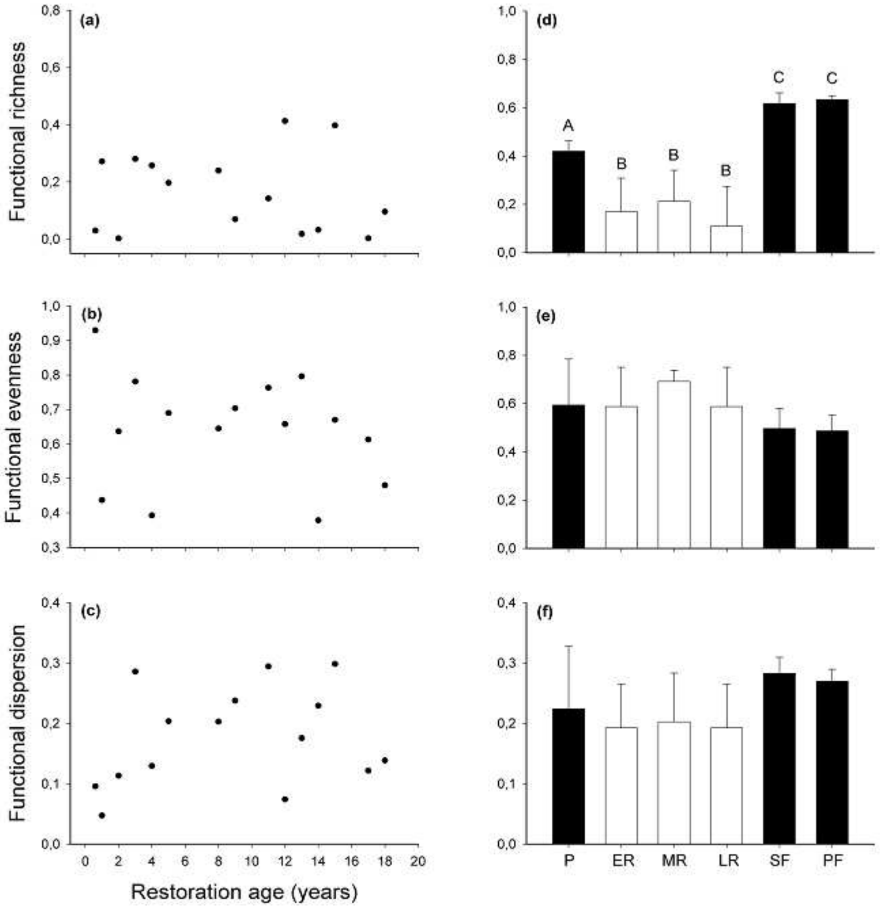

Fig. 5. a – c. Relationship between restoration age and functional richness, functional evenness and functional dispersion. **d – e.** Mean ± SD functional richness, functional evenness and functional dispersion recorded in the different habitat types (P = pasture; ER = early-stage restoration; MR = mid-stage restoration; LR = late-stage restoration; SF = secondary forest; PF = primary forest). Unlike letters indicate significant differences ($P < 0.05$). Black bars represent the reference and degraded sites and white bars the forest restoration areas.

4.Discussion

This is the first study, to our knowledge, to evaluate the efficacy of tropical forest restoration combining measures of species diversity, composition and functional diversity. Our results underscore the importance of utilizing more than one metric to characterize assemblages found in restored areas in order to better evaluate restoration success. The increasing similarity of dung beetle species composition to primary and old secondary forest with increasing time since restoration suggests that these areas are successfully progressing towards the reference systems. However, analyses of species diversity and functional diversity reveal that dung beetle assemblages are severely impoverished in the restored sites, and even after 18 years remain the same or worse in relation to the starting point of restoration (e.g. pasture).

4.1 Species composition and categories of habitat specificity

We demonstrated a clear trajectory of the restored areas, according to similarity in dung beetle species composition, from pasture to the preserve forests. The gradient of forest restoration ages in our study represents a transition from open environment to close-canopy forest habitats. Thus, increasing similarity to reference forests with restoration age can be attributed to a transition from open environment specialists to forest specialist species over the course of succession in these restored areas, consistent with patterns found when tropical forests have been allowed to regenerate naturally (Dent and Wright, 2009). This is supported by our results showing an increase in the proportion of species classified as forest specialists with restoration age and a decrease in the proportion of species classified as open environment specialists. Dung beetles are extremely sensitive to changes in vegetation structure, with species often showing patterns of fidelity to specific environmental properties (e.g. canopy cover, understorey vegetation, soil type and moisture) (Gardner et al., 2007; Halffter and Arellano, 2002; Horgan, 2007; Nichols et al., 2007; Noriega et al., 2007; Sowig, 1995). A higher degree of canopy cover can serve as a filter preventing the entry of open area species and increasing richness of forest-restricted species (Halffter and Arellano, 2002). Our results suggest that increasing similarity of the restored areas to the reference systems was also due to the decline of habitat generalists with restoration age.

While the proportion of species classified as forest specialists increased with restoration age, the proportion of individuals in this group did not. Rather, we found an increase in the proportion of individuals classified as forest generalists with forest age. Forest generalists are those species that depend on a certain degree of forest cover, however are matrix tolerant species and can establish in degraded forested systems. These results suggest that, in contrast to forest generalists, forest specialists are arriving in lower numbers and/or not surviving and reproducing well in the restored forests. Arrival of species into the restored forest areas will be highly influenced by the surrounding matrix, which can be extremely important in the local recovery of tropical forests (Chazdon, 2003). Although the restored areas in our study were typically located near forest fragments, our study region is dominated by human-managed habitats such as pastures and *Eucalyptus* plantations. Forest generalists may be poor competitors, but possess much better dispersal abilities compared to forest-restricted species and are also less sensitive to habitat change (Krauss et al., 2003; Larsen et al., 2008; Warren et al., 2001). Therefore, they can take advantage and dominate newly available environments that have some degree of canopy cover. In contrast, forest specialists avoid the landscape matrix and often stay confined to the forest habitat (Feer and Hingrat, 2005; Klein, 1989; Larsen et al., 2008). The lower abundance of forest specialists in restored forests in our study system may therefore result from their reluctance or inability to cross non-forested areas and degraded forested systems (e.g. *Eucalyptus* plantations) in order to reach the restored forest areas.

4.2 Species richness, abundance and biomass

Contrary to expectations, we found that species richness, number of individuals and biomass in the restored areas were similar to or lower than in pastures and substantially lower than in forest reference sites. Our results are markedly different from a recent meta-analysis by Rey Benayas et al. (2009), which concluded that restoration efforts tend to increase species richness, diversity, abundance and biomass relative to degraded systems. Our results also contrast with another meta-analysis by Nichols et al. (2007), which found that land-use systems with a high degree of forest cover (such as secondary forests) can harbor dung beetle assemblages similar, in terms of species richness and abundance, to those found in intact tropical forest.

In contrast to total species richness, rarefied species richness was similar in all land-use systems, indicating that differences in number of individuals is driving observed differences in species richness (see Gotelli and Colwell, 2001). Both number of individuals and total biomass were substantially higher in the primary and secondary forest areas compared to restored forests. This suggests that the carrying capacity of restoration areas is still limited. In particular, availability of food resources may be restricting population sizes and limiting dung beetle species richness in the restored areas. Dung beetles depend on other groups of organisms, mainly vertebrates (especially mammals) and trees, for adult and larval food resources (Halffter and Matthews, 1966; Hanski and Cambefort, 1991). Therefore, the recovery of dung beetle assemblages in the restored areas also depends on the recovery of these groups. Culot et al., 2013 and Nichols et al. (2009) demonstrated the strong association between dung beetles and mammals, reporting a co-declining relationship between mammals and dung beetles. In our study, recovery time of the restoration areas (18 years) may not have been sufficient to successfully recuperate intact assemblages of dung beetles and the organisms on which they depend. Although all restored areas had significantly lower dung beetle biomass than primary and secondary forests, there was a significant positive relationship between biomass and restored forest age, suggesting that forests may eventually recover sufficient resources to support a diverse dung beetle assemblage. Continued monitoring of dung beetle populations, along with studies quantifying vertebrate densities and fruit availability in restored vs. reference systems are needed to confirm this hypothesis.

4.3 Functional diversity

FRic in the restoration sites was significantly lower than both the degraded and reference systems, suggesting that these areas may have low stability through time and be deficient in ecosystem processes provided by dung beetles (Cadotte et al., 2011; Díaz and Cabido, 2001; Montoya et al., 2012). A greater variety of functional traits translates into a higher amount of resources being used, representing stronger effects of diversity on ecosystem functioning (Díaz and Cabido, 2001). Also, greater functional trait richness can help to safeguard ecosystems against abiotic variation, since species with different traits may respond differently to environmental constraints, ensuring the long-term maintenance of ecosystems processes in a changing environment (Díaz and Cabido, 2001). When studying changes in ground-foraging ant assemblages along a successional gradient of secondary Atlantic Forest, Bihn et al. (2010) found that the recovery of species richness and diversity was accompanied by a proportional increase in functional richness. In our study, functional richness is significantly correlated with species richness ($r^2 = 0.42$, $p = 0.004$), and therefore is unlikely to rebound unless species richness increases in these forests.

Most studies have found a reduction in functional evenness and dispersion with higher disturbance intensity (see Mouillot et al., 2013). One explanation for this pattern is that highly disturbed areas only support species with traits that allow them to tolerate the environmental conditions created by disturbance. This generates clustering and irregular distribution of abundances of co-occurring species in functional space, decreasing values of functional evenness and dispersion (Gerisch et al., 2012; Mouillot et al., 2013). However, we found no differences among study sites in FEve or FDis of dung beetle assemblages. Barragán et al. (2011) similarly found that FEve and FDis remained the same among pastures, forest fragments and continuous rainforest and between small and large forest fragments. This lack of difference between the systems can be an indication that only the identity of traits (functional richness) is being influenced by the environment and not the structure of the functional assemblage (i.e. abundance distribution and dispersion of traits in functional space). Similar values of FEve to the reference sites can suggest that niche space occupied in the restoration areas is being evenly exploited by the species and is not underutilized (Mason et al., 2005). According to Fonseca and Ganade (2001), assemblages with higher functional evenness can present more functional redundancy, because species are regularly distributed among functional groups. Similar values of FDis to the reference sites may indicate a higher dispersion of the functional traits in the restored areas, corresponding to a gain in response diversity (variability of responses to disturbances among species that contribute similarly to ecosystem function) (Elmqvist et al., 2009; Laliberté et al., 2010). Both high functional redundancy and high response diversity can increase the resilience of communities in the face of environmental change (Laliberté et al., 2010), including human and natural disturbances, and represent an interesting result from a conservation perspective.

4. Conclusions

Tropical forest restoration of degraded pastures can represent an important strategy to conserve biological diversity, but the knowledge we have about this strategy is still limited. Our study demonstrates that restored areas have the capacity to host forest-restricted species, but additional recovery time is likely needed to allow for the complete recovery of all biodiversity aspects. However, restored areas did not show any progress through time in relation to the starting point of the restoration, and after 18 year still harbor extremely depauperate dung beetle assemblages in terms of species and functional richness. Thus, it is unclear when the dung beetle assemblage will fully recover in restored forests, if ever. Since dung beetles are considered good indicators of environmental quality and overall biodiversity, our results suggest that further action may be needed to restore faunal diversity in this region. Our results also demonstrate how measures of composition, species diversity and functional diversity can complement each other and contribute to a better understanding of the efficacy of restoration practices.

Acknowledgments

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Supplementary material

Appendix A. Influence of distance to RPPN Estação Veracel and size of restored areas on dung beetle assemblages.

Appendix B. Dung beetle trait assignment.

Appendix C. Identity of Scarabaeine dung beetles species, total captures per habitat type and species accumulation curves.

Appendix D. Results of the permutational analysis of variance (PERMANOVA).

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Appendix A. Influence of distance to RPPN Estação Veracel and size of the restored areas on dung beetle assemblages

The reference sites (primary and old secondary forest) of this study are located in one single reserve called Veracel Station Private Reserve of Natural Heritage (RPPN Estação Veracel). Our restoration areas are dispersed in the studied landscape, with one of them (restoration area of 15 years old) located inside the reserve at a distance of 5 m from the preserved rainforests, and the others situated between 20 km and 70 km from the RPPN Estação Veracel. We found a negative relationship between restoration age and distance to RPPN ($r^2 = 0.42$, $p = 0.004$), which means that older restoration areas are closer to the reserve in relation to the younger ones. However, this relationship is being influenced by the 15 years old restored area, and when we exclude this site from the analysis we find no significant correlation between distance and restoration age ($r^2 = 0.20$, $p = 0.06$). Nevertheless, it is important to examine the potential impact that distance to RPPN may have on the dung beetle community in the restored areas.

Restoration areas also varied widely in size: 0 years (64 ha), 1 year (400 ha), 2 years (64 ha), 3 years (15 ha), 4 years (191 ha), 5 years (7 ha), 8 years (106 ha), 9 years (5 ha), 11 years (36 ha), 12 years (3 ha), 13 years (54 ha), 14 years (14 ha), 15 years (3 ha), 17 years (9 ha) and 18 years (11 ha). Since this factor on its own can influence dung beetle assemblages in the restoration areas, it is also important to test for possible effects of this variable.

We used generalized linear models (GLMs) to investigate the influence of distance to RPPN, size of the restoration areas and restoration age on dung beetle community parameters (community similarity, species diversity, habitat specificity and functional diversity). We used as explanatory variables restoration age, size of the restoration areas and distance to RPNN in the same model and the dung beetle community parameters as responses (see Methods for more details). All GLMs were performed in the R software package, followed by residual analysis to check for the error distribution and adequacy of the model.

The results are detailed in the table below and show that neither distance to RPPN or size of the restoration areas influences any of the dung beetle community parameters studied. Restoration age had similar effects in models with and without distance to RPPN and size of the restoration areas (see Results).

Table A.1. Results of the generalized linear models investigating the influence of distance to RPPN, size of the restoration areas and restoration age on dung beetle assemblage parameters (assemblage similarity, species diversity, habitat specificity and functional diversity). *= p-values < 0.01

GLM: Y ~ Distance + Age + Size	**Results**		
	Age	**Distance to RPPN**	**Size**
Similarity to primary forest ~ Age + Distance + Size	**F = 13.43; p = 0.003***	F = 0.99; p = 0.34	F = 0.19; p = 0.66
Similarity to secondary forest ~ Age + Distance + Size	**F = 12.97; p = 0.004***	F = 1.06; p = 0.325	F = 0.26; p = 0.61
Similarity to pasture ~ Age + Distance + Size	**F = 11.98; p = 0.005***	F = 0.01; p = 0.91	F = 0.02; p = 0.87
Richness ~ Age + Distance + Size	χ^2 = 10.98; p = 0.16	χ^2: 10.09; p = 0.34	χ^2 = 10.00; p = 0.76
Rarefied richness ~ Age + Distance + Size	F = 1.80; p = 0.20	F = 1.79; p = 0.20	F = 3.72; p = 0.07
Number of individuals ~ Age + Distance + Size	F = 0.92; p = 0.35	F = 0.64; p = 0.43	F = 0.07; p = 0.79
Biomass ~ Age + Distance + Size	**F = 6.53; p = 0.02***	F = 0.50; p = 0.49	F = 0.41; p = 0.53
% forest specialists richness ~ Age + Distance + Size	**F = 7.74; p = 0.01***	F = 2.26; p = 0.16	F = 0.03; p = 0.85
% pasture specialists richness ~ Age + Distance + Size	**χ^2 = 10.30; p = 0.01***	χ^2 = 8.29; p = 0.15	χ^2 = 7.43; p = 0.35
% forest generalist richness ~ Age + Distance + Size	F = 1.91; p = 0.19	F = 0.08; p = 0.77	F = 0.09; p = 0.76
% habitat generalists richness ~ Age + Distance + Size	**F = 10.06; p = 0.008***	F = 3.23; p = 0.09	F = 0.28; p = 0.60
% forest specialists individuals ~ Age + Distance + Size	F = 1.93; p = 0.19	F = 1.01; p = 0.33	F = 0.01; p = 0.89

GLM: Y ~ Distance + Age + Size	**Results**		
	Age	**Distance to RPPN**	**Size**
% habitat generalists individuals ~ Age + Distance + Size	**F = 11.24; p = 0.006***	F = 0.04; p = 0.83	F = 0.05; p = 0.82
Functional richness ~ Age + Distance + Size	F = 1.20; p = 0.29	F = 0.11; p = 0.73	F = 0.24; p = 0.62
Functional evenness ~ Age + Distance + Size	F = 0.22; p = 0.64	F = 3.23; p = 0.09	F = 4.02; p = 0.08
Functional dispersion ~ Age + Distance + Size	F = 1.12; p = 0.31	F = 2.37, p = 0.15	F = 2.61; p = 0.13

Appendix B. Dung beetle trait assignment

Species were characterized in terms of five ecological attributes: habitat specificity, food relocation habit, diet, diel activity and biomass. Protocols for trait assignments are described below. When necessary, we also obtained additional information on dung beetle traits from the published literature (Costa et al., 2009; Edmonds and Zidek, 2010; Génier, 2009; Gillett et al., 2010; Hernández, 2006, 2002; Koller et al., 2007; Korasaki et al., 2012; Lopes et al., 2011; Louzada and Silva, 2009; Marchiori et al., 2003; Matavelli and Louzada, 2003; Nichols et al., 2013; Rodrigues and Flechtmann, 1997; Scheffler, 2005; Silva, 2011; Spector and Ayzama, 2003), from unpublished literature (Audino, 2011) and personal observations of specialists (Fernando Vaz-de-Mello and Fernando Augusto Barbosa Silva).

- *Habitat specifity*: Habitat specificity was based on the collections carried out in primary forest, secondary forest and pasture and complemented with a survey conducted in 5 areas of *Eucalyptus* plantations, using the same trap design. Species collected only in primary and secondary forests were considered forest specialists and only in pastures considered open environment specialists. Those trapped both in natural forests and in eucalyptus plantations were considered forest generalists and the ones collected in natural forest, pasture and eucalyptus systems were considered habitat generalists;
- *Food relocation habit*: Food relocation habit assignment followed the classifications of Bornemisszа 1969 and Hanski & Cambefort 1991 who categorized dung beetle species as rollers (telecoprids), tunnellers (paracoprids) or dwellers (endocoprids) (Bornemissza 1969; Hanski & Cambefort 1991). Rollers construct balls of the food resource, roll them

some distance away and then bury them. Tunnellers carry pieces of the resource into the interior of tunnels that they dig directly underneath or near the food source. Dwellers feed and reproduce inside or beneath the food source;

- *Diet*: Species were categorized as coprophages, necrophages or carpophages if at least 80% of the beetles were captured in traps baited with human feces, carrion or banana, respectively. Species with similar numbers of individuals in more than one type of baited trap were considered generalists. Only dung beetle species with more than 10 individuals were assigned to diet categories.
- *Diel activity*: We sampled one area each of primary forest, old secondary forest, pasture and Eucalyptus plantation using the same sampling design described in the Materials and Methods section. However, specimens were removed from the traps every 12h, at dawn (05h40am) and dusk (05h40pm). Traps were left in the field for 48h and baits were replaced every 12h. Species were then classified as diurnal or nocturnal based on when they were captured;
- *Biomass*: 30 individuals of each species were dried at 60°C for one week and weighed using a balance accurate to 0.0001 g.

Table B.1. Identity and traits for 52 species of dung beetles (Scarabaeinae: Coleoptera) sampled in the south Bahia region. **NA:** missing data.

Species	**Habitat specificity**	**Food relocation habit**	**Diet**	**Period of fly activity**	**Biomass (g)**
Anomiopus sp.	NA	NA	NA	NA	0.002988
Ateuchus sp.1	Forest specialist	Paracoprid	Generalist	Nocturnal	0.017324
Ateuchus sp.2	Forest specialist	Paracoprid	Coprophage	Nocturnal	0.009423
Ateuchus sp.3	Forest generalist	Paracoprid	Coprophage	Nocturnal	0.017907
Canthidium aff. *depressum*	NA	Paracoprid	NA	NA	0.03515
Canthidium aff. *korschefskyi*	Forest specialist	Paracoprid	Necrophage	NA	0.014123
Canthidium aff. *lucidum*	Forest specialist	Paracoprid	Generalist	Diurnal	0.02315
Canthidium aff. *trinodosum*	Forest specialist	Paracoprid	Coprophage	Diurnal	0.007337
Canthidium sp.1	Forest specialist	Paracoprid	Coprophage	Nocturnal	0.025493
Canthidium sp.2	NA	Paracoprid	NA	NA	0.0081
Canthidium sp.3	Forest specialist	Paracoprid	Coprophage	NA	0.003074
Canthidium sp.4	Forest generalist	Paracoprid	Coprophage	Diurnal	0.005842
Canthidium sp.5	NA	Paracoprid	Coprophage	NA	0.01106
Canthon aff. *viidus*	Habitat generalist	Telecoprid	Coprophage	NA	0.007377
Canthon chalybaeus	Habitat generalist	Telecoprid	Generalist	Diurnal	0.020763
Canthon histrio	Habitat generalist	Telecoprid	Coprophage	Diurnal	0.033247
Canthon lituratus	Open environ. specialist	Telecoprid	Generalist	Diurnal	0.005577
Canthon mutabilis	Open environ. specialist	Telecoprid	Generalist	Diurnal	0.010583
Canthon sulcatus	Forest specialist	Telecoprid	Coprophage	Diurnal	0.051913

Canthonella silphoides	Forest specialist	Telecoprid	Coprophage	Nocturnal	0.002893
Chalcocopris hespera	Forest specialist	Paracoprid	Coprophage	Diurnal	0.073753
Coprophanaeus bellicosus	Forest generalist	Paracoprid	Necrophage	Nocturnal	2.17035
Coprophanaeus cyanescens	Habitat generalist	Paracoprid	Necrophage	Nocturnal	0.81719
Coprophanaeus dardanus	Forest generalist	Paracoprid	Necrophage	Nocturnal	0.731263
Coprophanaeus punctatus	Forest specialist	Paracoprid	Necrophage	NA	0.40528
Deltochilum aff. *calcaratum*	Forest specialist	Telecoprid	Necrophage	NA	0.19914
Deltochilum granulosum	Forest specialist	Telecoprid	NA	NA	0.46858
Diabroctis mimas	Habitat generalist	Paracoprid	Coprophage	Diurnal	0.11215
Dichotomius aff. *laevicollis*	NA	Paracoprid	Coprophage	Nocturnal	0.11536
Dichotomius aff. *sericeus*	Forest generalist	Paracoprid	Generalist	Nocturnal	0.11765
Dichotomius bos	Open environ. specialist	Paracoprid	Coprophage	Nocturnal	0.441
Dichotomius depressicolis	Forest specialist	Paracoprid	Coprophage	Nocturnal	0.2902
Dichotomius geminatus	Open environ. specialist	Paracoprid	Generalist	Nocturnal	0.111706
Dichotomius irinus	Forest specialist	Paracoprid	Generalist	Nocturnal	0.053277
Dichotomius mormon	Forest specialist	Paracoprid	Coprophage	Nocturnal	0.6559
Dichotomius nisus	Open environ. specialist	Paracoprid	Coprophage	Nocturnal	0.26296
Dichotomius quadrinodosus	Forest specialist	Paracoprid	Coprophage	Nocturnal	0.375853
Dichotomius schiffleri	Forest specialist	Paracoprid	Coprophage	Nocturnal	0.092733
Dichotomius semisquamosus	Habitat generalist	Paracoprid	Coprophage	Nocturnal	0.2787
Eurysternus calligrammus	Forest specialist	Endocoprid	Generalist	Diurnal	0.04395
Eurysternus hirtellus	Forest specialist	Endocoprid	Coprophage	Diurnal	0.011273
Eurysternus nigrovirens	Habitat generalist	Endocoprid	Generalist	NA	0.00831

Eutrichillum hirsutum	Habitat generalist	Endocoprid	Necrophage	Nocturnal	0.003173
Holocephalus sculptus	NA	Paracoprid	NA	NA	1.0104
Ontherus azteca	Forest specialist	Paracoprid	Coprophage	Nocturnal	0.060646
Ontherus irinus	Forest specialist	Paracoprid	NA	NA	0.0694
Onthophagus aff. *catharinensis*	NA	Paracoprid	NA	NA	0.006
Paracanthon sp.	Forest specialist	NA	Coprophage	Diurnal	0.0046
Pseudocanthon sp.	Open environ. specialist	NA	Coprophage	Nocturnal	0.003653
Streblopus opatroides	Forest specialist	NA	Coprophage	Nocturnal	0.093923
Trichillum externepunctatum	Habitat generalist	Endocoprid	Coprophage	Nocturnal	0.002823
Uroxys sp.	Forest specialist	NA	Coprophage	Nocturnal	0.00196

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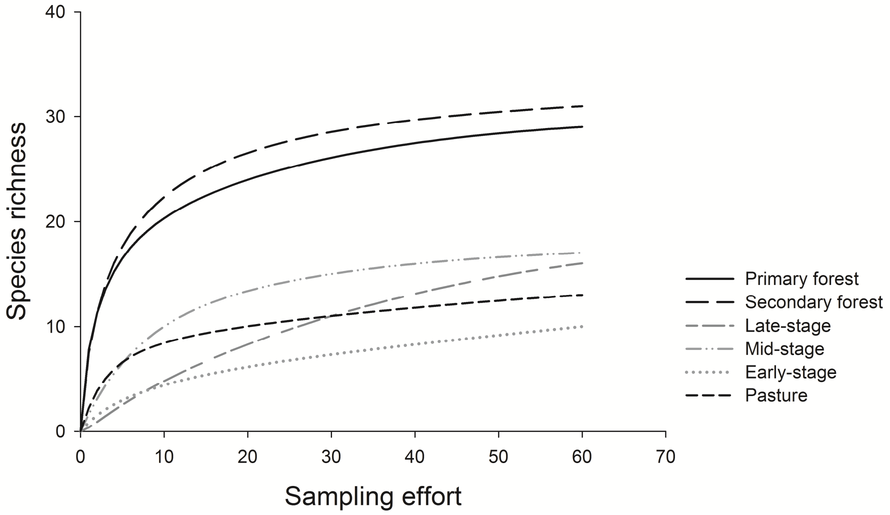
Appendix C. Identity of Scarabaeine dung beetles species, total captures per habitat type and species accumulation curves.

Table C.1. Identity of Scarabaeine dung beetles species and total captures per habitat type: primary forest (PF), old secondary forest (SF), late-stage restoration (LR), mid-stage restoration (MR), early-stage restoration (ER) and pasture (P).

Species	**PF**	**SF**	**LR**	**MR**	**ER**	**P**	**Total number of individuals**
Anomiopus sp.	2	5	0	0	1	0	8
Ateuchus sp.1	192	119	2	0	0	0	313
Ateuchus sp.2	55	68	48	10	0	0	181
Ateuchus sp.3	2	7	3	13	0	0	25
Canthidium aff. *depressum*	2	0	0	0	0	0	2
Canthidium aff. *korschefskyi*	40	6	0	0	0	0	46
Canthidium aff. *lucidum*	92	64	0	0	0	0	156
Canthidium aff. *trinodosum*	609	214	11	0	0	0	834
Canthidium sp.1	18	36	1	0	0	0	55
Canthidium sp.2	0	1	0	0	0	0	1
Canthidium sp.3	0	22	0	0	0	0	22
Canthidium sp.4	0	0	1	19	0	0	20
Canthidium sp.5	0	0	0	433	0	0	433
Canthon aff. *viidus*	0	0	0	16	114	32	162
Canthon chalybaeus	0	0	0	0	1	0	1
Canthon histrio	0	0	0	46	20	0	66
Canthon lituratus	0	0	0	0	1	91	92
Canthon mutabilis	0	0	0	0	5	1	6
Canthon sulcatus	286	444	0	0	0	0	730
Canthonella silphoides	552	582	31	75	0	0	1240
Chalcocopris hespera	3	11	0	0	0	0	14
Coprophanaeus bellicosus	18	19	0	0	0	0	37
Coprophanaeus cyanescens	0	0	0	4	0	13	17
Coprophanaeus dardanus	8	10	3	9	1	0	31
Coprophanaeus punctatus	5	2	0	0	0	0	7
Deltochilum aff. *calcaratum*	7	11	0	0	0	0	18

Deltochilum granulosum	1	3	0	0	0	0	4
Diabroctis mimas	0	0	0	0	0	2	2
Dichotomius aff. *laevicollis*	0	0	0	64	0	0	64
Dichotomius aff. *sericeus*	1990	1762	141	31	0	0	3924
Dichotomius bos	0	0	0	0	0	1	1
Dichotomius depressicolis	0	1	1	0	0	0	2
Dichotomius geminatus	0	0	0	0	6	76	82
Dichotomius irinus	156	27	0	0	0	0	183
Dichotomius mormon	0	0	2	3	0	0	5
Dichotomius nisus	0	0	1	0	0	76	77
Dichotomius quadrinodosus	1	2	0	0	0	0	3
Dichotomius schiffleri	3	163	0	0	0	0	166
Dichotomius semisquamosus	0	1	3	3	1	0	8
Eurysternus calligrammus	112	127	2	0	0	0	241
Eurysternus hirtellus	91	98	7	6	0	0	202
Eurysternus nigrovirens	0	0	15	2	0	3	20
Eutrichillum hirsutum	15	17	0	0	0	2	34
Holocephalus sculptus	0	0	1	0	0	0	1
Ontherus azteca	2	0	3	9	0	0	14
Ontherus irinus	3	4	0	0	0	0	7
Onthophagus aff. *ranunculus*	0	0	0	0	0	14	14
Paracanthon sp.	20	27	0	0	0	0	47
Pseudocanthon sp.	0	0	0	0	0	80	80
Streblopus opatroides	52	29	2	0	0	0	83
Trichillum externepunctatum	0	0	0	1	21	160	182
Uroxys sp.	130	59	2	0	0	0	191
Number of individuals	**4467**	**3941**	**280**	**744**	**171**	**551**	**10154**
Number of species	**29**	**31**	**20**	**17**	**10**	**13**	**52**

Figure C.1. Sample-based species accumulation curves for dung beetles in primary, old secondary forest, late-stage, mid-stage , early-stage restoration and pasture.



Appendix D. Results of the permutational analysis of variance (PERMANOVA).

Table D.1. Results of the permutational analysis of variance (PERMANOVA) indicating whether the categories of habitat types are different according to species composition. Pseudo-F and p-value are presented for the main test and test statistic (t) and p-values for each pair-wise comparison. * = p-values < 0.05

Source of variation	**Pseudo-F**	**p**
Land use systems	7.45	0.0001*
Post hoc comparison of systems		
Land use systems	**t**	**p**
Primary forest vs. secondary forest	1.04	0.41
Primary forest vs. pasture	5.04	0.008*
Primary forest vs. late-stage restoration	2.32	0.006*
Primary forest vs. mid-stage restoration	2.56	0.008*
Primary forest vs. early-stage restoration	4.40	0.008*
Secondary forest vs. pasture	4.77	0.007*
Secondary forest vs. late-stage restoration	2.22	0.006*
Secondary forest vs. mid-stage restoration	2.45	0.01*
Secondary forest vs. early-stage restoration	4.19	0.006*
Pasture vs. late-stage restoration	3.49	0.009*
Pasture vs. mid-stage restoration	2.53	0.007*
Pasture vs. early-stage restoration	2.15	0.008*
Late-stage restoration vs. mid-stage restoration	1.61	0.02*
Late-stage restoration vs. early-stage restoration	3.19	0.009*
Mid-stage restoration vs. early-stage restoration	1.99	0.01*

ARTIGO 2

Drivers of dung beetle community assembly in tropical forest restoration areas: role of local environment and landscape structure

Preparado de acordo com as normas da revista Ecological Applications
Versão preliminar

ABSTRACT

Forest restoration approaches not based on scientific theory are unlikely to advance. Yet, there is still a lot of work to do to reduce the disconnection between theory and practice. We assessed the effectiveness of assembly rules theory to guide restoration efforts, evaluating the relative importance of local environment conditions, landscape context and spatial descriptors (used here to estimate neutral dispersal-assembly or unmeasured spatially structured processes) for determining dung beetle species and functional trait composition in a gradient of 15 restoration areas at tropical Atlantic Forest, Brazil. We also verified how local environment and landscape influence restoration areas similarity to the reference system (primary forest), indicating potential threshold values. Assembling of both species and functional trait composition were predominantly driven by niche-based processes, mainly by the influence of local environment. Landscape and spatial descriptors showed little independent effects. Most of the variation explained by space was also co-explained by environment and landscape, ruling out the potential influence of stochastic factors. Almost all variance explained by landscape was environmentally structured, showing that dung beetle dispersal is mostly determined by species specific environmental responses, depending on appropriate environmental conditions surrounding the restoration areas. Despite the little evidence on neutral dispersal limitation in variance partitioning analysis, the large amount of ‘‘unexplained’’ variation may reflect the occurrence of stochastic processes and/or of unmeasured environmental variables. Only two individual functional traits were influenced by the environmental variables measured and these traits exhibited different responses to the different environmental filters. Restoration areas that are more similar to primary forest according to species and trait composition generally presents a high forest canopy (> 69%), small distance among trees (< 221 cm), a well developed leaf litter layer (> 0.90 cm), are located in sites containing more than 20% of forest cover surrounding the landscape and closer to environmental reserves (< 30 km). This study emphasizes that assembly rules assumptions can help to better understand restoration processes, enabling to improve future restoration efforts. Our results demonstrates that before taking into account the effects of stochastic events, it is necessary to prioritize the restoration of desired environmental and landscape conditions.

Key words: Atlantic Forest; dispersal limitation; environmental filtering; restoration practices; functional traits; Scarabaeinae.

INTRODUCTION

The science of restoration ecology only exists for a few decades and is already considered a global priority to reverse human impacts on biodiversity and ecosystems functioning (Bullock et al. 2011, Galatowitsch 2012, Aronson and Alexander 2013). Despite its rapid scientific growth and consolidation (Suding 2011), there is still a need to advance in studies on restoration theoretical basis in order to guide its practices (Hobbs and Norton 1996, Palmer et al. 1997, Halle and Fattorini 2004, Rodrigues et al. 2009, Montoya et al. 2012). Ecological theories can contribute to improve restoration techniques and create more adequate practical management guidelines (Hobbs and Harris 2001, Halle and Fattorini 2004). In this context, community assembly theory has been widely recognized in the literature as one of the most important theoretical basis for restoration ecology (Young et al. 2001, Temperton et al. 2004). Assembly theory and restoration ecology are complementary fields, since the first seeks for rules that governs community assembly and the second the reconstruction of biologically functional communities (Temperton et al. 2004). Nevertheless, there have been few studies attempting to link assembly rules theory to restoration ecology (e.g. Moir et al. 2005, Funk et al. 2008, Matthews et al. 2009, Helsen et al. 2012, Barnes et al. 2014, Laughlin 2014).

Assembly theory predicts that species distribution can be affected by niche and/or neutral-based processes (i.e. deterministic vs. stochastic factors) (Belyea and Lancaster 1999, Weiher et al. 2011). Niche theory mainly demonstrates that species composition will be determined by environmental factors as a result of species-specific differences (Chase and Leibold 2003). In contrast, neutral theory assumes that species are ecologically equivalent and patterns of community assembly will occur randomly, specifically driven by dispersal limitation (colonization chance) (Hubbell 2001). Traditionally, these studies have been performed using a taxonomic perspective (i.e. species composition), but more recently a functional trait-based approach have become the focus to understand the underlying mechanisms of community assembly (McGill et al. 2006, Mouillot et al. 2013, Cadotte et al. 2013). When functional traits are used, species are grouped together according to their ecological similarities (i.e. resource use, habitat requirements), which can provide a better insight of niche-based processes (Cadotte et al. 2011, 2013, Mouillot et al.

2013). Generally, environmental filtering act on trait composition, and not on the species composition *per se* (Siefert et al. 2013, Cadotte et al. 2013). Besides, measures of functional traits can reflect aspects of ecosystem functioning (De Bello et al. 2010). Therefore, combined with traditional approaches, functional trait composition can improve the understanding of community assembly processes (Mouchet et al. 2010).

There is evidence in the literature that local environment and landscape context are the main drivers of species distribution in restored sites (e.g. Matthews et al. 2009, Brudvig 2011, Montoya et al. 2012, Leite et al. 2013, Shackelford et al. 2013). Site level conditions can act as a series of ecological filters determining whether a species will be able to colonize, establish and survive there (Hobbs and Norton 2004, Brudvig 2011). Landscape context, such as distance to source populations and land-use composition surrounding restoration sites, can highly influence the species power of dispersal, determining its probability to reach a site (Moir et al. 2005, Brudvig 2011, Leite et al. 2013, Shackelford et al. 2013). Dispersal constraints can also be driven by colonization chance, generating patchy spatial patterns of populations, where closer sites will be more similar in relation to species composition (Hubbell 2001). In general, spatial descriptors derived from geographic coordinates (PCNMs, Borcard et al. 1992) have been used to help understand these spatial patterns derived from dispersal limitation. Conceptually, stochasticity is considered an important factor influencing community assembly in restoration sites, but empirically has been relatively unexplored. Despite the recognized importance of local environment, landscape and spatial descriptors, there have been no studies investigating their relative influence on community assembly in restored sites.

The aim of this study was to test assembly rules theory assumptions in a forest restoration context, in order to guide restoration actions. We used dung beetles (Coleoptera: Scarabaeinae) as a focal taxon because they exhibit clear responses to environmental gradients, depend on other groups of organisms for food resources, and provide a set of ecological functions to ecosystems (Nichols et al. 2007, 2008, 2009). They are also excellent for the search for patterns in community ecology, being well known both taxonomically and functionally (Spector 2006). We evaluated the importance of local environmental data, landscape metrics and spatial descriptors for determining dung beetle species composition and functional trait composition in tropical forest restoration areas. We also verified how environmental and landscape variables influence the similarity of the restoration areas to the reference system (primary forest) according to species and trait composition, indicating potential threshold values that guarantee a higher similarity. Specifically we asked: (1) What is the relative importance of local environmental filters, landscape metrics and spatial descriptors on structuring species composition and traits composition of dung beetle communities in tropical forest restoration areas? (2) How do environmental factors and landscape structure influence the multiple functional traits of dung beetle communities? (3) How environmental filters and landscape descriptors influence the similarity of the restoration areas to the reference system (primary forest) according to species and trait composition? (4) Are there environmental and landscape characteristics thresholds associated with increasing similarity of the restoration areas to the reference system?

MATERIAL AND METHODS

Study area

The study was carried out within Veracel Celulose S.A. Company landholding, located in the south of Bahia state, Brazil (16°06' - 16°23' S, 039°09' - 039°49' W) (Figure 1). The company occupies near 210.000 hectares across 10 municipalities, of which 96.000 are covered by *Eucalyptus* plantation and 105.000 hectares were allocated for conservation of native vegetation (New Generation Plantations Project 2007, Veracel 2011).

The region lies within the Atlantic Forest biome, one of the most threatened tropical forests worldwide, that supports one to eight percent of the world’s total species and also present high levels of endemism (Myers et al. 2000, Sloan et al. 2014). Most of the original forest of the south Bahia has been logged and subsequently replaced by pastures during the 1960s and 1970s. When the company was installed in the region (1990s) the landscape was dominated by pastures and presented less than 7% of the original Atlantic Forest (New Generation Plantations Project 2007). Veracel generally plants *Eucalyptus* in areas that has been previously used for cattle grazing and that are almost exclusively associated with plateaus. The company is also committed to restore Atlantic rainforest vegetation and until 2011 it had replanted a total of 4.300 hectares. The restoration program started in 1994 and since 2004 it compromises to restore a minimum of 400 hectares per year. The restoration consist of active planting of Atlantic rainforest tree species seedlings in areas of degraded introduced pasture (New Generation Plantations Project 2007, Veracel 2011, for more details, see Appendix A).

The studied region presents a tropical rainforest climate, type Af, with rains well distributed throughout the year and temperatures high and fairly constant (Kottek et al. 2006). It receives approximately 1600 mm of precipitation annually, with the temperatures ranging from 18.9–27.9°C, achieving an average of 22.6° per year (Veracel 2007).

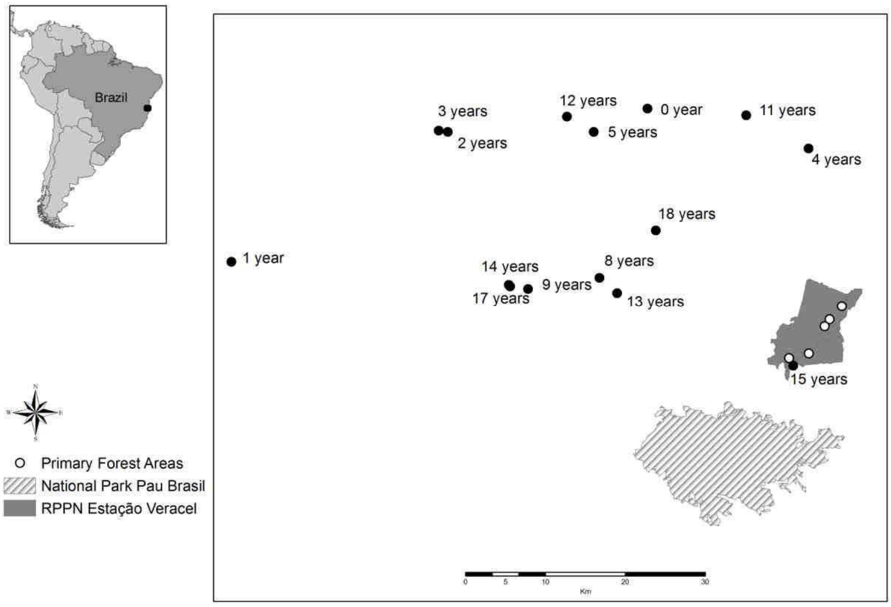


FIG. 1. Map of the study region (south of Bahia state, Brazil) showing the location of the 15 forest restoration areas, five areas of primary forest and the two largest environmental reserves of the landscape (RPPN Estação Veracel and Pau Brasil National Park).

Dung beetle sampling

Sampling was conducted between May 12th and June 3th 2012. We sampled dung beetles in 15 forest restoration areas, ranging from 0 to 18 years, representing different successional stages (Figure 1). These ages were classified according to the initiation of restoration process, in other words, since planting of native tree seedlings. Due to different ages, these restoration areas exhibit differences in relation to vegetation structure. The sampled restoration areas are distributed through the studied landscape, being located at a minimum distance of 500 m from each other. The collections were also conducted in five areas of primary forest (reference system) at least 1 km apart. These primary forest areas are located in the Veracel Station Private Reserve of Natural Heritage (RPPN Estação Veracel), which contains around 6000 hectares of preserved forest and it is considered one of the largest reserves in the Atlantic forest biome. One sampled restoration area (15 years) was located inside RPPN at a distance of 5 m from the preserved rainforests, but >1 km from the sampled primary forest sites. The others were situated between 20 km and 70 km from the RPPN Estação Veracel (Figure 1).

In order to sample dung beetles we used pitfall traps baited with 25 g of human feces, carrion (bovine spleen) or rotten banana. The pitfalls consisted of a plastic container (11 cm height, 19 cm diameter) buried flush with the ground, and a bait recipient (5 cm diameter, 5 cm height) suspended in the center of the trap. To protect the trap from rain and sun a plastic lid cover was held 20 cm above it using wooden stakes. Dung beetles attracted by the bait fell into a saline and detergent solution.

Each restoration and primary forest area received a total of 12 pitfalls traps disposed in a linear transect placed 50 m from the edge, whenever possible. The transects presented four sample points spaced 100 m apart. Each sample point received three pitfall traps distanced by 3 m from each other, one with each bait type (feces, carrion, fruit). Traps were left in the field for 48h. Dung beetles were identified to the species level by Dr. Fernando Z. Vaz-de-Mello (Universidade Federal do Mato Grosso).

Trait data

We used four ecological attributes to quantify functional trait composition of dung beetles: food relocation habit, diet, period of fly activity and biomass. These four characteristics reflect the response of organisms to environmental conditions and have significant effects on ecosystem function (Slade et al. 2007, 2011, Barragán et al. 2011, Nichols et al. 2013). Dung beetle traits were determined through this study using different methodologies and, when necessary, we also obtained additional information from the literature and specialists (for more details and list of species with its respective traits, see Audino et al. 2014).

Food relocation habit was categorized into three main groups: tunnelers, rollers and residents, according to Bornemissza (1969) and Hanski and Cambefort (1991). Information on species diet were obtained according to the percentage of individuals attracted to each bait. Species were categorized as coprophages, necrophages or carpophages if at least 80% of the beetles were captured in traps baited with human feces, carrion or rotten fruit, respectively. Species with similar abundance in more than a type of baited trap were considered generalists (Halffter and Favila 1993, Halffter and Arellano 2002). Only dung beetle species with more than 10 individuals sampled were assigned into diet categories. To obtain information about diel fly activity we performed a supplementary experiment, sampling dung beetles in natural and modified systems of the studied region. We sampled one area of primary forest, old secondary forest, introduced pasture and *Eucalyptus* plantation using the same sampling design described before. However, specimens were removed from the traps every 12h, at dawn (05h40am) and dusk (05h40pm). Traps were left in the field for 48h and baits were replaced every 12h. Species were then classified as diurnal or nocturnal. Furthermore, biomass was obtained weighting a sample of 30 individuals of each species (whenever possible) after drying it at 60°C for one week.

Local environmental data

The restoration sites and primary forest areas were characterized according to six environmental variables: canopy cover, understory cover, distance among trees, tree basal area, leaf litter depth and percentage of sand in soil samples. We measured canopy cover above traps using hemispherical photographs taken with a Nikon D40 coupled with a fisheye hemispherical lens 0.20 x and analyzed with the software Gap Light Analyzer 2.0 (Frazer et al. 1999). To measure understory cover we took photographs of the understory beside the sample points using a black sheet (1 x 1 m) arranged perpendicularly to the ground as background. The photographs were analyzed with the software Sidelook 1.1 (Nobis 2005). We calculated distance among trees and basal area recording the distance from the center of each sample point to the nearest four trees (circumference higher or equal to 10 cm at 1.3 m above soil) and measuring the perimeter of those trees. Distance among trees was estimated as the average distance (cm) between the center of the sample points and trees, serving as a proxy of tree density in the sampled areas. Basal area is related to the mean size of the trees and was calculated using the following formula: $AB = P^2/4\pi$, which AB is tree basal area and P the perimeter. Leaf litter depth was measured within 3 m from the sample points using a digital pachymeter. Sand percentage in the soil was quantified through the collections of soil samples (20 cm depth), obtained beside the sample points, in each study area. These samples were analyzed for texture (proportion of sand, silt and clay) at the Universidade Federal de Lavras, Departamento de Ciências do Solo.

Landscape metrics

All 15 forest restoration areas were examined regarding the percentage of native forest cover surrounding the landscape and distance to the closest environmental reserve. Percentage of native forest cover was calculated within five buffers (100, 250, 500, 750 m and 1 km). Then, we performed a forward selection procedure to determine which buffer size has the highest explanatory power of species composition and functional trait composition data. The 250 m buffer was the only one retained in forward selection ($p < 0.05$), describing the most amount of variation. For this reason, the 250 m buffer will be the one that is going to be used in subsequent analysis. Distance from the closest environmental reserve was considered as a proxy of distance to species source pools. The environmental reserves considered to calculate the distance were the largest reserves found in the studied region, RPPN Estação Veracel (described above) and Pau Brasil National Park. Pau Brasil National Park is even larger than RPPN Estação Veracel, presenting 19.000 hectares of preserved Atlantic forest (Figure 1). The landscape metrics were quantified in Q-GIS using a digital map from a series of aerial photos (1:100.000) provided by Veracel Celulose SA. Forward selection was computed using the “packfor” package, function “forward.sel”, in software R (Dray 2011, R Development Core Team 2014).

Spatial descriptors

Geographical coordinates of the 15 restoration areas were used to run principal coordinates of neighbor matrices (PCNM) analysis (Borcard and Legendre 2002), computed with vegan package, function pcnm, in the software

R (Oksanen et al. 2013, R Development Core Team 2014). From the geographical positions, this analysis generates PCNM eigenfunctions that describes the spatial patterns among the sampling areas at different scales (Dray et al. 2006). These are obtained through principal coordinate analysis (PCoA) of a truncated geographic distance matrix, retaining eigenfunctions with positive eigenvalues. The PCNM analysis resulted in a total of 8 positive eigenfunctions and these were used as explanatory variables.

Restoration age

Restoration age was initially considered in this study as a possible group of predictor variables, given its potential to influence community assembly in restoration areas. However, we did not find any direct influence of this variable on dung beetle species and functional trait composition. The influence of restoration age is only associated to its correlation with environment, landscape and space variables (Appendix B). Therefore, restoration age was not included in subsequent analysis.

Statistical analyses

All statistical analyses were performed in the software R version 3.1.1 (R Development Core Team 2014), and the statistical tests conducted at a significance level of 0.05.

Relative importance of local environment, landscape and space

The potential for local environment, landscape and space to explain the patterns of dung beetle species composition and functional trait composition (abundance of each trait in the sampling sites) in forest restoration areas was evaluated using variance partitioning analysis (Peres-Neto et al. 2006). This method uses canonical redundancy analysis (RDA) in order to decompose the variation in species and trait composition matrices into independent and joint effects of local environment, landscape and space (Borcard et al. 1992, Peres-Neto et al. 2006). Variance partition have been widely used to understand the guiding mechanisms of community assembly (e.g. Gilbert and Lechowicz 2004, Legendre et al. 2009, Louzada et al. 2010, Baldeck et al. 2013, Myers et al. 2013). The predominance of local environment and/or landscape effects suggest that niche based processes (e.g. environmental filtering, Chase and Leibold 2003) are likely influencing the assembly of dung beetle communities. The predominance of space may reflect the influence of stochastic factors (neutral theory, Hubbell 2001), specifically dispersal limitation, and also of unmeasured environmental variables that are spatially structured (Anderson et al. 2011, Baldeck et al. 2013). Since intraspecific aggregation can be driven by both neutral dispersal limitation and environmental variables, authors have recently warned the difficulties to interpret the relative roles of niche and neutral processes (Baldeck et al. 2013, Siefert et al. 2013). Dispersion limitation driven by landscape is different from the one described by neutral theory, because the distribution of species are not random, but influenced by species-specific environmental responses.

Prior to variance partitioning analysis, response variables (species and functional trait composition) were Hellinger-transformed and each group of predictor variables (local environment, landscape and space) were submitted to permutational forward selection procedure. Forward selection was applied because of the high number of possible predictors (16) relative to the number of sites (15). This procedure allows to identify the predictor variables that are significantly correlated with the response variables, avoiding type I errors and overestimating the amount of explained variance (Dray 2011). Variance partitioning analysis was performed using vegan package, function varpart (Oksanen et al. 2013).

Functional trait individual responses to local environment and landscape

The effects of local environment and landscape variables on the multiple functional traits of dung beetle communities was evaluated using hierarchical partitioning analysis (Chevan and Sutherland 1991). Hierarchical partitioning is an analytical method of multiple-regression that uses all possible model combinations, changing the order of the predictor variables, to identify the variables that have the greatest independent influence on the dependent variable (Chevan and Sutherland 1991, Mac Nally 2000, Olea et al. 2010). To calculate the independent contribution, the analysis separates it from joint contributions resulting from correlation with other variables (Olea et al. 2010). Models used gaussian errors for biomass and quasi-binomial errors for the remaining traits, and we evaluated competing models based on the R2 goodness of fit statistic. The significance of independent effects was calculated using a randomization test with 1000 iterations (Mac Nally 2002). We tested the independent effects of eight predictor variables (all local environment and landscape metrics, see above) on the total biomass and the percentage number of individuals of each dung beetle trait in the restoration areas (diurnal/nocturnal, tunnelers, rollers and dwellers, coprophages, necrophages and generalists). Hierarchical partitioning was implemented using the hier.part package (Walsh and Mac Nally 2007).

Environment and landscape variables influence on similarity to the reference system

We used generalized linear models to verify how environmental filters and landscape descriptors influence restoration areas similarity to primary forest according to species and trait composition. We calculated the mean similarity of the restoration areas to primary forest according to species and functional trait composition using Bray-Curtis similarity index. Abundance data was standardized and square root transformed prior to the construction of Bray-Curtis triangular matrix. First, we tested if restoration areas that present a higher environmental dissimilarity to primary forest have a smaller species and functional trait composition similarity to primary forest. We calculated environmental dissimilarity of the restored areas to primary forest based on all local environmental variables measured, using Euclidean distance. Secondly, we tested how each environmental and landscape variable influence this similarity. Species composition and functional trait composition similarity to primary forest were considered the response variables and environmental dissimilarity to primary forest, all environmental and landscape predictors as the explanatory variables. We used quasi-binomial errors for both response variables.

Similarity to the reference system: threshold values

We performed univariate regression tree analysis to identify local environmental and landscape characteristics thresholds associated with high similarity of the restoration areas to the primary forest according to species and functional trait composition. This method uses dichotomous keys creating break points of the predictor variables and partitioning the data set into mutually exclusive groups. Groups within the same break point present similar values of the response variable (De'ath 2002). Trees were determined by using 1000 cross-validations and pruned based on the 1-SE (standard error) error rule, whereby selection of the best tree was performed within one standard error of the minimum. This analysis was implemented using the mvpart library, function rpart (De'ath 2013).

Variables correlations

We investigated the existence of possible correlations among the environmental, landscape and spatial variables using Pearson correlation analysis. Pearson correlation values are presented in Appendix C. Correlated variables were kept in our study, since all statistical analysis used here accept collinearity.

RESULTS

Across all restoration and primary forest areas, we collected a total of 5662 dung beetles from 46 species (Appendix D). In the restoration areas we found 1195 individuals distributed in 31 species and in primary forest we recorded 4467 individuals of 29 species. Only 14 species (30%) were shared by the restoration and primary forest areas. The mean species richness found in the restoration areas was 5.7 per site and in primary forest areas 20.2 per site. The most abundant species in all sampling sites was *Dichotomius* aff. *sericeus* (2162 individuals), *Canthonella silphoides* (658 individuals) and *Canthidium* aff. *trinodosum* (620 individuals), representing 60% of all sampled individuals.

Relative importance of local environment, landscape and space

Forward selection procedure yielded four significant predictor variables for dung beetles species composition data: PCNM3 among the set of space descriptors, canopy cover and understory cover among the set of local environment descriptors and percentage of forest cover among the set of landscape metrics. The same number of predictor variables were selected as significant in explaining functional trait composition: PCNM3, canopy cover, basal area of the trees and percentage of forest cover.

Space, landscape and local environment explained together 26% of the variation in dung beetle species composition at the forest restoration areas (Fig. 2a). Nearly half of this total (12%) was attributed to environment alone. The independent effects of space and landscape was substantially smaller, accounting for 1% and 0% of explanation respectively. The other half of the total variation was explained by the joint effects among the three sets of predictor variables: spatially structure landscape variables (2%), spatially structured environmental variables (2%) combined variation of landscape-environment (2%), joint fraction of space-landscape-environment (8%). When accounting for independent and joint effects together, local environment explained the largest amount of variation (24%), followed by space (13%) and landscape (11%).

Functional trait composition presented similar assembly patterns (Fig. 2b). The total amount of variation explained by the model was slightly higher (32%). Local environment was again more important than space and landscape, explaining a total of 32% of the variation and 18% alone. However, at this time, landscape presented more total explanation than space (13% and 12%, respectively). For both, this total explanation was basically due to the joint effects with the other sets. Landscape presented an independent effect of 0% and space of 1%.

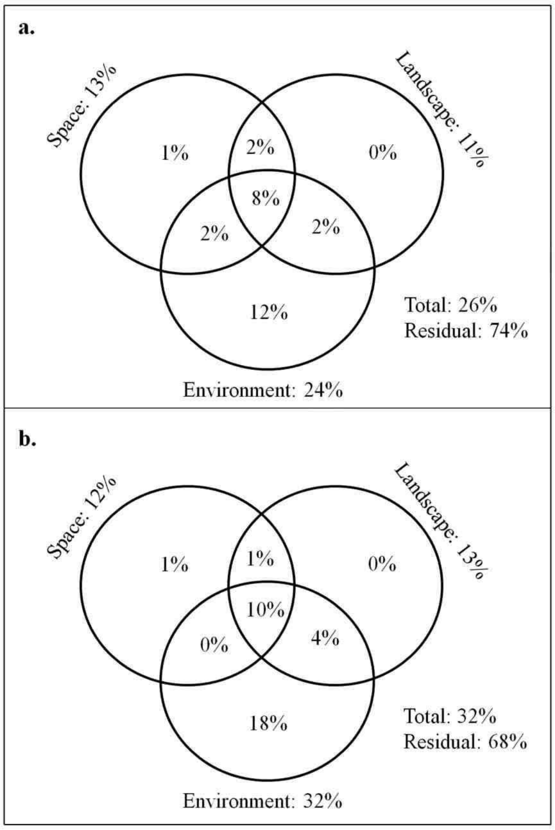


FIG. 2. Fractions of explained variation for species composition (a) and functional trait composition (b). Total fractions are listed above the circles, and individual fractions are indicated within the Venn-diagrams.

Functional trait individual responses to local environment and landscape

Only two out of eight hierarchical partitioning randomizations tests showed a significant influence of the predictor variables on dung beetle traits (Fig. 3). Canopy cover presented an independent and positive effect on the percentage of tunnelers individuals. Tree basal area had an independent and positive influence on the percentage of necrophages individuals. Total biomass, percentage of diurnal/nocturnal, rollers, residents, coprophages and generalists number of individuals were not significantly influenced by any of the predictor variables tested. None of the landscape-related variables affected individual dung beetle traits.

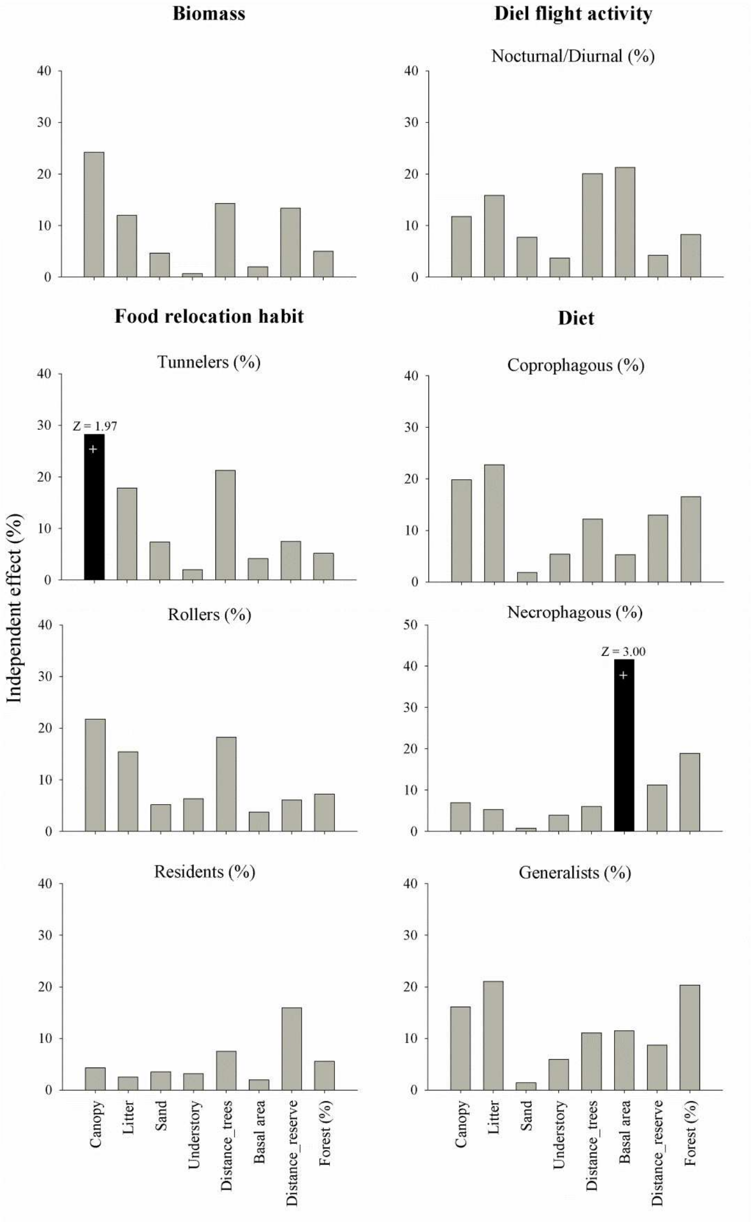


FIG. 3. Distribution of the percentage of independent effects of environmental and landscape variables on dung beetle community functional traits (biomass and number of individuals percentage of each dung beetle trait). Black bars

represent significant effects ($p < 0.05$) as determined by randomization tests. Z-scores for the generated distribution of randomized I's (I value = the independent contribution towards explained variance in a multivariate dataset) and an indication of statistical significance. Z-scores are calculated as (observed – mean (randomizations))/SD(randomizations), and statistical significance is based on upper 0.95 confidence limit ($Z \geq 1.65$). Positive or negative relationships are shown by + or –, respectively.

Environment and landscape variables influence on similarity to the reference system

According to generalized linear models, restoration areas that are more environmentally similar to primary forest also present a higher similarity in relation to species and functional trait composition (Fig. 4, Table 1). The local environmental variables that showed a significant relationship with species and functional trait composition similarity to primary forest was: canopy cover, leaf litter depth and distance among trees. Similarity of the restoration areas to primary forest increased with canopy cover and leaf litter depth and decreased with the distance among trees (smaller degree of tree density). We found no relationship between species and trait composition similarity to primary forest and tree basal area, understory cover and sand percentage. In relation to the landscape metrics, restoration areas that are closer to the environmental reserves and have more forest cover surrounding its landscape also presented a higher similarity to primary forest according to species and functional trait composition (Fig. 4, Table 1).

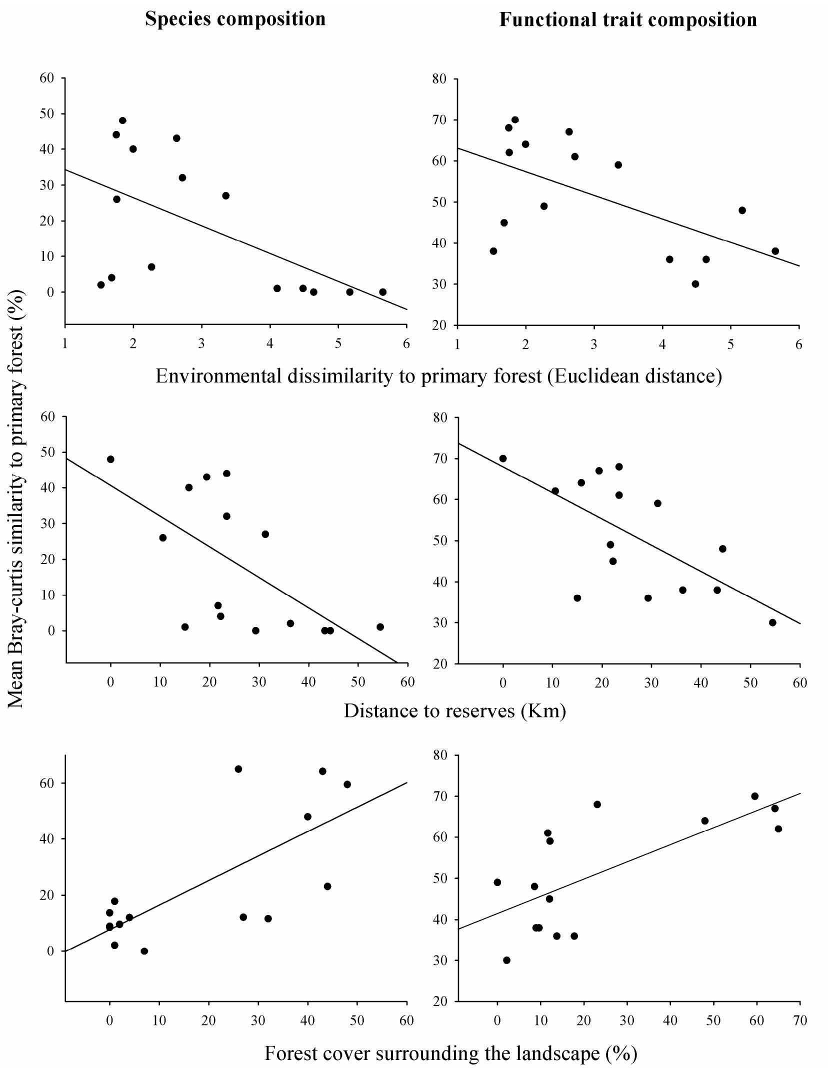


FIG. 4. Relationship between species composition and functional trait composition similarity of the restoration areas to primary forest and environmental dissimilarity to primary forest (measured as Euclidean distance), distance from the closest environmental reserve, and percentage of forest cover surrounding the restoration areas.

TABLE 1. Generalized linear models results showing the relationship between species composition and functional trait composition similarity of the restoration areas to primary forest and environmental dissimilarity to primary forest (measured as Euclidean distance), canopy cover, leaf litter depth, distance among trees, tree basal area, understory cover, soil sand distance to the closest environmental reserve, and percentage of forest cover surrounding the restoration areas.

Similarity to primary forest (Bray-Curtis)

	Species composition		**Trait composition**	
	F	**P**	**F**	**P**
Local environment				
Environmental dissimilarity to PF	**7.78**	**0.01**	**6.87**	**0.02**
Canopy cover (%)	**25.46**	**0.0002**	**19.51**	**0.0006**
Leaf litter depth (cm)	**13.88**	**0.002**	**18.93**	**0.0007**
Sand (%)	2.65	0.12	1.20	0.29
Understory cover	0.15	0.70	0.01	0.90
Distance among trees (cm)	**20.16**	**0.0006**	**7.12**	**0.01**
Tree basal área	0.80	0.38	0.62	0.44
Landscape				
Distance to reserves (km)	**9.07**	**0.01**	**9.86**	**0.007**
Forest cover (%)	**9.46**	**0.008**	**12.67**	**0.003**

Similarity to the reference system: threshold values

Species composition similarity

Only canopy cover and distance among trees were selected in the tree regression model for species composition similarity (Fig. 5a). Canopy cover was the splitting factor at the first node and the most influential variable. According to this model, restoration areas with a forest canopy higher than 69.4% presented a mean similarity to primary forest (0.38) almost 10 times higher than the areas with a smaller percentage of canopy cover (0.04). Areas presenting less than 69.4% of canopy cover was further split by distance among trees: areas with a higher density of trees (distance < 221.9 cm) were more similar to primary forest (0.15) in relation to the ones with a smaller density of trees (distance > 221.9 - 0.01). Within the larger distance among trees (> 221.9), regression tree analysis provided the final split, indicating that areas with a much higher distance (> 463.2) were greatly less similar to primary forest (0.004) in relation to areas with a distance among tress smaller than 463.2 (0.04).

Both variables of the landscape metrics (percentage of forest cover and distance to reserves) were retained in regression tree analysis as significant to explain species composition similarity to primary forest (Fig. 5b). In this model we also obtained a tree formed by three splits. The first split was based on percentage of forest cover, presenting the largest influence on the response variable. Similarity to primary forest was higher in restoration areas presenting more than 20.43% of forest cover surrounding its landscape (0.40). Areas with a smaller percentage of forest cover presented an average similarity of 0.04 and was next split by distance to reserves. Restoration areas distanced by more than 33.7 km to the environmental reserves presented a really small average similarity to primary forest (0.007) in relation to the ones localized closer to the reserves (distance > 33.7 km – 0.11). These restored sites closer to the reserves provided the last split, again explained by percentage of forest cover: areas with more than 12.9% of forest cover were more similar to primary forest (0.17) in relation to the ones containing a smaller percentage of forest (0.005).

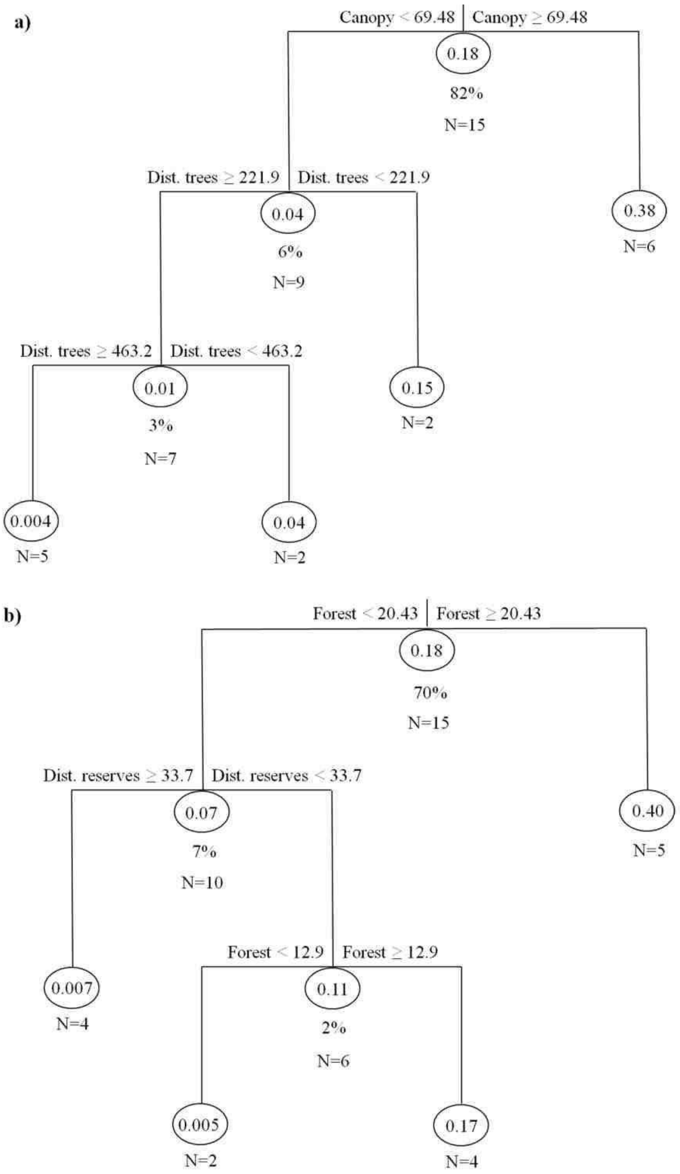


FIG. 5. Regression trees analysis for predicting species composition similarity (Bray-Curtis index) of dung beetle communities in the restoration areas to primary forest (reference system). a) Variables tested were canopy cover (%), leaf-litter (cm), sand (%), understory vertical structure, distance among trees

(cm) and tree basal area; b) Variables tested were distance to reserves (Km) and percentage of forest cover surrounding the restoration areas. Values inside the circles indicate the average similarity to primary forest and the percentage values of each split indicate the variation explained.

Functional trait composition similarity

Functional trait composition similarity to primary forest was best described by a two leaf regression tree containing two environmental variables: canopy cover and leaf litter depth (Fig. 6a). Canopy cover was again the most influential variable, explaining 74% of the model. The threshold values obtained for canopy were the same as the ones found for species composition (<69.48% and > 69.48%), however the differences in average similarity between the two groups were not so high (0.42 – 0.65, respectively). Areas below 69.48% of forest cover was further split by leaf litter depth. The smallest values of similarity to primary forest (0.35) were found in areas containing a percentage of forest cover smaller than 69.48% and leaf litter depth smaller than 0.90 cm. Areas containing higher values of leaf litter presented an average similarity of 0.47.

The same threshold values found for species composition in relation to the landscape metrics was found for functional trait composition similarity (Fig. 6b). The only differences between the two models were the mean similarity values and the regression tree size. For functional trait composition it was generated a tree formed by two splits: the first split based on percentage of forest cover (< 20.43 and > 20.43) and then, for low forest cover rates, a second split based on distance to reserves (>33.47 and < 33.47).

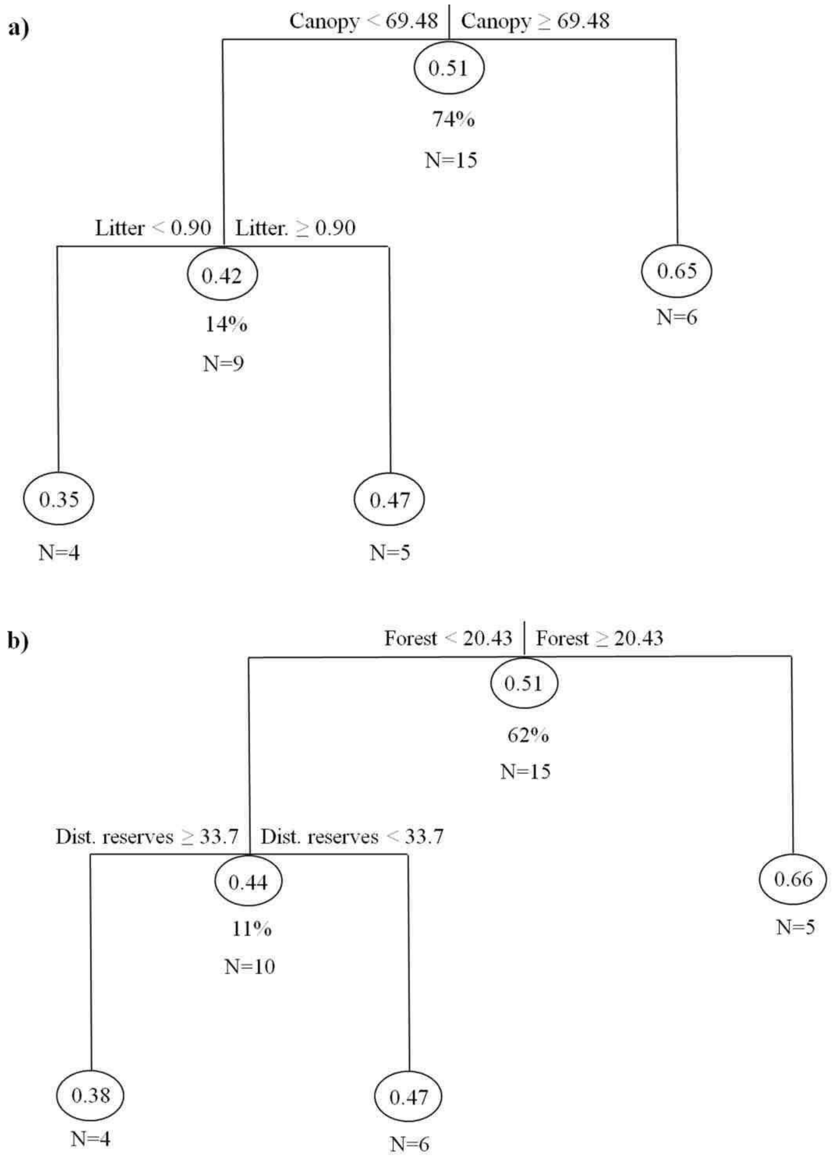


FIG. 6. Regression trees analysis for predicting functional trait composition similarity (Bray-curtis index) of dung beetle communities in the restoration areas to primary forest (reference system). a) Variables tested were canopy cover

(%), leaf-litter (cm), sand (%), understory vertical structure, distance among trees (cm) and tree basal area; b) Variables tested were distance to reserves (Km) and percentage of forest cover surrounding the restoration areas. Values inside the circles indicate the average similarity to primary forest and the percentage values of each split indicate the variation explained.

DISCUSSION

We demonstrate that assembly rules theory can certainly help to guide restoration practices, enabling to improve future restoration efforts. Our study provides valuable insights into the mechanisms influencing dung beetle community assembly in tropical forest restoration areas, evaluating for the first time the importance of local environmental conditions, landscape context and spatial descriptors to recover species and functional trait composition. The assembly of both species and functional trait composition were predominantly driven by niche-based processes, mainly by the influence of local environmental filters. Landscape and spatial descriptors had little or no independent contributions, presenting mostly shared effects with each other and local environment. However, the importance of stochastic factors cannot be completely ruled out, because of the large amount of unexplained variation. We also document how these environment and landscape variables make the restoration areas more similar to the reference system (primary forest) in relation to species and functional trait composition, indicating threshold values. These findings suggest that quite simple management practices, by manipulating site level conditions, landscape connectivity and permeability, can be effective in making restoration areas more similar to primary forest.

Relative importance of local environment, landscape and space

Local environmental conditions had a stronger influence on dung beetle community assembly in relation to landscape context and spatial structure. Nearly all the total variation explained by space was also co-explained by environment and landscape, resulting in a small effect of pure spatial variation (only 1%). This indicates that an intraspecific spatial aggregation exists along the restoration areas, being driven by the influence of local environmental conditions, landscape context or a combination of both processes, and not by neutral dispersal limitation. These results reflect the importance of niche-based processes in structuring dung beetle species and functional trait composition in the restoration areas, ruling out the potential influence of stochastic factors.

Generally, the relative importance of stochastic processes (e.g. dispersal constraints) decreases when dispersal abilities of the organisms are high and in the presence of strong environmental filters (Chase 2007). Very little is known about the dispersal capacity of dung beetles, however it is assumed that they are good dispersers mainly because of the random distribution and ephemeral nature of their food resources (Roslin and Viljanen 2011). Dispersal abilities of dung beetles differ substantially from species to species (records indicate that distance dispersed can range from 50 m to 1000 m in two days inside the same environment, Peck and Forsyth 1982, Larsen 2005) and can be affected by species specific environmental responses (Nichols et al. 2007, Larsen et al. 2008). According to Chase (2007), strong environmental filters are frequently found in modified environments and represent their harsh conditions. In those habitats just a small number of species from the regional pool will be able to tolerate the harsh conditions, establish and survive. Thus, community assembly will be highly determined by niche-selection processes instead of colonization chance. On the contrary, physical conditions of preserved environments will not work as a strong filter, allowing the establishment of most species from the regional pool. In such cases, stochastic colonization can play a larger role in community assembly. Despite the re-establishment of forest cover in the studied restoration areas with time (gradient ranging from 0 and 18 years), those areas are still very different from the preserved Atlantic forests in relation to habitat structure, generally have a small area and are immersed in a modified landscape (matrix mainly composed by pasture and *Eucalyptus* plantations) (Audino et al. 2014). In most cases, just a small number of the species from the regional pool of our study region are able to establish in the restoration areas, and those are usually good dispersers that can tolerate modified conditions (Audino et al. 2014). This is supported by our results where only few species are found in each restoration site (mean species richness of 5.7 per site), whereas in primary forest areas this number can be almost four times higher (mean species richness of 20.2 per site).

Our results show that site level conditions are fundamental in structuring dung beetle communities, however this is not a new result in the literature (e.g Nichols et al. 2007, Gardner et al. 2007, Louzada et al. 2010, Silva and Hernández 2014). It is widely recognized that dung beetles are influenced by vegetation structure, microclimate, soil characteristics and availability of food resources (Sowig 1995, Halffter and Arellano 2002, Noriega et al. 2007, Horgan 2007, Nichols et al. 2009). Landscape context did not have an independent effect on dung beetle community assembly, however we cannot dismiss its importance. Almost all variance explained by landscape was environmentally structured, indicating that this aspect have a potential influence on dung beetle communities through the interaction with local environmental conditions. This is not surprising, since the variable selected to compose variance partitioning model was percentage of forest cover surrounding the restoration areas. This result shows that dung beetle dispersal is mostly determined by niche-selection, where species movement will depend on appropriate environmental conditions surrounding the restoration areas. A high percentage of the variation in species composition and functional trait composition was unexplained, which may reflect the effects of unmeasured environmental variables and/or an indication for the occurrence of stochastic processes (Legendre et al. 2009, Baldeck et al. 2013, Chang et al. 2013, Myers et al. 2013).

Species and functional trait composition presented similar responses in relation to the relative importance of environment, landscape and space, and also retained practically the same variables in forward selection. This was expected, since species composition and functional trait composition were correlated (Mantel's r = 0.76; p<0.001). Dung beetle functional traits were better explained by the predictor variables than species composition, and this result is similar to the findings of Siefert et al. (2013) and Helsen et al. (2012) for plants and Pakeman and Stockan (2014) for carabid beetles.

Functional trait individual responses to local environment and landscape

Contrary to expectations, only two dung beetle traits were influenced by the recorded environmental and landscape variables. However, these results possibly reflect the high unexplained portion of functional trait compositional variance in variance partitioning analysis. As mentioned before, this unexplained fraction can decrease with the inclusion of other variables that are or might be relevant for dung beetle communities, such as mammals diversity as a proxy for resource availability (Nichols et al. 2009, Barlow et al. 2010, Culot et al. 2013), historical events (e.g. fire disturbance, land-use history, Louzada et al. 2010, Murphy et al. 2015) and soil moisture (Sowig 1995). These results can also be an indication that stochastic effects may be playing an important role in driving functional trait composition of dung beetles. Therefore, the low influence of neutral dispersal limitation showed in variance partitioning must be interpreted carefully.

We found that abundance of tunneler dung beetles increased with canopy cover and abundance of necrophages with basal area of the trees. This shows that different environmental filters influence the various components of community functional traits in different ways (Louzada et al. 2010, Siefert et al. 2013, de Bello et al. 2013). This result provides an important practical information, showing that to recover distinct functional traits in the restoration sites it is necessary to manipulate different environmental components. We could not find any information in the literature about the influence of canopy cover on tunneler dung beetles. In general, rollers are more sensitive to environmental disturbances and consequently to modifications in canopy cover, because they construct shallower tunnels a distance away from the food resource (Nichols et al. 2013). What might explain this result is that the majority of our tunneler species are also forest species (see Audino et al. 2014). Sites presenting high tree basal area usually have a fairly diverse, mature and undisturbed forest, and these characteristics can greatly determine the presence of a diverse mammal and bird community (Laidlaw 2000, Lees and Peres 2008). The presence of mammals and birds can, in turn, enable the existence of a higher number of necrophage species.

Similarity to the reference system

Restoration areas presenting similar environmental characteristics to primary forest are also more similar according to species and functional trait composition. Of all environmental variables measured, the ones considered more important to drive this similarity were canopy cover, distance among trees and leaf litter depth. These three variables are highly correlated to each other, as already stated in Appendix C. Restoration sites with an elevated percentage of canopy cover (> 69%) are more similar to primary forest according to both species and trait composition. For species composition, distance among trees was also important, where a smaller distance (< 221 cm) ensures a greater similarity to primary forest in relation to larger distances (> 221 cm/ > 463 cm). For functional trait composition, leaf litter depth determined the similarity of the areas with lower canopy cover (< 69%), where a greater depth (> 0.90 cm) promotes a higher similarity in relation to a smaller depth.

As in other studies (e.g. Silveira et al. 2010, Hosaka et al. 2014), our results suggest that forest canopy is the most important variable influencing dung beetle community assembly. Canopy cover is one of the key determinants of the microclimate and humidity within the forest (Jennings et al. 1999). Increased canopy openness leads to greater incidence of light, increasing the temperature of the whole forest, decreasing air humidity, soil and leaf littler moisture (Jennings et al. 1999, Laurance et al. 2009). It also have a direct effect on the understorey plant community, and may drive the proliferation of disturbed-adapted vines, weeds and pioneer species (Jennings et al. 1999, Laurance et al. 2009). Tree density is also related to these factors, since a greater space among trees will also lead to a smaller amount of forest canopy. Lastly, a well developed litter layer can be found in mature forest areas due to a higher quantity of trees, and consequently higher forest cover.

With regard to landscape context, our results shows that restoration areas containing more forest cover in its surrounding (> 20.43%) and that are closer to environmental reserves (distance < 33 km) are more similar to primary forest according to species and trait composition. Percentage of forest in a 250 m buffer around sites was the strongest predictor, probably because they can serve as a source of species, increasing the colonization of forest-dependent species to the restored ecosystem (Grimbacher and Catterall 2007, Louzada et al. 2010, Woodcock et al. 2010, Shackelford et al. 2013). A higher percentage of forest fragments nearby can also buffer from disturbances and increase the availability and probability to reach potential sources of food resources, since it allows the movement of species between patches and across the landscape (Debinski and Holt 2008, Matthews et al. 2009, Shackelford et al. 2013). The environmental reserves considered in this study are the largest preserved Atlantic forest remnants found in the landscape. They probably hold the majority of species from the regional pool and can serve as an importance source of species to the restored sites as well, which can greatly improve biological communities recovery.

Our results clearly corroborates the need for a more integrated view between management of site level conditions and a landscape perspective in restoration decision-making process. Both factors seem to be extremely important for dung beetle community assembly in restoration areas, affecting its arrival, establishment and survival. The first priority is to create more rainforest-like environmental conditions. In primary forest areas we generally find a practically continuous forest canopy (in average 86%), a small distance among trees (in average 118 cm) and a well developed leaf litter layer (in average 3.76 cm). Thus, maximizing canopy cover, tree density and leaf litter will produce suitable conditions for the establishment and survival of forest dependent species in the restored sites. This could be accomplished through high-density planting, which can create favorable conditions for later successional species, closing a canopy rapidly, and impede the proliferation of weedy early successional species (Galatowitsch 2012). Revegetation techniques implemented by Veracel Company include the active planting of fast growing species and mid and late successional species in intercalated lines, using a planting spacing of 3 x 3 m (Appendix A). Probably diminishing the space among native tree seedlings can help to create restored sites more similar to preserved forests (Grimbacher and Catterall 2007). It is also possible that future enrichment plantings may be necessary to fill the canopy gaps left in the fast growing species lines.

Secondly, it is necessary to plan restoration practices in a landscape context, choosing potential sites for the establishment of restoration areas (Rodrigues et al. 2009, Woodcock et al. 2010). As shown here, the most appropriate sites are the ones with a higher percentage of forest fragments around (> 20%) and/or closer to potential species sources (< 30 km). Being close to forest fragments, mainly the larger and preserved ones, can also contribute to natural forest regeneration processes and reduce restoration costs (Chazdon 2003, Rodrigues et al. 2009, Metzger and Brancalion 2013). Although considered a more difficult approach, management of landscape composition and connectivity can also help to create more biodiversity-friendly restored areas (Leite et al. 2013, Metzger and Brancalion 2013). For example, the inclusion of biological corridors as part of restoration efforts and the encouragement to the use of a high quality agroecological matrix can allow species movements between the restored sites and forest fragments (Beier and Noss 1998, Perfecto and Vandermeer 2008). This is extremely important to be taken into account, mainly in tropical forest landscapes (such as Atlantic Forest), where most of the remnants corresponds to small and disturbed forest fragments immersed in a highly modified matrix (Wright 2005, Ribeiro et al. 2009, Tabarelli et al. 2010).

Although restoration practices have greatly improved due to the direct influence of ecological theories (Rodrigues et al. 2009), restoration ecology still face some challenges concerning the link between theory and practice (Montoya et al. 2012). The patterns we present here demonstrates the predominance of niche-based processes in structuring dung beetle communities in restored sites, which is a relevant practical information for biological diversity restoration (Chase 2007). Therefore, before taking into account the effects of stochastic events, it is necessary to prioritize the restoration of desired environmental and landscape conditions. Stochastic factors must still be considered in restoration actions, however the focus should be in the manipulation of ecological filters. Our study also provides a series of environmental and landscape threshold values that can greatly help to guide tropical forest restoration efforts.

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SUPPLEMENTAL MATERIAL

Appendix A. Restoration techniques
Appendix B. Relative importance of restoration age in dung beetle assembly
Appendix C. Correlations

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Appendix A: Restoration techniques

Veracel Celulose company restores Atlantic forest in areas of degraded introduced pasture located generally next to Permanent Protected Areas (riverside and waterways forest strips that must be protected according to Brazilian environmental law), Legal Reserves (areas located in a rural property that has to be maintained as native vegetation) and other protected areas. Restoration techniques involves the active planting of native tree species seedlings (1.111 seedlings per hectare). If the area that it is going to be restored already have arboreal and shrub plants, they are not removed from the site, being considered as planted seedlings. The restoration model used by the company consists of “filling” and “diversity” planting lines (see Rodrigues et al. 2009). Species from the “filling” lines are considered fast-growing trees, producing some degree of canopy cover and improving environmental conditions next to the ground. Species from the “diversity” lines are represented by late secondary, climax or poor coverage pioneers species, being responsible for the self-perpetuation of the forest along time. Seedlings are planted at a distance of 3 m from each other in intercalated lines, using 50% of fast-growing species (“filling” group) and 50% of late successional species (“diversity” group). Prior to planting, areas are submitted to a series of management measures, such as: a) control of ants using formicide baits; b) application of herbicides in areas where grasses and herbaceous weeds occur in high densities (2 kg/ha); c) manual mowing in areas containing weeds ≥ 1 m tall; d) subsoiling to reduce soil compaction, and e) fertilization. Monitoring of planting success is frequent in the first 3 years of the restoration process and after this period, it is conducted every 5 years.

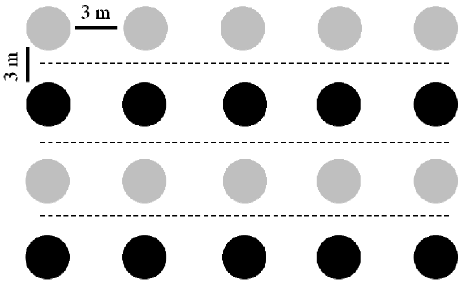

FIG. A1. Restoration model used by Veracel Celulose. Grey circles represent fast-growing species from the “filling” lines and black circles late-successional species from the “diversity” lines. Planting spacing corresponds to 3 x 3 m.

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Appendix B: Relative importance of restoration age in dung beetle assembly

Time can be an important factor to determine dung beetle community assembly in restored sites, because opportunities for colonization of an area increases over time. For example, the habitat for certain forest-dependent species might be suitable as soon as there is minimal canopy cover, but it takes time for all the species to colonize the site. However, restored areas also develop with time a more favorable habitat structure, making difficult to separate the effects of site age from environmental variables (Grimbacher and Catterall 2007). So, we used variance partitioning analysis to disentangle the relative importance of restoration age, space, landscape and environment in structuring dung beetle species and trait composition in restoration areas (for more details about the analysis, see Materials and Methods section). This analysis will allow to understand how much restoration age affect dung beetle community alone and together with the environmental, landscape and space variables.

We found a high correlation between restoration age and canopy cover (Pearson's, $r = 0.91$; $p < 0.05$), distance among trees ($r = -0.72$; $p < 0.05$) and leaf-litter depth ($r = 0.89$; $p < 0.05$). Restoration age was also correlated to distance to environmental reserves ($r = - 0.61$; $p < 0.05$) and forest cover surrounding the landscape ($r = 0.55$; $p < 0.05$). Variance partitioning analysis showed that restoration age had no independent effects on species and functional trait composition of dung beetles. All variance explained by age was also co-explained by local environment, space and landscape (see Table B1).

Table B1. Variance partitioning results for restoration age, space, landscape and local environment. R-adjusted values are showed for each total, independent and joint effects.

Partition table	**Species composition**	**Trait composition**
Total age	0.1957	0.28379
Total space	0.13582	0.12665
Total landscape	0.10937	0.1264
Total environment	0.24685	0.32465
Individual fractions		
Isolated age	-0.007	0.00095
Isolated space	0.007	0.01569
Isolated landscape	-0.031	-0.03549
Isolated environment	0.05	0.03399
Age+Space	0.00006	-0.00111
Space+Landscape	0.03201	0.01236
Age+Landscape	0.01184	0.00627
Age+Environment	0.07283	0.14859
Environment+Space	0.00413	-0.00699
Environment+Landscape	0.01095	0.01105
Environment+Age+Space	0.02051	0.00584
Age+Space+Landscape	-0.00413	-0.00196
Space+Landscape+Environment	-0.01187	0.00695
Age+Landscape+Environment	0.01458	0.03134
Age+Space+Landscape+Environment	0.08751	0.09388
TOTAL	**0.25523**	**0.32535**
RESIDUAL	**0.74477**	**0.67465**

Appendix C. Correlations

TABLE C1. Correlations (Pearson) among environmental, landscape and spatial variables. R values are presented for each comparison and bold values are the ones statically significant ($p < 0.05$). CA = canopy cover; LI = leaf-litter depth; SA = sand; UN = understory; DT = distance among trees; BA = basal area; DR = distance to environmental reserves; FC = forest cover surrounding the landscape.

	CA	LI	SA	UN	DT	BA	DR	FC	PCNM1	PCNM2	PCNM3	PCNM4	PCNM5	PCNM6	PCNM7	PCNM8
CA																
LI	**0.927**															
SA	-0.398	-0.292														
UN	-0.176	-0.020	0.269													
DT	**-0.845**	**-0.716**	0.374	**0.515**												
BA	0.176	-0.005	-0.208	-0.274	-0.040											
DR	**-0.639**	**-0.595**	-0.088	0.272	**0.683**	0.076										
FC	**0.542**	**0.576**	-0.006	-0.146	-0.412	-0.221	**-0.704**									
PCNM1	0.010	-0.144	-0.008	-0.367	-0.262	0.121	-0.181	-0.020								
PCNM2	-0.294	-0.182	-0.154	-0.091	0.401	0.114	**0.516**	-0.163	0.000							
PCNM3	**-0.575**	-0.658	-0.156	-0.175	0.312	0.193	0.485	**-0.563**	0.000	0.000						
PCNM4	-0.315	-0.227	**0.517**	0.147	0.194	-0.479	0.011	-0.026	0.000	0.000	0.000					
PCNM5	-0.439	-0.450	0.165	**0.596**	**0.681**	0.014	0.479	-0.196	0.000	0.000	0.000	0.000				
PCNM6	-0.245	-0.147	0.130	-0.213	0.114	-0.347	0.023	-0.013	0.000	0.000	0.000	0.000	0.000			
PCNM7	0.377	0.339	**-0.535**	0.167	-0.273	-0.146	0.018	0.051	0.000	0.000	0.000	0.000	0.000	0.000		
PCNM8	-0.128	0.002	-0.123	0.245	0.072	-0.216	0.244	-0.327	0.000	0.000	0.000	0.000	0.000	0.000	-0.255	

Appendix D. Dung beetles sampled in primary forest and restoration areas

Table D.1. Number of individual of dung beetles sampled in primary forest and restoration areas of south Bahia, Brazil

Species	**Primary forest**	**Restoration areas**
Anomiopus sp.	2	1
Ateuchus sp.1	192	2
Ateuchus sp.2	55	58
Ateuchus sp.3	2	16
Canthidium aff. *depressum*	2	0
Canthidium aff. *korschefskyi*	40	0
Canthidium aff. *lucidum*	92	0
Canthidium aff. *trinodosum*	609	11
Canthidium sp.1	18	1
Canthidium sp.4	0	20
Canthidium sp.5	0	433
Canthon aff. *viidus*	0	130
Canthon chalybaeus	0	1
Canthon histrio	0	66
Canthon lituratus	0	1
Canthon mutabilis	0	5
Canthon sulcatus	286	0
Canthonella silphoides	552	106
Chalcocopris hespera	3	0
Coprophanaeus bellicosus	18	0
Coprophanaeus cyanescens	0	4
Coprophanaeus dardanus	8	13
Coprophanaeus punctatus	5	0
Deltochilum aff. *calcaratum*	7	0
Deltochilum granulosum	1	0
Dichotomius aff. *laevicollis*	0	64
Dichotomius aff. *sericeus*	1990	172
Dichotomius depressicolis	0	1

Dichotomius geminatus	0	6
Dichotomius irinus	156	0
Dichotomius mormon	0	5
Dichotomius nisus	0	1
Dichotomius quadrinodosus	1	0
Dichotomius schiffleri	3	0
Dichotomius semisquamosus	0	7
Eurysternus calligrammus	112	2
Eurysternus hirtellus	91	13
Eurysternus nigrovirens	0	17
Eutrichillum hirsutum	15	0
Holocephalus sculptus	0	1
Ontherus azteca	2	12
Ontherus irinus	3	0
Paracanthon sp.	20	0
Streblopus opatroides	52	2
Trichillum externepunctatum	0	22
Uroxys sp.	130	2
Abundance	**4467**	**1195**
Number of species	**29**	**31**