UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

INFLUÊNCIA DO TIPO E DO MANEJO DA MATRIZ SOBRE A DIVERSIDADE DE INSETOS E SUAS RESPOSTAS AO EFEITO DE BORDA

FELIPE MARTELLO RIBEIRO

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Zoologia

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Julho de 2016

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Programa de Pós Graduação em Zoologia

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Rio Claro, _____de__________de_______

Dedico esta tese ao meu filho, Pedro, e aos milhares de besouros e formigas que foram sacrificados nos estudos aqui apresentados

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RESUMO

A fragmentação atualmente é uma das maiores ameaças a biodiversidade, reduzindo a quantidade de habitat nativo, dividindo o habitat nativo em fragmentos pequenos e isolados. Apesar de boa parte de estratégias de conservação focarem preferencialmente nos remanescentes das áreas nativas, esta prática ignora a relevância que ambientes antrópicos (matrizes) podem têm para biodiversidade: tipos diferentes de matriz diferentemente os movimentos de organismos entre remanescentes de habitat nativo; provêm certa quantidade de recurso que é utilizada por algumas espécies, assim como criam diferentes áreas de transição com os remanescentes (bordas) que influenciam na biodiversidade encontrada nessas áreas. Nesta tese estudei como matrizes diferentes afetam a diversidade de besouros escarabeídeos e de formigas, dois grupos de insetos com alta biodiversidade, considerados importantes bioindicadores ambientais por serem sensíveis à alterações ambientais, essenciais em diversos processos ecológicos e por representarem eficientemente a resposta de outro organismos à tais alterações. Nos primeiros dois capítulos foquei em entender como os besouros e formigas respondiam à distância de borda em bordas compostas por cerrado e diferentes tipos de matrizes. Como resultados encontrei que a biodiversidade de ambos insetos foi afetada pelo tipo de ambiente que se encontravam (cerrado ou matriz), porém nem sempre suas respostas evidenciaram o efeito de borda. No caso das formigas, pude constatar que o tipo de resposta que as comunidades mostraram foi influenciada pelo tipo de matriz que compunha a borda, sugerindo que a resposta que os organismos têm á borda é dependente dos ambientes que a compõe. No terceiro capítulo procurei mostrar que mesmo ambientes que podem ser considerados como a mesma matriz, nesse caso eucalipto, podem afetar de forma diferente a biodiversidade. Utilizando a riqueza de espécies e medidas de diversidade funcional, descobri que comunidades de formigas em áreas de eucalipto abandonadas por 28 anos tinham a mesma riqueza que comunidades localizadas em mata atlântica nativa, porém uma menor riqueza funcional. Além disso, tais comunidades eram mais similares à aquelas localizadas em plantações de eucalipto manejadas do que as comunidades na mata atlântica. De forma geral, procuro discutir a relevância de se considerar paisagens como ambientes heterogêneos tanto em estudos de fragmentação como em estratégias de manejo, visto que ambientes aparentemente iguais (bordas de cerrado e plantações de eucalipto) podem afetar de forma diferente os organismos.

ABSTRACT

Fragmentation, nowadays, is one of the major threat to biodiversity, reducing the native habitat amount, separating native habitat in small and isolated fragments. Although most of conservation strategies preferably focus in remnants of native areas, this practice ignores the relevance the relevance that anthropic environments (matrixes) would have for biodiversity: different matrix can facilitates or difficult the movement of organisms between native habitat remaining; it provide resources that is used for many species, as well as create different transitional areas adjacent to the remnants (edges) that influence the. In this thesis I studied how different matrices affect the diversity of dung beetles and ants, two groups of insects with high biodiversity, considered important environmental bioindicators since they are sensitive to environmental changes, essential in many ecological processes and efficiently represent the response of other organisms to environmental changes. In the first two chapters I focused in understanding how dung beetles and ants respond to distance to edge, in transitional areas composed by cerrado (Brazilian savannah) and different types of matrixes. I found that the biodiversity of both insects was affected by the type of environment (cerrado or matrix), but not always their answers showed the presence of edge effect. In the case of ants, I found that the type of response that communities showed was influenced by the type of matrix that composed the edge, suggesting that the answer of organisms to edge distance is specific of the environments that compose it. In the third chapter I showed that even environments that can be regarded as the same matrix, in this case eucalyptus, may affect differently biodiversity. Using species richness and functional diversity indexes, I found that communities of ants located in abandoned eucalyptus plantations for 28 years had the same richness that communities located in the native rain forest, but small functional richness. Furthermore these communities were more similar to those located in managed eucalyptus plantations than communities in the Atlantic. In general, I discussed the importance of considering landscapes as heterogeneous environments both in fragmentation studies and in conservation strategies, since environments apparently similar (savannah edges and eucalyptus plantations) can affect differently the organisms.

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APRESENTAÇÃO

Esta tese de doutorado foi concebida com o objetivo de compreender como a paisagem, mais especificamente os tipos de usos de solo que compõe as paisagens, influenciam na comunidade de insetos. Dessa forma dividi esta tese em quatro capítulos, onde no primeiro contextuo, de forma sucinta, a importância de considerar a paisagem em estudos de ecologia e como que o tipo de usos de solos influenciam na respostas dos organismos à fragmentação. Neste primeiro capítulo apresento uma síntese sobre os três estudos que realizei (capítulos dois a quatro), bem como uma discussão sobre a implicação dos resultados dessa tese para a conservação.. Nos três capítulos seguintes apresento os estudos que desenvolvi durante o doutorado,sendo que os manuscritos estão no formato das revistas científicas selecionadas. O manuscrito do segundo capítulo já foi submetido para a revista *Journal of Insect Conservation*. Os capítulos três e quatro estão formatados para as revistas *Biological Conservation* e *Forest Ecology and Managment,*respectivamente.

CAPÍTULO 1: INTRODUÇÃO

1.1 Referencial teórico

A conversão de áreas naturais em ambientes antropotizados atualmente é uma das mais maiores ameaças a biodiversidade (Chaplin III et al. 2000). Como consequência ocorre a redução de habitat nativo de diversas espécies, causando fragmentação, aumento do isolamento e redução do tamanho das manchas de habitat (Fahrig 2003). Historicamente, a teoria de biogeografia de ilhas (MacArthur & Wilson 1968) tem sido a principal referência para estudos de fragmentação e estratégias de restauração, evidenciando a importância do tamanho do fragmento e de seu isolamento na manutenção da biodiversidade (Laurance 2008). Assumindo que a riqueza de espécies de uma ilha resulta da interação entre a taxa de extinção de espécies e a frequencia com que novas espécies chegam à ilha (taxa de imigração), os autores postulam que a taxa de extinção é inversamente proporcinal ao tamanho da ilha (ilhas maiores suportam mais espécies) e que a taxa de imigração é inversamente proporcinal ao isolamento da ilha (quanto mais isolada, menor a taxa de colonização) (MacArthur & Wison 1967).

Apesar de intuitivamente esta teoria parecer se aplicar às paisagens fragmentadas atuais,onde fragmentos menores e mais isolados tenderiam a ter menos espécies que fragmentos maiores, sua aplicação neste contexto apresenta algumas limitações por não contemplar, por exemplo a facilitação pelo homem na dispersão de algumas espécies, a quantidade de fragmentos na paisagem, a variação da taxa de migração entre espécies e a interação entre espécies (Mack & Lonsdale 2001, Laurance 2008). Todavia, talvez a maior limitação da apliacação desta teoria em à paisagens fragmentadas seja considerar paisagens heterogêneas como oceanos, em que fragmentos (ilhas) estão imersos em um mar de ambientes não habitáveis. Dessa forma, dois fragmentos de mesmo tamanho e com o mesmo grau de isolamento deveriam ter a mesma diversidade, mesmo que um estejam imersos em ambientes antrópicos distintos: área urbana, pastagem, agrofloresta, cana-de-acúcar, mineração, silvicultura etc. Porém, sabe-se que os ambientes antrópicos que compõem as paisagens, chamados daqui para frente de matrizes, têm grande influência na conectividade da paisagem, de forma que matrizes que estruturalmente diferem mais dos ambientes nativos são mais hostis à espécies nativas (Ricketts 2001, Kupfer et al. 2006, Laurance 2008,). Além disso, as matrizes não são ambientes totalmente hostis à biodiversidade: muitas espécies encontram uma série de recursos, como abrigos e alimentos, nesses ambientes, de forma que o quanto as matrizes se diferenciam dos habitats nativos, pode ser um indicador da quantidade de recursos disponíveis para espécies nativas nessas matrizes (Brotons et al. 2003). Apesar disso, boa parte das estratégias de conservação atuais focam apenas em conservar reservas de habitat nativos ou em definir áreas prioritárias para conservação baseadas principalmente no tamanho da área natural e no grau de isolamento que essas áreas estão (Kupfer et al. 2006).

Além de influenciar na movimentação de espécies nativas entre fragmentos e de prover recursos para espécies, a matriz adjacente a um fragmento influencia também na natureza e magnitude do efeito de borda (Laurance 2008). Este efeito é mais uma das consequências da fragmentação, que acarreta alterações microclimáticas no fragmento, oriundas da interação da área nativa com a matriz adjacente (Murcia 1995). Em função disto, nas áreas de contato entre o fragmento e a matriz ocorrerem mudanças na composição de espécies e na estrutura das comunidades (Murcia 1995). Assim, em regiões próximas a bordas, espécies mais sensíveis a tais mudanças ambientais tendem a ter sua população reduzida ou localmente extintas, como é o caso de alguns grupos de plantas, aves (Banks-Leite et al 2010), pequenos mamíferos (Santos-Filho et al. 2008) e besouros (Ewers e Didham 2008). O grau no qual a matriz contrasta estruturalmente com ambientes nativos também influencia em como os organismos irão responder a borda, de forma que espera-se um efeito mais intenso quando uma matriz seja mais contrastante com o ambiente nativo (Ries et al., 2004, Harper et al., 2005). Apesar da extensa literatura sobre o efeito de borda, para muitos organismos ainda não existem um consenso sobre como estes respondem a borda, de forma que especialistas vem alertando sobre considerar de forma explícita, em estudos de borda, este efeito como um processo gradiente (que se intensifica ou suaviza de acordo com a distância da borda), bem como o tipo de matriz que compõe a borda (Ries 2004, Ewers & Didham 2006, Harper & MacDonald 2011).

Nesta tese busquei compreender o papel da matriz sobre a biodiversidade utilizando dois grupos de insetos como modelo: os besouros escarabeídeos e as formigas. Tais insetos são considerados bons indicadores de alterações ambientais, além de refletirem a respostas de outros organismos à tais alterações. Estes insetos são de grande relevância para a manutenção de diversas funções ecossistêmicas como controle de parasitas, decomposição de matéria orgânica e enriquecimento das propriedades do solo, no caso dos besouros escarabeídeos; e a ciclagem de nutrientes, aeração do solo e dispersão de sementes.

1.2 Efeito da borda e do uso das terras sobre besouros escarabeídeos

No primeiro estudo (Capitulo 2) desta tese busquei compreender como comunidades de besouros escarabeídeos respondem ao efeito de borda em fragmentos de cerrado adjacentes a três tipos de usos de solo agrícolas: plantações de cana, plantações de eucalipto e pastagens. A partir de coletas feitas por armadilhas de queda, dispostas ao longo de transectos (que começavam dentro do fragmento e se adentravam na matriz adjacente) assumi três possíveis respostas que os besouros poderiam ter à distancia: a) uma resposta discreta (influência do tipo de ambiente: fragmento ou matriz), b) uma resposta gradiente (influência do efeito de borda), e c) uma resposta nula (sem alteração ao longo do transecto). A partir disso, minhas hipótese eram que o tipo de resposta que estes insetos teriam à distância de borda seria influenciada pelo contraste entre a matriz que compunha a borda e o fragmento de cerrado. Com base nos resultados, observei que apesar de na maior parte dos fragmentos as comunidades de besouros mostrarem padrões diferentes de diversidade no fragmento e na matriz adjacente, nem sempre a resposta que considerava o efeito de borda (resposta gradiente) foi a selecionada. Além disso, o tipo de resposta que essas comunidades não foi influenciado pelo contraste entre a matriz e o cerrado. Embora os resultados encontrados tenham ido na direção oposta das minhas expectativas, exponho neste capítulo como estes besouros são severamente impactados pelo tipo de ambiente que se encontram e como a presença de recursos em matrizes, a natureza efemera dos principais recursos utilizados pelos besouros (fezes de mamíferos) e outras variáveis podem ter influenciado nas respostas observadas.

1.3 Tipo de matriz influencia a resposta da comunidade de formigas ao efeito de borda

O terceiro capítulo também focou sobre o efeito de borda em fragmentos compostos por cerrado e diferentes tipos de matrizes, porém tendo se as formigas como organismo alvo. O desenho experimental e as hipóteses deste capítulo são semelhante ao do capítulo anterior, porém com um tratamento dos dados e análises diferentes, de forma a garantir. Assim como o capítulo anterior, utilizei modelos estatísticos para expressar os potenciais tipos de respostas à distancia de borda (discreta, gradual ou nula). Porém aqui, diferente do capítulo anterior, realizei dois tipos de análises: o primeiro juntando todas as paisagens - incorporando no grupo de modelos possíveis a variável “tipo de matriz que compunha a borda” - e uma segunda análise, onde investiguei as respostas das comunidades de formigas separadamente em cada tipo de borda (cana-cerrado, pasto-cerrado e eucalipto-cerrado). Esta abordagem me indicou que a resposta que a comunidade de formigas mostra a distância de borda é específica à matriz que compõe a borda, e que a tentativa de buscar padrões entre comunidades localizadas em bordas compostas por matrizes diferentes podem ocultar os padrões que esses insetos têm em cada borda, mesmo que o tipo de matriz seja considerado nos tipos de respostas. Pude ainda constatar uma grande diferença em como as duas variáveis respostas (riqueza e composição) responderam a borda, e que uma interpretação dos resultados que considere os respostas dessas duas variáveis pode auxiliar a compreender como comunidades de formigas respondem ao efeito de borda.

1.4 Homogeneização taxonômica e funcional de formigas em plantios de eucalipto

Entre os resultados que encontrei no capítulo anterior, observei que em fragmentos de cerrado adjacentes a plantações de eucalipto as comunidades de formigas não apresentavam alterações ao longo do transecto quanto a riqueza de espécies. Tal resultado alia-se a tantos outros estudo que evidenciam pouca, ou nenhuma, diferença na biodiversidade entre comunidades amostradas em áreas nativas e em plantações de eucalipto, e alimenta o ferrenho debate sobre o real papel de plantações de eucalipto na conservação da biodiversidade (Lindenmayer & Hobbs 2004 , Paquete 2010). Dessa forma, neste quarto capítulo busquei compreender como plantações de eucalipto com diferentes manejos e idades influenciam a comunidade de formigas. Para tanto calculei a diversidade taxonômica e funcional de cada comunidade de formigas (diversidade alfa) e quanto essas comunidades se assemelhavam, também taxonômica e funcionalmente, (diversidade beta), onde hipotetizei que comunidades de formigas localizadas em plantações de eucalipto abandonadas teriam uma diversidade (taxonômica e funcional) intermediária entre aquelas localizadas em florestas nativas (Mata Atlântica) e plantações de eucalipto manejadas. Nos resultados observei que comunidades de formigas em plantações de eucalipto têm diversidade taxonômica e funcional reduzidas quando comparadas a comunidades de fragmentos de Mata Atlântica. Constatei ainda que comunidades em eucalipto abandonado tinham a riqueza e a estrutura funcional semelhante às de comunidades localizadas em Mata Atlântica, porém com uma riqueza funcional menor. Apesar disso, observei que mesmo após 28 de abandono dos plantios de eucalipto, as comunidades de formigas eram mais semelhantes (diversidade beta), tanto taxonômica como funcionalmente, com as comunidades localizadas em eucalipto manejados. Assim finalizo este capítulo discutindo qual o real papel da plantações de eucalipto em estratégias de conservação, e como a regeneração natural, aliada a outras técnicas de restauração podem contribuir para ações de conservação e restauração.

1.5 Implicações para conservação da biodiversidade

Nos estudos desenvolvidos nesta tese pude constatar que tanto as comunidades de besouros escarabeídeos como de formigas são afetados pela matriz que compõe as paisagens, alterando os padrões de diversidade, a estrutura das comunidades localizadas nesses ambientes e as respostas que esses insetos apresentam a alterações ambientais. Todavia, essa alteração nem sempre levou a uma redução da diversidade: nos três estudos encontrei comunidades de matrizes que tinham maior ou igual diversidade (seja abundância, riqueza de espécies ou diversidade funcional) que comunidades encontradas em áreas nativas. Uma vez que esses insetos são essenciais em diversos processos ecológicos (ex. decomposição de matéria orgâncica, controle de parasitas e ciclagem de nutrientes) e que podem refletir como outros organismos são afeados pela conversão de áreas naturais em ambientes antrópicos, meus resultados indicam que, mais do que não considerar fragmentos de áreas nativas como ilhas de biodiversidade imersas em um oceano de ambientes inóspitos, estratégias de conservação devem considerar as comunidades que habitam as matrizes que compõe a paisagem e como essas comunidades interagem com as comunidades localizadas em áreas naturais.

Outro questionamento que me fiz ao final dessa tese foi quanto a efetividade da variável riqueza de espécies como preditora do impacto da matriz sobre organismos: esta foi a única variável resposta comum aos três estudos e, em alguns casos (em todos os capítulos) não mostrou variações entre os ambientes, mesmo que outras variáveis respostas (abundância, composição de espécies e índices de diversidade funcional) tenham indicado mudanças. Uma vez que a riqueza considera apenas o número de espécies presente na comunidade, esta medida, assim como outras tradicionais de diversidade (índice de Shannon e Simpson) ignoram as diferenças que existem entre as espécies, conseqüentemente desconsiderando as diferentes contribuições que cada espécie têm para serviços ecossistêmicos (Cianciaruso et al. 2009). Dessa forma, nas últimas décadas estudos vêm mostrado que medidas que considerem essas diferenças entre espécies (traços funcionais) podem mostrar variações , provenientes de alterações ambientais, mesmo quando não existe alteração na riqueza de espécies (Cadotte et al. 2011). Assim, atualmente existe uma tendência de estudos que foquem em compreender como alterações ambientais impactam a biodiversidade utilizares mais traços funcionais e índices provenientes desses (diversidade funcional), do que em medidas tradicionas de biodiversidade (Cianciaruso et al. 2009). Todavia, esta tarefa não é simples, uma vez que exige uma extensa pesquisa em ecofisiologia, sobre quais traços dos organismos que expressam as funções (processos ecológicos) que os organismos desempenham nos ecossistemas, ou que expressam as respostas desses às alterações ambientais. Apesar de estudos nessas áreas para formigas e besouros serem ainda incipientes, mostram-se bastante promissores tanto para se compreender como as comunidades são afetadas por alterações ambientais, como para traçar planos de manejo que visem em conservar não só um grande número de espécies, mas as funções ecológicas.

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CAPÍTULO 2: EDGE AND LAND USE EFFECTS ON DUNG BEETLES (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE) IN CERRADO, BRAZIL

Edge and land use effects on dung beetles (coleoptera: scarabaeidae: scarabaeinae) in brazilian savannah, cerrado, brazil

Felipe Martello, Fernando Andriolli, Thamyrys Bezerra de Souza Pavel Dodonov, Milton Cezar Ribeiro

2.1. Abstract

Edge influence is one of the most pervasive effects of habitat fragmentation, as many forest remnants in anthropogenic landscapes are within 100 m from edges. Forest remnants may also affect the surrounding anthropogenic matrix, possibly resulting in a matrix – edge – remnant gradient diversity of some species groups. We sampled dung beetles in 15 agricultural landscapes in São Paulo, Brazil, using pitfall placed along transects in matrix – edge – remnant gradients. The remnants were a native savanna-like vegetation, the *cerrado,* and the matrix were composed of three human-dominated environments (sugarcane, eucalypt and pasture). More species were observed in cerrado remnants than in adjacent land uses. Dung beetles were more abundant in the cerrado than in the matrix in the landscapes of sugarcane and eucalypt, but not of pasture. Our results show that dung beetles are severely affected by anthropogenic land uses, and notwithstanding it high abundance in some land uses such as pastures, the number of species living in these areas tends to be smaller than in the cerrado remnants. We also find that edge influence was evident (only for abundance) mainly in pasture landscapes, although this land use causes species composition disruption in communities indicating that edge alters communities located in fragments, but also those located in matrix, phenomenon called as "forest effect". Thus, anthropogenic land uses may severely affect dung beetles, and this impact can extend to communities located both inside cerrado remnants and in matrices, with possible consequence for ecological processes such as decomposition and nutrient cycling.

Keywords: Brazilian savannah; sugarcane; pasture; eucalyptus; Akaike's Information Criterion

2.2. Introduction

Habitat fragmentation is one of the major threats to biodiversity. Among its most pervasive effects are those related to edge influence at the interface between natural and anthropogenic land uses. Over 20% of the remaining forest vegetation worldwide is located within 100 m of an edge (Haddad et al. 2015) and therefore may be subject to severe edge influence (Harper et al. 2005). This situation may be even worse in some tropical forests —for example, nearly 50% of the Brazilian Atlantic forest area is 100 m or less from the edge of the forest (Ribeiro et al. 2009). Vegetation edges in human-dominated landscapes are characterized by changes in species composition (Foggo et al. 2001, Harper et al. 2005), with a greater abundance of generalist and invasive species than in undisturbed areas (Laurance et al. 2002). Soil insects, which are responsible for important ecological processes such as decomposition and nutrient cycling (Whitford 1996, Brussaard et al. 1997), are among the groups affected by edges in both tropical and temperate regions (Meyer et al. 2009; Delgado et al. 2013a, b; Barrera et al. 2015). Still, notwithstanding the large number of studies showing edge influence on different organisms, many others have failed to detect edge-related gradients, and there is still no consensus on how edges affect some organisms (Ries et al. 2004).

Edge influence may depend on the type of matrix surrounding the forest fragments (Delgado et al. 2007; Pohlman et al. 2007; Kowal and Cartar 2012). Edge influence is expected to be greater when the fragment and the adjacent land use are more dissimilar in terms of vegetation structure, ecological processes and/or microclimate (Ries et al. 2004; Harper et al. 2005). For example, higher-contrast edges exerted a stronger edge influence than lower-contrast edges on air moisture in the Brazilian cerrado (Dodonov et al. 2013), on dung beetles in Argentinian Atlantic Forest (Peyras et al. 2013), and on flying insects in New Zealand (Campbell et al. 2011). Thus, when edge contrast is lower, the microclimate and vegetation at the edge may be similar to the reference conditions, and an organism may occur with equal abundance at the edge and in the fragment’s interior, even if it has greater or smaller abundance in the matrix. The same applies to the effects exerted by the vegetation remnant on the surrounding matrix. Conversely, some studies failed to detect a relationship between edge contrast and vegetation structure (Dodonov et al. 2013) or plant litter biomass (Dodonov et al. in press) in the cerrado, showing the this relationship is not universal.

Furthermore, a number of organisms, particularly the more generalist ones, may use the matrix habitat as well as the native vegetation remnants. For example, matrix habitats may be important, or at least usable as complementary habitat (Ries et al. 2004), by non-volant small mammals (Martin et al. 2012; Cooney et al. 2015), birds (Hansbauer et al. 2009), and several arthropod species (Borges and Brown 2001). Even organisms that survive better in forested environments may use the matrix, albeit with lower abundances than in the vegetation fragments. The abundance of different organisms and the number of species of a given group in the fragments and in the matrix will depend on the resources available in each environment and will therefore vary between matrix types (Ries et al. 2004; Driscoll et al. 2013). For example, in comparison to a monoculture matrix, an agroforestry matrix may offer a larger quantity of resources and will likely harbor a greater number of species occurring in greater abundances. Both the edge contrast and matrix suitability may affect the existence and shape of edge-related gradients in agricultural landscapes, with edge contrast affecting the gradient's degree of conspicuousness, and the matrix quality affecting the difference in abundance between the forest and the matrix.

To aid in understanding the effects of different matrices on edge influence and the distribution of organisms, we addressed the variation in richness and abundance of an important group of soil insects — the dung beetles (Coleoptera: Scarabaeinae) — in Brazilian cerrado fragments and the surrounding human-dominated environments in Southeast Brazil. We focused on this group of organisms because they are highly diverse in tropical regions and provide several ecosystem functions, such as decomposition of organic matter in nutrient cycling, improvement of physical and chemical properties of soil, parasite suppression, and secondary seed dispersion (Nichols et al. 2007; Nichols et al. 2008; Campos and Hernández 2013). In addition, due to their association with vegetation structure (Hanski and Camberfort 1991; Nichols et al. 2007; Gardner et al. 2010; Almeida et al. 2011), they are sensitive to habitat alteration and are one of the first organisms to be affected by anthropogenic disturbance (Larsen and Forsyth 2005). For that reason and because dung beetles are easily sampled and have a well-known ecology and taxonomy, these insects are widely used for biodiversity monitoring, especially in agricultural or anthropogenic environments (Audino et al. 2014; Figueiras et al. 2015).

Coprophagy, the consumption of feces, is the fundamental feature of the biology of Scarabaeinae and determines characteristics of behavior, morphology, development and distribution (Halffter and Matthews 1966). Dung beetles use faeces for feeding or oviposition (Hanski and Cambefort 1991) and the resource partitioning through different dung-manipulation strategies allows the coexistence of many species (Hanski and Cambefort 1991). Regarding dung manipulation strategies, this group is divided into three guilds: telecoprids (rollers - adults group an amount of faeces into a ball and roll it some distance from the point of origin); paracoprids (tunnelers - adults dig tunnels in the soil under the faeces); and endocoprids (dwellers - adults and larvae feed within the fresh faeces deposits). The several ecosystem functions provided by dung beetles are more dependent on the functional properties and combinations of species than on species richness by itself (Slade et al. 2007), whereas within these dung-manipulation strategies there is much variation regarding the depth, speed and amount of faeces buried (Doube 1990) and habitat loss and fragmentation may result in a decrease of this functional richness (Barragán et al. 2011)

We assessed how the abundance, richness and composition of dung beetles as a whole and of the different dung-manipulation strategies (telecoprids, paracoprids and endocoprids) in Brazilian *cerrado* (a savanna-like vegetation) fragments are affected by different land uses: pasture; sugarcane plantations; and eucalypt plantations. We expected species richness, both for total of dung beetles and for each guild, to be greater in the cerrado than in the adjacent matrices due to increased resource variability. We expected total dung beetle abundance to be greater in the pasture than in the cerrado due to resource availability, but to be lower in the other matrices compared to the cerrado. This hypothesis also reflects the pattern expected for paracoprids, as this guild usually is the most abundant and its behavior of allocating the feces in underground tunnels enables these species to survive in drier environments. Finally, we expected to observe a edge-related gradients in the low-contrast matrix, namely eucalypt (due to its forest-like phytophysionomy) and pasture (few management and open are environment, such some *cerrado* phytophysionomy), as in these environments the smaller difference between the cerrado and the adjacent matrix may allow species characteristic of both environments to use the edge zone. In the high-contrast matrix, namely sugarcane we expect a discontinuous pattern, as many species would be restricted either the cerrado or the matrix (Figure 1).

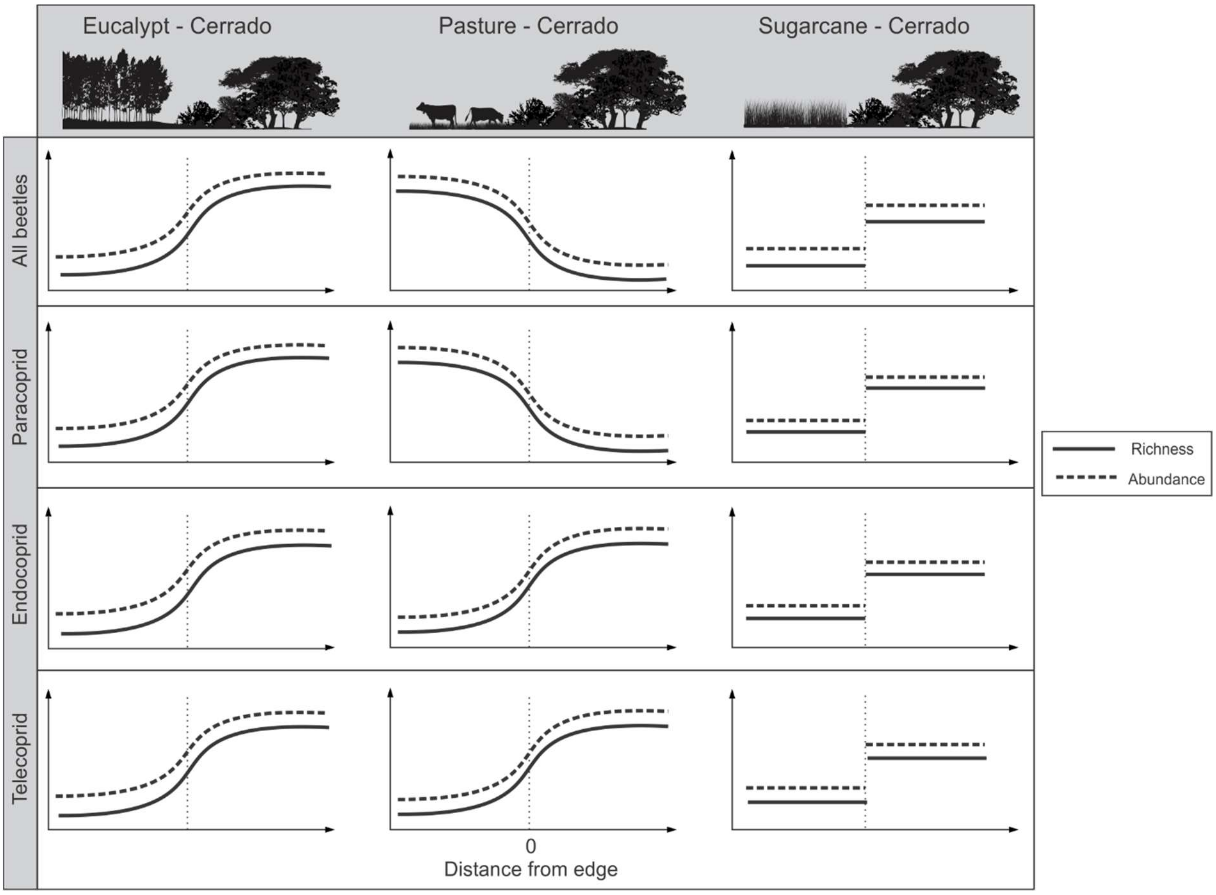

Figure 2. 1 Schematic representation of our expectations of total and guilds of dung beetle abundance and species richness response to distance from edge for three different land uses (pasture, eucalypt and sugarcane). Two horizontal line represent the categorical fragment-matrix model and a non-linear curve represents the gradient model

2.3. Methods

2.3.1. Study area

We performed this study in 15 agricultural landscapes composed of fragments of cerrado *sensu stricto* vegetation surrounded by different land uses. The landscapes are located in the Corumbataí river basin, São Paulo State, Southeast Brazil, between latitudes 22°04’46’’S and 22°41’28’’S and longitudes 47°26’23’’W and 47°56’15’’ W (Figure 2). The cerrado *sensu stricto* is characterized by researches as a savanna woodland characterized by a discontinuous canopy layer and tree heights between 5 and 8 m, and a ground layer occupied by heliophilous grasses, sedges, herbaceous species and subshrubs (Coutinho 1978; Ribeiro and Walter 2008). Three of the studied fragments were surrounded by pastures, five by eucalypt plantations and seven by sugarcane plantations (Table 1). This pasture is characterized by large open areas without intensive management area (application of herbicides or pesticides), and an extensive use of the pasture (between 0.3 and 1.14 cattle per hectare) (Sparovek et al, 2011). This region is characterized by a subtropical climate with a dry winter and a wet summer (Valente 2001), with a average yearly precipitation is about 1400 mm, 80% of which is concentrated between October and February (Zavatini and Cano 1993).

Table 2.1. Characteristics of the study areas, including the dominant matrix, its municipality (all in São Paulo State, Southeastern Brazil), coordinates of each landscape (decimal degrees) and total number of species found in each study site and in the corresponding fragment and matrix. Landscapes P1−P3 are occupied by a pasture matrix, E1− E5 by eucalypt and S1− S7 by sugarcane.

Landscape	Matrix	Municipality	Coordinates		Number of species		
			Latitude	Longitude	Total	Cerrado	Matrix
P1	Pasture	Analândia	-22.115	-47.646	17	14	13
P2	Pasture	Corumbataí	-22.27	-47.656	35	34	21
P3	Pasture	Analândia	-22.244	-47.688	20	16	14
E1	Eucalypt	Itirapina	-22.252	-47.759	23	14	19
E2	Eucalypt	Brotas	-22.301	-47.896	23	19	17
E3	Eucalypt	São Carlos	-22.092	-47.877	23	12	16
E4	Eucalypt	Analândia	-22.146	-47.649	30	19	17
E5	Eucalypt	Analândia	-22.135	-47.634	25	19	15
S1	Sugarcane	Itirapina	-22.247	-47.707	21	16	7
S2	Sugarcane	Itirapina	-22.184	-47.876	28	17	25
S3	Sugarcane	Brotas	-22.259	-48.154	25	21	14
S4	Sugarcane	Brotas	-22.31	-48.12	26	18	15
S5	Sugarcane	Brotas	-22.291	-48.161	35	27	16
S6	Sugarcane	Brotas	-22.294	-48.095	34	22	22
S7	Sugarcane	Analândia	-22.146	-47.64	18	15	9

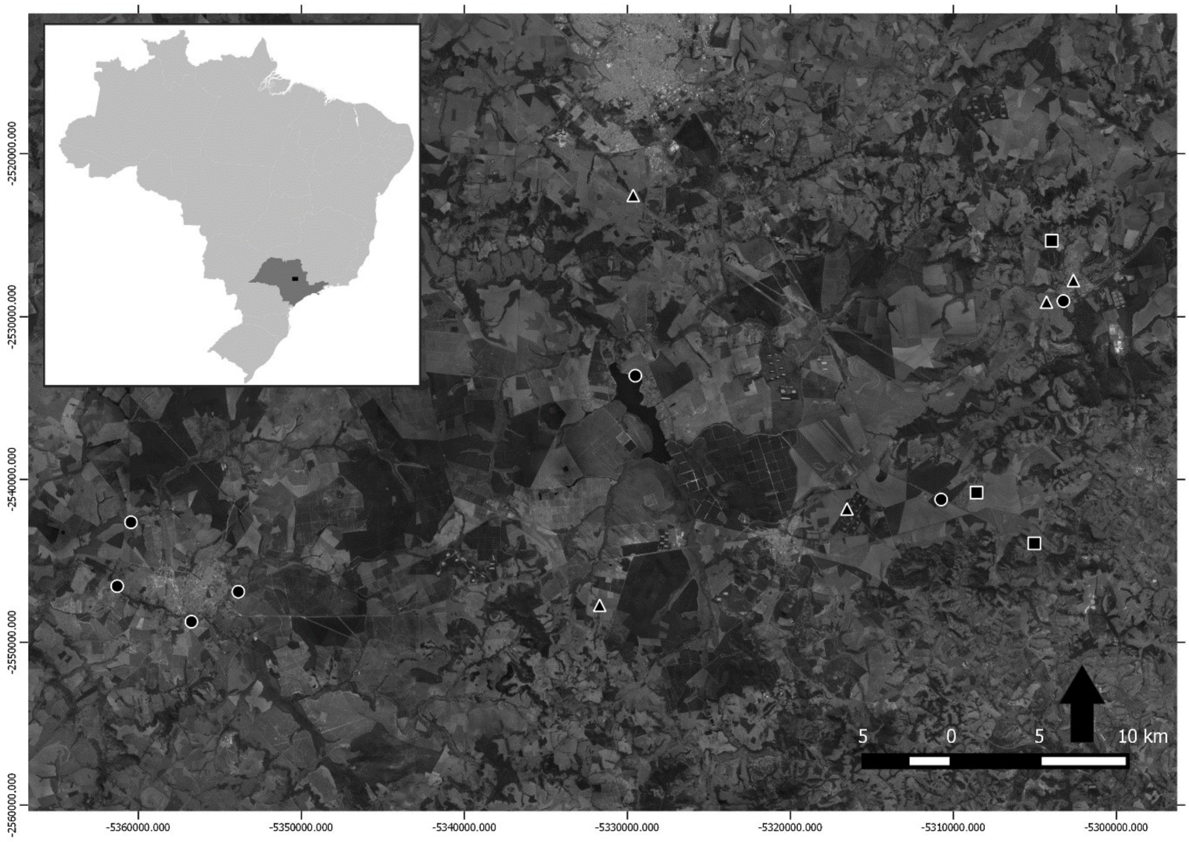

Figure 2. 2 Satellite image of the location of the study landscapes. The small map indicates the location of the image (black rectangle) within the State of São Paulo (dark grey), Brazil (light grey). Polygons represent the type of matrix that composed the cerrado boundaries, wherein squares represent pasture, triangles represent eucalyptus plantations, and circles represents sugarcane plantations

2.3.2. Dung beetle sampling and identification

In each of the study fragments, we established two transects placed 50 m apart and perpendicular to the fragment's edge. Each transect contained eight pitfall traps, four in the matrix and four in the fragment, with 25 m between adjacent traps. Although the distance between traps was smaller than recommended for independent samples (Larsen and Forsyth 2005; Silva and Hernández 2015), a wider spacing could have precluded the detection of edge-related gradients. The traps closest to the fragment-matrix boundary within each transect were positioned in both the fragment and the matrix at 12.5 m from the boundary. The traps were composed of a 1-liter cylindrical receptacle holding 250 mL of water with 2% detergent, saturated with sodium chloride to minimize decomposition. At the center of the receptacle, we placed human feces as bait in a 50-millilitre plastic cup suspended from a wire, and we covered the trap with a tilted Styrofoam disk for protection against rain and to keep the bait from drying up (Hernandez and Vaz-de-Mello 2009). As only human feces were used as an attractant, only coprophagous Scarabaeinae were sampled. The traps were exposed for 48 hours, after which their contents were passed through a fine mesh and deposited in plastic bags with 70% alcohol for posterior processing and species identification in the lab. Each transect was sampled three times between December 2011, January 2012, and February 2012, periods of highest abundance of this group in southern Brazil (Hernández and Vaz-de-Mello 2009).

Dung beetles were then identified to the most detailed taxonomical level possible, and information on their guilds was obtained from the literature (Halffter and Matthew 1966; Doube 1990; Vulinec 2002; Alcorón et al. 2009; Liberal et al. 2011; Beiroz 2012).

2.3.3. Data analysis

For the analyses, we pooled the data for each distances at each landscape, thus combining the data for the three campaigns and the two transects corresponding to each distance. We then used the landscapes with each dominant land use (pasture, eucalypt or sugarcane) as replicates, thus having three to eight replicates at each distance for each land use. We used total abundance and richness and the abundance and richness of each guild as response variables.

We analyzed the relationship of each response variable with position along the transect by adjusting cerrado to each land use three competitive models: a null model, a categorical "fragment–matrix" model, and a continuous "interior–edge–matrix" model, which we called the "gradient" model. The adjustments were made as generalized linear or additive mixed models with a Poisson distribution. The null model assumes that the response variable is homogeneous along the transect and is not affected by the position along the transect nor by the environment. The fragment–matrix model assumes that the response variables do not vary with distance into the fragment nor into the matrix, but may vary between these two environments (*e.g.* total abundance in sugarcane landscapes in Figure 1). The gradient model assumes that the response variables are related to their position along the transect (from -85 m into matrix to 85 m into the interior of the cerrado, where zero is the edge transitional zone), without explicitly differentiating between fragment and matrix (*e.g.* total abundance in eucalypt and pasture landscapes in Figure 1). Thus, the fragment-matrix model considers only differences between the two environments (habitat and matrix), whereas the gradient model is able to account for edge influence and for continuous variation along the transect. The null model was represented by a linear intercept-only model; the fragment–matrix model by a generalized linear model, with the two habitat types modeled as categorical variables; and the gradient model by an additive model with a smoothing function for distance along the transects. In all analyses we included the sampling landscape as a random factor and calculated the (Laplace approximate) maximum likelihood. The optimal amount of smoothing in the gradient model was defined by means of a cross-validation procedure (Zuur et al. 2011).

We calculated Akaike's Information Criterion corrected for finite sample size (AICc) values for the three models and calculated the difference in the AICc of each model compared to the model with the smallest AIC (ΔAICc). We selected the model with the lowest AICc when the ΔAICc of other models was greater than 2.0, as models with a ΔAIC of two or less may be considered as having "substantial" support (Burnham and Anderson 2002). Although there are several criticisms to the use of an arbitrary cutoff to determine which model is best (Burnham and Anderson 2014; Murtaugh 2014; Valpine 2014), we chose to define an *a priori* cutoff because of the large number of response variables, which would make a more thorough assessment of the support for each model too subjective. When two or more models had small ΔAICc values, we selected the simplest model. When both the gradient and the fragment–matrix models had ΔAICc of 2.0 or lower, we selected the simpler fragment–matrix model because it assumes that there are differences between the two areas but no edge influence. When the simplest null model was among the models with a ΔAICc of 2.0 or lower, we considered it as the best model because it assumes neither edge influence nor differences between the two areas.

When either the fragment–matrix or the gradient model was selected, we also noted whether species richness was greater in the fragment or the matrix. There were thus five possible outcomes for each response variable at each landscape type: no response (null model); greater abundance in the matrix, with no gradient; greater abundance in the fragment, with no gradient; greater abundance in the matrix, with a gradient indicating edge influence; or greater abundance in the fragment, with a gradient indicating edge influence.

We also performed a non-metric multidimensional scaling ordination (NMDS), using Bray-Curtis distance, with all plots to describe and interpret the patterns of community composition along the edge distance.

All analyses were performed in R 3.2.4 (R Core Team 2015). The null and fragment-matrix model were adjusted with the glmer function of the lme4 package (Bates et al. 2015), whereas the gradient models were adjusted with the gamm4 package (Wood and Sheipl 2014), base on the mgcv (Wood 2011) package. The AICc values were obtained with the MuMIn package (Barton 2015). The NMDS ordination were performed with the vegan package (Oksanen et al. 2007)

2.4. Results

In the 15 study agricultural landscapes, we sampled a total of 8,423 individuals, belonging to 57 species and 21 genera. We observed between 3 and 165 (mean of 25.1 ± 40.1 SD) individuals per pitfall in the different matrices and between 13 and 118 (mean of 44.9 ± 26.9) individuals per pitfall in the fragments (Figure 3). The mean number of species per pitfall ranged from 2.3 to 10.9 (mean of 5.5 ± 2.4) species in the matrix and from 5 to 15.1 (mean of 8.9 ± 2.8) in the *cerrado*. Paracoprid was the richest guild (32 species), followed by telecoprid (18 species) and endoprid (seven species), and the abundance of most species differed between the matrix and the remnants (Figure 3). The most abundant guild in both cerrado and matrix (regardless the type of land use) was the paracoprid, with 3496 individuals in cerrado (mean of 10.53 ± 12.56 per pitfall) and 1578 individuals in different matrices (mean of 5.42 ± 9.65 per pitfall). Endocoprid guild had 986 individuals sampled in cerrado (mean of 2.97 ± 7.09 per pitfall) and 807 individuals in different matrices (mean of 2.77 ± 12.61 per pitfall). The telecoprid was the less abundant guild with 907 individuals sampled in cerrado (mean of 2.73 ± 3.67 per pitfall) and 624 individuals in different matrices (mean of 2.14 ± 7.01 per pitfall).

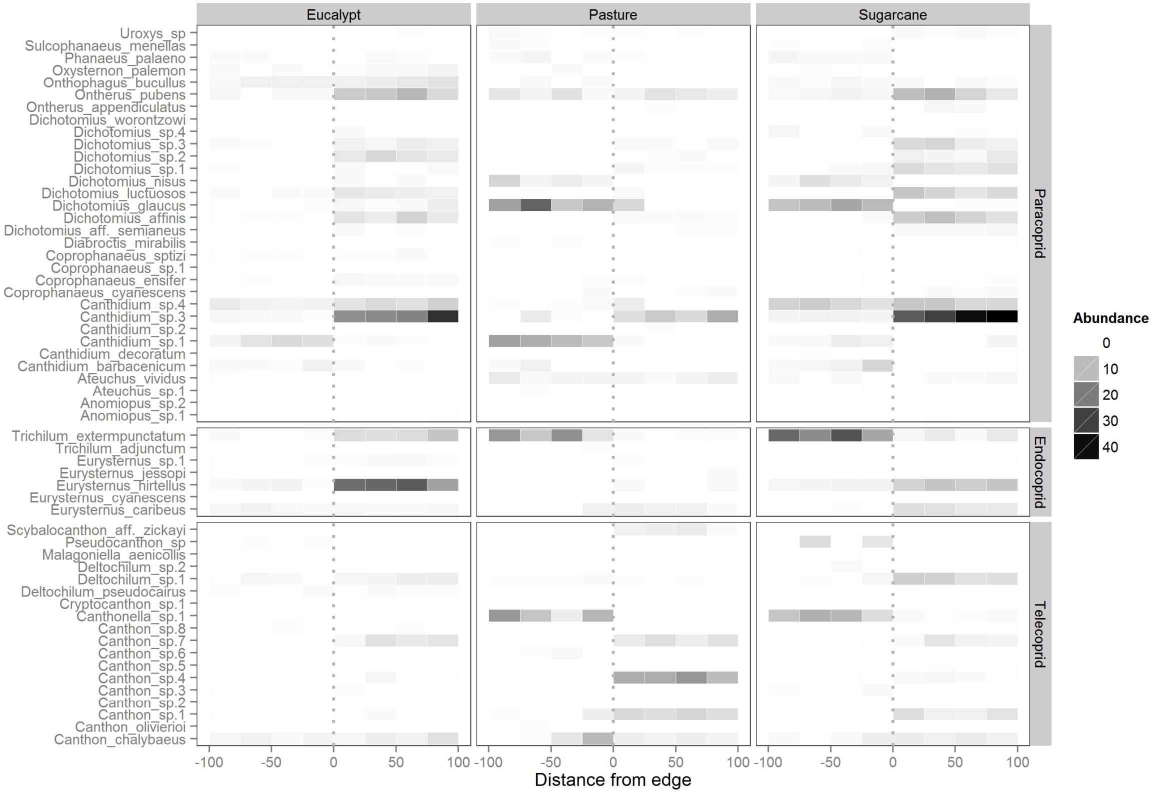

Figure 2. 3 Abundance of dung beetle species, per source allocation guild, sampled in landscapes composed by the Brazilian savannah, cerrado (positive values of distance from edge), and three different land use (negative values of distance from edge). Vertical dotted lines represent edges between *cerrado* and its adjacent matrix.

The patterns of total abundance and richness varied among land uses and it responses to edge distance always followed the same response that the paracoprid guild had shown. Total and paracoprid abundances decreased linearly from the matrix into the *cerrado* in the pasture landscapes (gradient model) but was greater in the *cerrado* than in the matrix at the eucalypt and sugarcane landscapes, with no edge influence detected (Figure 4). The total and paracoprid number of species did not vary between matrix and *cerrado* in the pasture landscapes and was smaller in the matrix in the other landscapes (Figure 5). The abundance of endocoprids was greater in matrices than in cerrado in pasture and sugarcane landscapes, but smaller in matrices in eucalypt landscapes, with no detectable edge influence in any landscape (habitat-matrix model) (Figure 4). The richness of this guild was greater in matrices than cerrado in eucalypt and sugarcane landscapes, with no edge influence detected, and it did not change between habitat in pasture. The ΔAICc values of the models are presented as supplementary material.

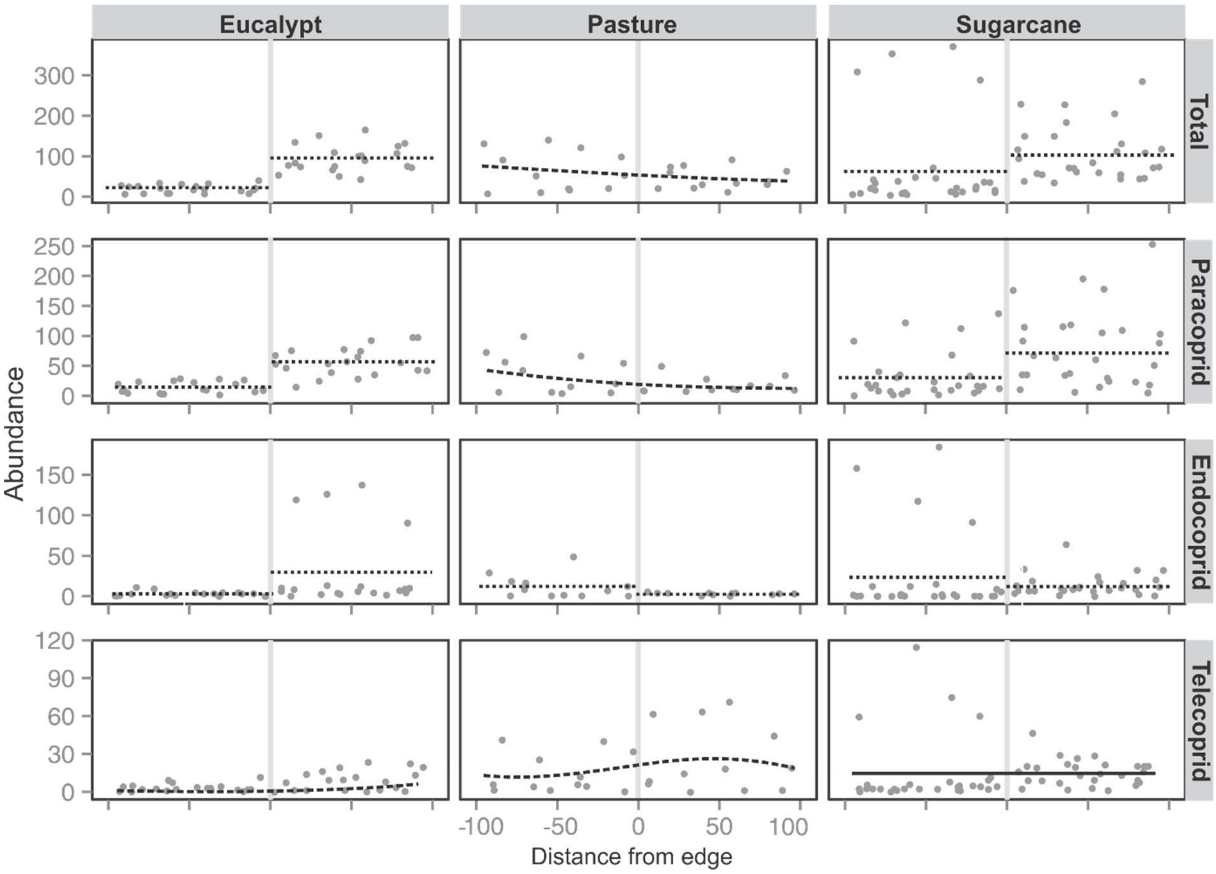

Figure 2. 4 Abundance of dung beetle source allocation guilds sampled in landscapes composed by the Brazilian savannah, cerrado (positive values of distance from edge), and three different land use (negative values of distance from edge). Vertical lines at zero value of x axes represent the edge between the two environments composing the landscape. Black lines represent the selected model, which express the response of dung beetles to edge distance, wherein: dashed line is the gradient model, two dotted lines is the fragment-matrix model, and continuous lines is the null model.

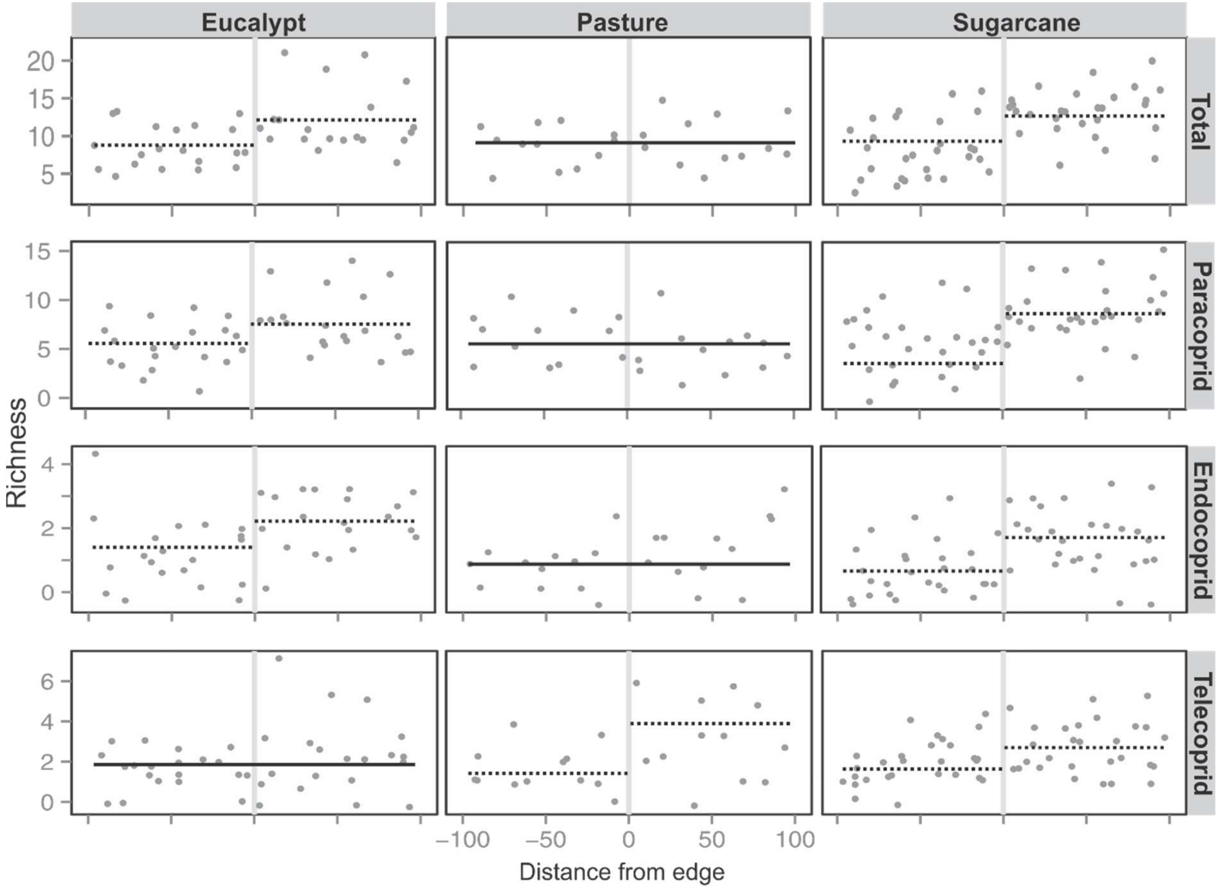

Figure 2. 5 Richness of dung beetle source allocation guilds sampled in landscapes composed by the Brazilian savannah, cerrado (positive values of distance from edge), and three different land use (negative values of distance from edge). Vertical lines at zero value of x axes represent the edge between the two environments composing the landscape. Black lines represent the selected model, which express the response of dung beetles to edge distance, wherein: two dotted lines is the fragment-matrix model, and continuous lines is the null model.

The NMDS ordination revealed that patterns of dung beetle species composition along transects differ depending on the matrix adjacent to the remnant (Figure 6). In edges adjacent to sugarcane matrix there was either a gradual transition in dung beetle composition along transects or a fuzzy differentiation between the communities located in the matrix or the cerrado. Conversely, in pasture matrix the ordination analysis showed a much clearer differentiation between the matrix and the cerrado. The composition of dung beetles in the eucalypt matrix showed a differentiation between communities located in the matrix and cerrado, with a more evident edge zone (Figure 6).

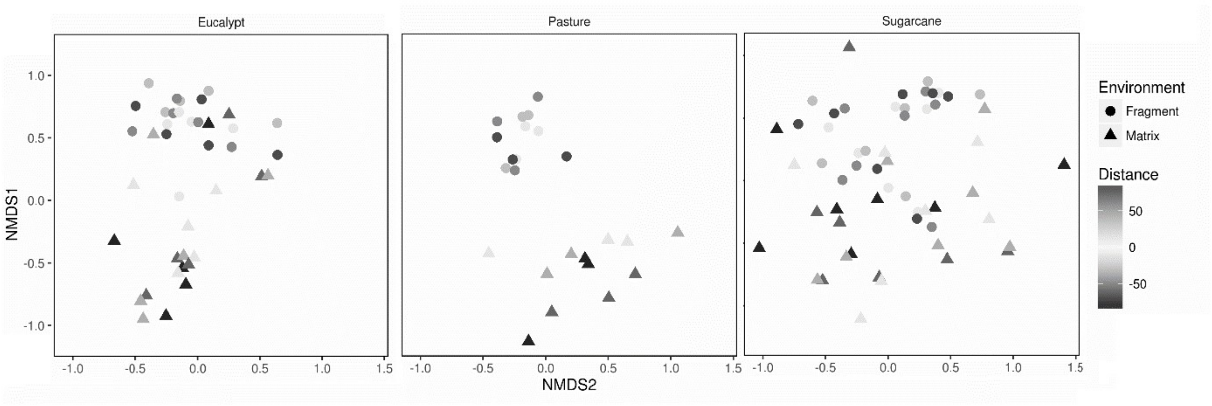

Figure 2. 6 Non-metric multidimensional scaling ordination (NMDS) of dung beetles sampled in transects in landscapes composed by the Brazilian savannah, cerrado (fragment), and three different land use (matrix).

2.5. Discussion

Our results showed great variation in the abundance and richness of dung beetles between the cerrado fragments and the adjacent matrix. This variation was observed for all beetles, for guilds and for some species. Our expectations regarding the number of dung beetles species were mostly confirmed, which were generally larger in the *cerrado* fragments than in the adjacent matrix and never higher in matrix. This indicates that, even though many dung beetle species are able to survive in the matrix, the natural vegetation offers a greater variety of resources and habitats for their survival. Although the cumulative function of the number of species with sampling effort being different according to habitat may be underestimated the richness in cerrado and overestimated in disturbed habitat, we believe that once we sampled in periods of highest abundance of dung beetle, this bias can be neglected. Regarding beetle abundances, our expectations also were mostly confirmed: dung beetles were frequently more abundant in pasture than in the adjacent *cerrado*, but less abundant in the other anthropogenic land uses. Dung beetle abundance depends on the specific land use being considered, and simply classifying land uses as either natural or anthropogenic does not provide an adequate description of the impacts on the community.

Scarabeinae differ in their preference regarding physical and chemical characteristics of feces (Gittings and Giller 1998) and have been shown to discriminate differences in nutritional value (Verdú and Galante 2004), dung shape (Gordon and Cartwright 1974), water and/or fibre content (Verdú and Galante 2004) and dung size (Peck and Howden 1984). Thus, elevating the diversity of feces (especially from large mammals) promotes elevation in the diversity of dung beetles (Nichols et al. 2009). Although pastures may have a greater abundance of resources than other land uses, these resources usually come from a single provider – cattle. The dominance of cattle in this matrix suggests high competition between species that prefer this resource, resulting in the dominance of few species (Louzada and Silva 2009; Almeida et al. 2011). Moreover, high cattle density causes soil compaction, and practices of installation and management in introduced pastures can have a negative impact on dung beetle diversity (Almeida et al. 2011). In this study, we detected an increase in the total abundance of dung beetles in pasture matrix, as would be expected from the increase in resource quantity. Contrarily to our expectations, the richness in the pasture landscapes did not changed between the matrix and the adjacent *cerrado* just. However, this outcome does not mean that there is no changes between dung communities located in these two habitat, since the NMDS ordination showed that the composition of communities located in these adjacent habitat were different - exposing a marked effect of pasture land use in dung beetle communities. Although most dung beetles in tropical savannah are not host specialist (Spector and Ayzama 2003), the characteristic of the habitat wherein the dung is located, as well as the competition between species, can play a key rule to determine the community composition (Roslin and Vijanen 2011).

Dung beetles communities in highly modified habitats are commonly characterized by a small number of the hyper-abundance of few small-bodied species that dominate the environment and tend to be more aggregated than large-bodied species, possibly as a result of having smaller niches differences (Koller et al. 1999; Scheffler 2005; Nichols et al. 2007; Simmons and Ridsdill-Smith 2011). The loss of large-bodied beetles may have significant secondary consequences for community structure and subsequent patterns of ecological function, for example, in the function of waste removal large-bodied beetles remove disproportionately more dung than smaller-bodied beetles (Larsen et al. 2005; Slade et al. 2007; Dangles et al. 2012). In this study, the small-bodied *Trichillum externumpunctatum* was an abundant species in pasture and sugarcane matrices. This species is generally found in pastures in Brazil (Flechtmann et al. 1995; Koller et al. 1999; Aidar et al. 2000), and its high abundance in environments with elevated temperatures, such as pastures and sugarcane plantations, may be an outcome of a different nidification behavior (Alcorón et al. 2009) compared to other endocoprids (Cambefort and Hanski 1991). In this species, neither brood masses nor balls are prepared by the female, and after the feeding stage the larva leaves the mass of faeces to pupate in the soil underneath it, thus moving to a more humid environment (De Maria et al. 1999; Alcorón et al. 2009).

The lower abundance and richness of dung beetles in most land uses expose the severe impact of land-use changes on dung beetles and reflect the contrast between the *cerrado* and the adjacent matrices. The differences between adjacent habitats in terms of physical conditions can explain our results. For example, soil humidity and structure play a key role in dung beetle reproduction, as these factors are essential for nest construction (Fincher 1973). Moreover, the biodiversity of both adults and larvae of dung beetles depends closely on the presence of mammals, since their faeces and carcasses are used as resources (food and nest) by many species (Hanski and Cambefort 1991). Although some mammals are able to use eucalypt plantations (Lyra-Jorge et al. 2010), this is not likely for higher-contrast matrices such as sugarcane. Considering that dung beetle abundance may be an indicator of the abundance of mammals (Andresen and Laurance 2007; Nichols et al. 2009), our results also indicate severe impacts of the eucalypt and sugarcane matrices on mammal abundance (Andresen and Laurance 2007; Nichols et al. 2009).

Regarding dung-manipulation strategies, the higher proportion of paracoprids compared to the other guilds has been also found in others studies in the Neotropics (Louzada and Lopes 1997; Liberal et al. 2011; Silva and Di Mare 2012). The higher abundance of this guild might be an outcome of low competition rate (Hanski 1991) and changes regarding the usage of both land and fecal resources (Halffter and Edmonds 1982) allowing the occurrence of ecologically similar species and increase regional diversity of paracoprids (Louzada and Lopes 1997). Paracoprids were most abundant in pasture matrix; this environment is more advantageous to them than to the other guilds because 1) endocoprids live inside faeces and are more sensitive to high temperatures in pasture due acceleration on faeces dryness (Klein 1989); 2) telecoprids roll large masses of faeces away in a short time span and this costs more energy per time than tunneling behavior (Krell et al. 2003). In pasture and sugarcane matrices the abundance of endocoprids was mainly due to *Trichillum externumpunctatum,* which has a different nidification behavior (Alcorón et al. 2009) in relation to other endocoprids (Cambefort and Hanski 1991), allowing the larvae and pupae to develop in an environment of considerable moisture conditions (De Maria et al. 1999; Alcorón et al. 2009)

In eucalypt landscapes there was higher abundance of all functional guilds in the *cerrado* than in the matrix, whereas different patterns were observed for other land uses depending on the guild. It is known that the presence of all guilds in an environment maximizes ecosystem functions (Slade et al. 2007), as the presence of paracoprids and telecoprids species causes increasing in the removal of faeces, seed dispersal, edaphic aeration, and incorporation of organic matter in the soil. Furthermore, the increasing in paracoprids may lead to lower seed predation (Estrada and Coates-Estrada 1991; Andresen 2002; Slade et al. 2007). Besides, combined effects of the endocoprids and paracoprids result in a synergistic pattern that facilitates faeces transference to the soil and stimulates microbial activity with important consequences for soil Carbon cycling (Menéndez et al. 2016). Thus, it appears that the services provided by dung beetles are most impaired in eucalypt land uses. Although eucalypt plantations are structurally similar to *cerrado* fragments and may have a large amount of natural regeneration (Dodonov et al. 2014), these landuse are large managed monocultures with application of agricultural inputs, such as fertilizers and pesticides and are clear-cut periodically (FAO 2006). In addition. these features, as well as the high the water demands and the release of allelopathic substances, that is characteristic of this three, cause a severe impact on soil structure, which reduces the resilience and biodiversity of communities (Lugo 1997)

The NMDS ordination showed that edge communities in eucalypt landscapes had an intermediate composition between those in the cerrado and the adjacent matrix. Thus, while decreasing the abundance of all guilds, eucalypt landscapes apparently change smoothly the species composition along the edge. Such a pattern reveals that the system that causes less drastic changes in vegetable structure and remains part of the forest cover may offer, in communities located near to the native habitat microclimate conditions more favorable for dung beetles fauna (Halffter and Matthews 1996; Halffter and Arellano 2002). This may also be related to the resources available, as different edge-related patterns are expected if the matrix resources are supplementary, with the same type of resource being found in the *cerrado* and the matrix, or complementary, with the matrix offering some resources that are absent from the cerrado (Ries et al. 2004). If near to *cerrado* eucalypt matrix contains the same type of resources than the adjacent cerrado, species composition is not likely to vary much, with most variation being due to changes in abundance. Conversely, species compositions may vary more when the matrix has different resources than the *cerrado*, which may be the case for pasture landscapes in which there was a clear differentiation between the cerrado and the matrix.

Our expectations regarding edge influence were only partially corroborated. The gradient model, indicating edge influence, was selected for abundance only in pasture landscape. This outcome indicates that, although pasture land use causes species composition disruption between pasture and *cerrado* and pasture influences negatively dung beetles abundance in communities located near the edge, the variation in abundance is more gradual. This may reflect both a negative effect of the pasture on the adjacent cerrado, for example due to altered microclimate (Dodonov et al. 2013), and an effect of the cerrado on the pasture matrix, in which the cerrado edge creates more favorable conditions in the matrix. This latter phenomenon has sometimes been called 'forest effect' and has been observed, for example, in areas disturbed by insect outbreaks (Franklin et al. 2015) and in agricultural areas adjacent to forest fragments (González et al. 2015). Forest effect may affect factors as diverse as vegetation composition (Bueno and Lambí 2015), microclimate (Baker et al. 2014) and predatory insects (González et al. 2015), which can provide resources for mammals in areas on this effects, consequently afford resources for dung beetles.

Unlike the patterns observed for dung beetle abundance, edge influence on species richness was never evident for any landscape, whether for the total of beetles or for the different guilds. Weak or non-significant edge influence is commonly observed for dung beetle diversity (Durães et al. 2005; Feer 2008; Campbell et al. 2011), and it seems that species richness is also little affected by edges in the cerrado. This pattern can be partially due to the patchy and ephemeral nature of their resources (manure and carcasses), which makes these insects mobile and efficient in tracking those resources throughout the landscape (Roslin 2000). In addition, similar to other savannas, the cerrado is a naturally patchy environment with alternating patches of greater or smaller woody plant cover (Wiegand et al. 2006; Gonçalves and Batalha 2011). Furthermore, small-sized cerrado mammals may not be affected by edges at the scale of this study (Di Napoli and Caceres 2012). Thus, the distribution of dung beetles in our study fragments may be sufficiently heterogeneous to preclude the detection of edge influence on the number of species (Harper et al. 2005).

Besides the fact that most of dung beetles in tropical savannas are not host specialists (Spector and Ayzama 2003), the differences in mammal communities between the different land uses (Lyra-Jorge et al. 2010; Martin et al. 2012) as well as the presence of the dung of generalist and edge-preferring mammals at the edge may aid in explaining our results. It must also be considered that dung beetles may use all of the studied matrices to some degree, albeit often with lower abundance, as shown by the results above. Edge influence on species richness could be more evident if we were to consider more inhospitable matrices such as urban areas or highways (Noreika and Kotze 2012). Still, a lack of relationship between edge contrast and edge influence has been observed for other variables in the cerrado, including vegetation height, canopy closure and plant litter biomass (Dodonov et al. 2013, Dodonov et al. 2016). The great diversity of this group of beetles results in a myriad of environmental and resource preferences as well as differences in movement capabilities among species, leading to a variation in edge-related patterns among the species such that the loss of some species at the edges is compensated by other species (Barbero et al. 1999; Peyras et al. 2013; Figueiras et al. 2015).

Finally, landscape features also play a key role in the detection of the edge influence on organisms, especially in highly fragmented and heterogeneous landscapes. One of the best-known landscape metrics to have an impact on edge influence is habitat area, since small patches have higher densities of edge area (Fletcher et al. 2007; Banks-Leite et al. 2010). As dung beetles are sensitive to patch size (Feer and Hingrat 2005; Horgan 2007), area and edge effects interact synergistically in such a way that small patches may be unable to sustain species that avoid edges; hence a misdetection of the edge influence (Ewers et al. 2007). Thus, the inclusion of larger fragments could have aided in the detection of edge influence on species richness. However, considering that small remnants dominate highly fragmented regions such as Southeast Brazil, our results are representative of the patterns that may be observed in this region.

In conclusion, we showed clear effects of different land uses on dung beetle abundance, richness and composition of dung beetles as a whole and of the different dung-manipulation strategies in an agricultural landscape containing cerrado fragments. We also demonstrated the occurrence of edge influence on the abundance of this group, albeit only in pasture matrix. Although edge influence was not often observed for species richness, there were great differences between the vegetation remnants and the adjacent land uses for both richness and abundance. Thus, anthropogenic land uses, including low-contrast ones such as eucalypt plantations, tend to decrease the abundance and richness of dung beetles, with possible consequences for several ecological processes including decomposition and nutrient cycling. These effects may extend into the cerrado remnants, decreasing their core area, the impacts being especially severe considering the high degree of fragmentation of this vegetation.

2.6. Acknowledgments

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2.7. Supplementary material

Supplementary material S1. Values of the difference in the second-order Akaike information criterion between each model and the best model (dAICc) for the three models compared. Sample size was of three landscapes in pasture matrix, five in eucalypt matrix and seven in sugarcane matrix.

Response variable	Land use	Null model	Fragment-matrix model	Gradient model
Total abundance	Pasture	40.4	9.1	0.0
	Eucalypt	1066.2	0.0	86.8
	Sugarcane	249.8	0.0	48.5
Total richness	Pasture	0.0	2.2	5.4
	Eucalypt	12.4	0.0	7.8
	Sugarcane	33.9	0.0	4.7
Endocoprid abundance	Pasture	66.7	0.0	2.0
	Eucalypt	488.3	0.0	65.2
	Sugarcane	51.1	0.0	3.6
Endocoprid richness	Pasture	0.0	0.1	2.3
	Eucalypt	2.0	0.0	2.8
	Sugarcane	9.6	0.0	7.7
Paracoprid abundance	Pasture	104.0	17.7	0.0
	Eucalypt	568.4	0.0	43.6
	Sugarcane	569.9	0.0	54.3
Paracoprid richness	Pasture	0.0	0.4	2.9
	Eucalypt	6.5	0.0	5.9
	Sugarcane	19.2	0.0	2.8
Telecoprid abundance	Pasture	38.8	3.3	0.0
	Eucalypt	59.2	3.9	0.0
	Sugarcane	0.0	0.8	3.4
Telecoprid richness	Pasture	3.3	0.0	4.6
	Eucalypt	0.0	0.4	4.0
	Sugarcane	3.0	0.0	0.9

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CAPÍTULO 3: MATRIX TYPE INFLUENCES THE RESPONSE OF ANT COMMUNITIES TO DISTANCE FROM EDGE IN NATURAL AND HUMAN-MODIFIED ECOTONES

Matrix type influences the response of ant communities to distance from edge in natural and human-modified ecotones

Martello, Felipe R., Andriolli, Fernando, Campos, Ana E., Ribeiro, Milton C.

3.1 Abstract

As fragmentation has intensified in recent decades, the impacts of the edge effects on biodiversity has become a major topic within studies focused on the consequences of fragmentation as well as conservation strategies. Despite the wealth of studies that address edge effect, for many organisms there is no consensus about how they respond to this issue. This discordance has become a key topic among edge effect specialists, who point the importance of an appropriate statistical analysis as well as an experimental design that explicitly consider the adjacent matrix and distance from the edge as a continuous factor. In this study, ,we aimed to know how the biodiversity of ant communities located in matrix-patch ecotones to the distance from the edge in cerrado ecotone composed by different matrix. We also sought to understand if the type of matrix that composes the ecotone changes this response. Our results show that edge distance had a positive effect, a negative effect, or no effect on ant communities located in matrix-cerrado ecotones. Concerning of each ecotone, the pool of suitable models for richness and composition was always different, in a way that an analysis considering the two variables together provided a more precisely picture of how edge distance affect ant community in each ecotone, than if we used only one variable. We conclude that the type of response that ant communities show to edge distance are correlated to the type of matrix, especially because matrixes shelter exotic and generalist species. Our results showed that the response of ant communities to edge effect can be either linear or non-linear, and that this response are related to the type of matrix. Thereby we emphasize the importance of not only consider the matrix in experimental design, but also that this variable can play a key role in the response of ant communities to edge effect. Furthermore, we highlight that organisms can have a non-linear response to edge distance, which can be essential to elucidate the lack of consensus that exists in edge effect studies.

3.2 Introduction

The conversion of natural environments into human-modified landscapes is a key driver of global biodiversity loss (Fahrig 2003). In addition to reducing the natural land cover, it fragments continuous natural habitats into small patches. This fragmentation has a negative impact on biodiversity mainly by confining species within small patches and changing microhabitat conditions in the natural areas adjacent to the matrix (nonhabitat surrounding native habitat patches) (Fahrig 2003). These microhabitat changes are consequences of the interaction between the two environments (matrix and natural habitat) that composes these transitional areas (ecotones) and are known as edge effect (Ries 2004). As fragmentation has intensified in recent decades (Ewers and Didham 2006) the impacts of edge effect on biodiversity and the factors that influence this process have become major topics within studies focused on the consequences of fragmentation as well as conservation strategies (Murcia 1995, Ries 2004, Harper et al. 2005).

Ants are among the most common organisms in any environment, rising as key drivers in essentials ecological processes (e.g. seed dispersal and soil aeration) severely impacted by edge effect. Furthermore, edge effect benefits exotic ant species and, consequently, ecotones are a gateway for invasive species, which are a threat particularly to invertebrate fauna (Cole et al. 1992; Vega & Rust, 2001; Holway 2005). Despite many studies of ants within ecotones, there is no consensus about how ant communities respond to edge effect, wherein abundances, richness and composition could increase, decrease or remaining unchanged under these conditions (Majer et al. 1997, Holway 2005,Brandão et al. 2011,). This discordance between edge studies is not exclusive to ant research. In fact, it has become a key issue among edge effect specialists, who point to the importance of an appropriate statistical analysis and experimental design that explicitly consider the adjacent matrix response and distance from the edge as a continuous factor (Ries 2004, Ewers & Didiham 2006, Harper et al. 2011). Although such concerns have been reflected in studies of ants and edge effect, many of them considered distance from the edge as a discrete factor (Sobrinho & Schoereder 2007, Banschbach et al. 2012); they also sampled individuals only inside the patches (Holway 2005, Sobrinho & Schoereder2007, Bolger 2007, Ness & Morin 2008).

In this study, we aimed to know how the biodiversity of ant communities located in matrix-patch ecotones to the distance from the edge in cerrado ecotone composed by different matrix. We also sought to understand if the type of matrix that composes the ecotone changes this response. We hypothesized that the biodiversity of ant communities located in an ecotone composed by a less managed matrix (pasture) or containing a forest phytophysionomy matrix (eucalyptus) would change gradually along the ecotone. By contrast we expected that the biodiversity of ant communities located in an ecotone composed by a more managed and homogeneous matrix (sugarcane) would change abruptly along the ecotone.

3.3 Material and Methods

3.3.1 Studied area, experimental design and sampling

We conducted our study in the center of São Paulo State, in a region where the predominant land uses are pasture, sugar cane monoculture, and eucalyptus forestry. The preponderant native habitat is the Brazilian savannah (cerrado), which currently represents less than 7% of its original cover (Durigan et al. 2007).

We selected 15 landscapes with cerrado remnants surrounded by three types of human land use: sugar cane (N=7), pasture (N=3), and eucalyptus forestry (N=5). In each landscape, we designed two 175 m transects spaced at least 50 m apart and perpendicular to the edge of the cerrado remnant. Half of each transect was inside the remnant and half was inside the matrix (Figure 1).

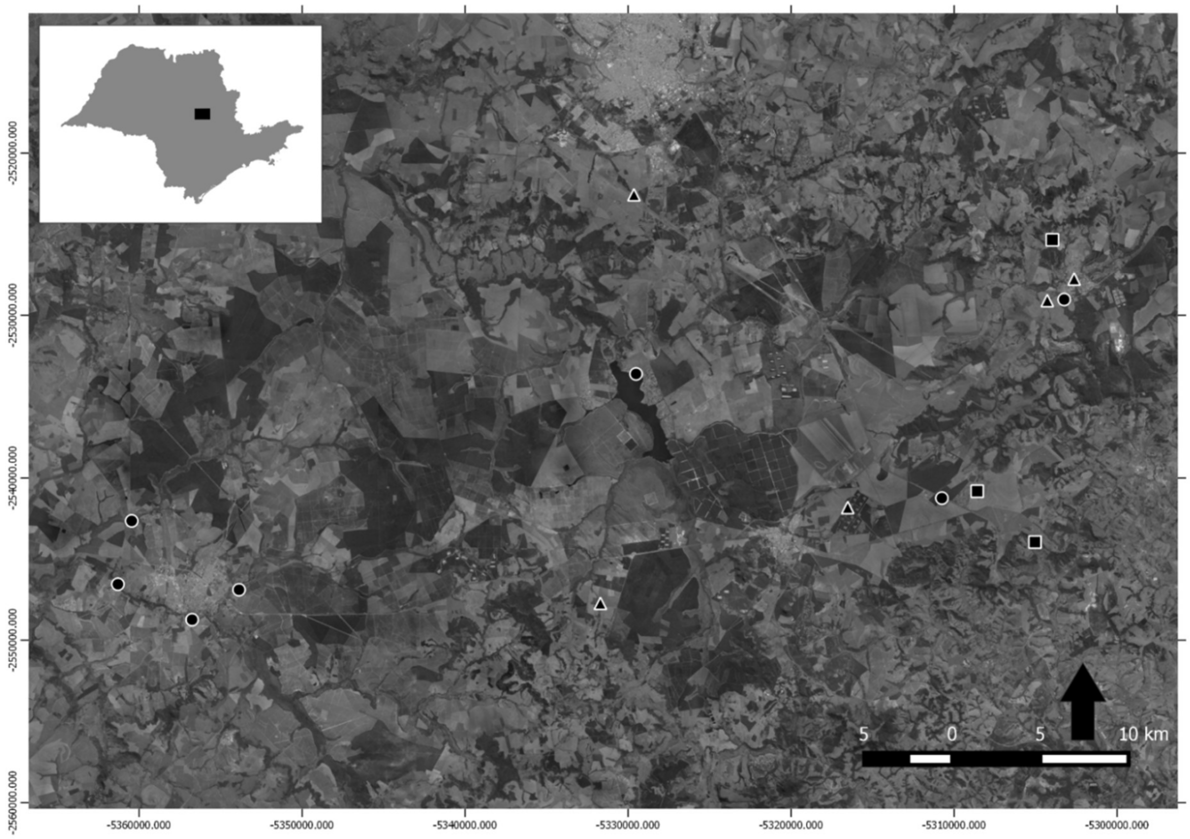

Figure 3.1. Satellite image of the location of the study landscapes. The small map indicates the location of the image within the State of São Paulo, Brazil. Polygons represent the type of matrix that composed the cerrado boundaries, wherein squares represent pasture, triangles represent eucalyptus plantations, and circles represents sugarcane plantations

On each transect, we set eight sample points 25 m apart, with one pitfall trap at each point, in a total of 16 pitfalls per landscape. The trap consisted of a circular receptacle (1000 ml) partially filled with detergent and water (250 ml water in a 2% solution), which was saturated with salt to minimize the decomposition of captured individuals. At the center of this receptacle, a disposable cup (50 ml) held human feces as bait. The cup was secured by wire to the receptacle to prevent contact with the water solution. We collected ants at each sample point on three dates: November and December 2011 and January 2012. All ant individuals in the pitfall were identified to morphospecies. Although the use of human feces as bait in a pitfall is not a typical procedure for ant sampling (Martello et al. [2016, submitted]), devised this experimental design to sample scarab beetles), we used it at all sample points to guarantee that the samples sufficiently represented the differences among the treatments. We also aggregated the data from the three dates at each sampling point to improve the data resolution. Thus, for each distance from the edge, we had 14 replicates for sugarcane, 6 for pasture, and 10 for eucalyptus. We calculated the ant richness from each one of these replicates.

3.3.2 Analyzes

To assess how communities of ants change to edge distance, we hypothesized the ant richness and composition could have three different responses: discrete, gradual or non-response (null model). For composition analysis we performed a Non-metric Multidimensional Analysis (NMDS – stress = 0.212) and we use the first axis as a response species composition variable. We performed linear models for each possible response. In the discrete model the predictor was the type of environment that composed the ecotone (cerrado or matrix). Hence, the assumption of this model is that ant changes between the environments, but not along the distance from the edge. In gradual model the predictor was the distance from the edge as a continuous variable, assuming a linear change in the ant biodiversity along the ecotone, thus considering that ants are affect by edge effect. The null model was composed only by the linear intercept, assuming no changes in ant edge effect affects ant community.

Since we expected that the type of matrix that composed the ecotone would changes how ant respond to edge effect, we first assessed whether models with the type of matrix as predictor were better than models without it. In this sense, we created, in addition to those formers models, three linear models. Two of these had the same predictors of the previous one (type of environment or distance) with the interaction with the type of matrix. The third model had only the type of matrix as predictor, assuming that there are no differences in ant diversity along the ecotone, just between ecotones composed by different matrixes.

We used the corrected Akaike Information Criterion to assess the weight of evidence (wAICc) of each model and we considered as suitable models those that had wAICc>0.10. We assumed that the type of matrix had influence in the communities ant response to edge distance if at least one of the suitable models had the matrix as predictor.

Whether the type of matrix affected the response variable we performed additional analysis to assess how the ant communities respond to the edge distance in each ecotone. Thus, we separated the sample sites by matrix type and generated for each sub-dataset the four models related to the expected response to edge distance: discrete, gradual, segmented and null. Again, we used wAICc considering as suitable models those that had wAICc>0.10. In case of the null model be considered suitable, we assumed that there was no changes in the ant community along the ecotone.

3.4. Results

We collected 15,497 ants of 106 morphospecies from seven subfamilies, being Myrmicinae and Formicinae the richest ones. The richest genres were Dorymyrmex (7 species), Camponotus (7 species) and Pheidole (19 species). Grouping all samples by type of environments, we found 93 ant species in cerrado and 96 in matrix. Regarding each matrix that composed the ecotone, the pasture matrix had the greater richness (80 species), followed by cerrado adjacent to the sugarcane matrix (77 species), the sugarcane matrix (75 species), cerrado adjacent to the eucalyptus matrix (70 species), eucalyptus matrix (67 species) and cerrado adjacent to the pasture matrix (77 species).

For ant community richness located in all ecotones, the only suitable model was whose predicted that ants changes discretely to edge distance with an interaction with the type matrix (Table 1). Since the plausible model included matrix as predictors, we performed a secondary analysis of communities located in each ecotones composed of different matrices. The richness of ant communities in both three ecotones had the discrete model as suitable, but for some of those ecotones others models was also suitable. While in pasture the discrete model was only the discrete as suitable model, for sugarcane the gradual model was also suitable. By contrast, all models were suitable in eucalyptus ecotone, including the null model, and thus we assumed that ant richness did not change in eucalyptus ecotone (Table 1 and Figure 2). As well as in richness, the model discrete with interaction with the matrix was the only suitable considering all ecotones (Table 1). Once more we conducted we performed secondary analysis for each ecotone, wherein ants located in the sugarcane ecotone was predicted only by the discrete model and ants located both in eucalyptus and pasture ecotones had both discrete and gradual response to distance from edge (Table 1 and Figure 2).

Table 3.1. Corrected Akaike Information Criterion weight of models performed for richness and composition of ant community located in ecotones composed by cerrado (Brazilian savannah) and three different matrix. Values in bold represent suitable models.

Ecotone	Variable	Discrete	Linear	Discrete & Matrix	Linear & Matrix	Matrix	Null
Totall	Richness	0	0	**0.923**	0.077	0	0
	composition	0	0	**1**	0	0	0
Eucalyptus	Richness	0.2476	0.262	-	-	-	**0.462**
	composition	**0.833**	**0.161**	-	-	-	0.005
Sugarcane	Richness	**0.482**	**0.454**	-	-	-	0.065
	composition	**1**	0	-	-	-	0
Pasture	Richness	**0.907**	0.092	-	-	-	0.001
	composition	**0.379**	**0.621**	-	-	-	0

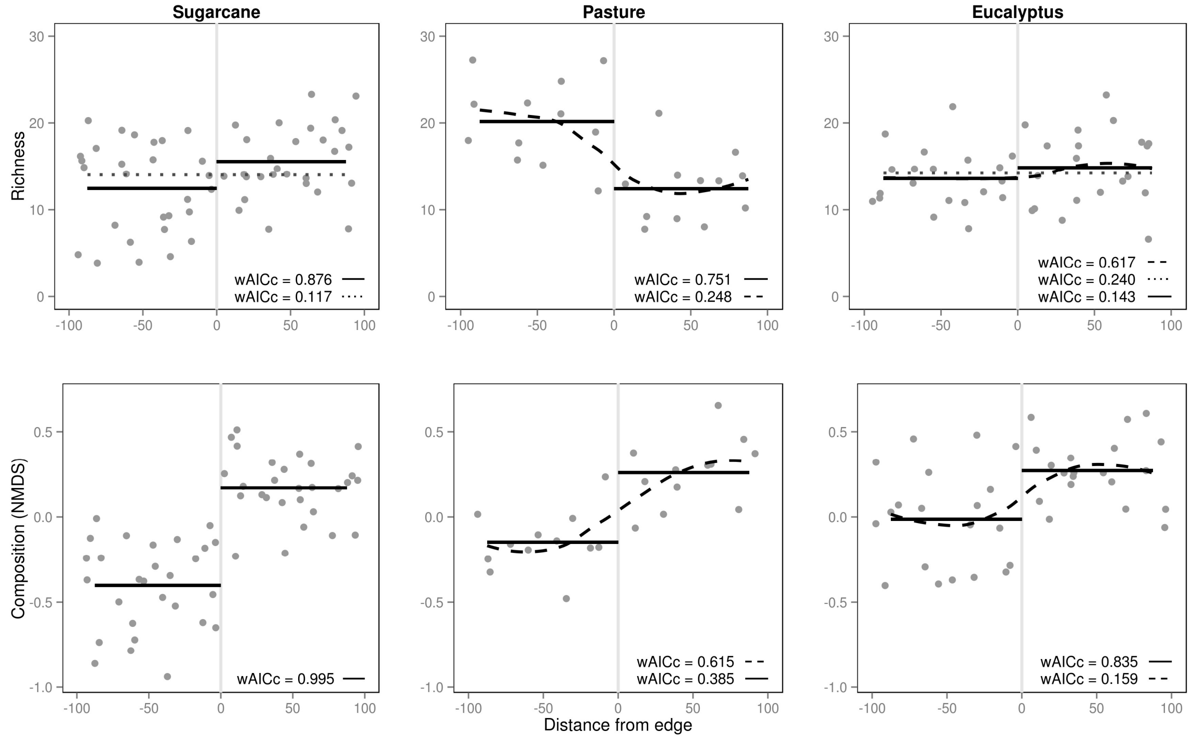

Figure 3.2. Species richness and composition of ant communities in transects located ecotones composed by cerrado (Brazilian savannah) and three matrix. Grey vertical lines represent the edge between the two environments that composed the ecotone. Black lines represent suitable model (AIC weight ≥ 0.10), wherein dashed lines represent discrete model, continuous line represent linear model and dotted line represents null model.

3.5 Discussion

Our results show that edge distance had a positive effect, a negative effect, or no effect on ant communities located in matrix-cerrado ecotones. This effect, as well in which way it occurred (discretely, gradually or segmented), were depend on the type of matrix, since this predictor was present in the best model for both response variables (richness and composition) and also the ant communities located in ecotones with different types of matrix showed different responses. Regarding all ecotones, for both richness and composition, the discrete model with matrix interaction was the only suitable model, suggesting that ant communities diversity changed between matrix and patch and also between different ecotones, but with no edge effect. For richness this result are similar to other studies that found no relationship between edge effect and ant richness (e.g. Daubers & Wolters 2004, Sobrinho & Schoereder 2007, Brandão et al. 2011). A common explanation to this no-effect result suggested by some authors is that edge effect could be affecting ant richness, but on a smaller scale to that used in their researches (50m) (Sobrinho & Schoereder 2007, Brandão et al. 2011). Here we used a scale that is the half of the scale used in those studies and, regarding all ecotones, we still not find relation of edge distance to ant richness. However, when we look for each ecotone separately it is became clear that for some of them models that assume the edge effect are also suitable. We found similar results for ant composition, wherein the unanimity of the discrete model regarding all ecotones was not found when we asses each ecotone separately. Hence, the disparity of the results found regarding all ecotones and for each of them highlights that the type of matrix are so important in edge effect studies as that, more than simply be considered in the experimental design, it should be assumed as specific for each ecotone, being the results interpreted in the light of the differences between the environments that compose the ecotone.

Concerning of each ecotone, the pool of suitable models for richness and composition was always different, in a way that an analysis considering the two variables together provided a more precisely picture of how edge distance affect ant community in each ecotone, than if we used only one variable. Eucalyptus plantation is a homogeneous environment dominated by just one plant species and has an expressive difference in phytophysionomy compared to cerrado (savannah). However, our analysis predicted that there were as many ant species in the eucalyptus forest as in the cerrado. This result can be related to the large amount of litter leaf that this forest presents (Ashton 1975), since there is a direct correlation between amount of litter leaf and ant richness (Campos et al. 2008, Silva et al. 2011). By contrast the composition of ant communities in this ecotone changed among the environments, and this change could be both gradual and discrete (the last one more likely). The impoverishment of litter leaf richness as well as the soil dryness and high concentration of substance allelopathic characteristic of these monocultures could decrease the richness some ant species that need resources that are reduced in this environment such as twigs in the litter leaf and soil mesofauna invertebrates (Souza et al. 2012). On the other hand eucalyptus forest shelters exotic generalist and leaf-cutting ant species and, this turnover of species between the communities along the distance from the edge explains the non-response of the richness in the eucalyptus-cerrado ecotone.

In both sugarcane and pasture ecotones one of the response variables was fitted just by the discrete model while the other variable by both non-null models. In these ecotones when both models were suitable the gradual model had similar or higher AIC weight than the discrete model. This pattern leave us a evidence that, for these ecotones, edge distance do affect the ant communities and we believed that the linear model would have higher AIC weight if the transect were longer. For the sugarcane ecotone the richness was the variable that respond both as discrete and linear, while ant composition change discretely along the ecotone. The evidence that richness changed gradually along this ecotone mask the abrupt difference in the ant composition in each environment that composed this ecotone. This suggest us that there are two ant communities in this ecotone, wherein edge effect acts increasing the richness of one of them (sugarcane) and decreasing of the other one (cerrado). These results were expected due to the severe impact on several ant communities of an ecotone composed of highly contrasting environments (Murcia 1995, Laurance et al. 2007, Noreika & Kotze 2012). By contrast, in the pasture ecotone the response variable explained by the discrete and linear model was the composition, while the richness only the discrete model was suitable. Here the communities tend to change gradually along the ecotone, but with an abruptly decreased of richness in the cerrado environment. This ecotone was the only that we found more species in the matrix than in the cerrado. We believed that this pattern occurred because pasture environments usually harbor exotic and open area ant species that are not found in native areas (Madureira et al. 2012). Beside that the absence of herbicides and the common presence of scattered trees in this environment that allow the survival of some ants species native from cerrado in this environment (Dias et al. 2012, Frizzo & Vasconcelos 2013).

This study underlined the influence of matrix type on ant communities' responses to the edge effect. We showed that the pool of possible responses of ant communities to edge distance varied among ecotones were different, suggesting that the response of ant to edge effect is specific for each ecotone. This assumption would help to explain the non-consensus about how ants respond to edge effect. The common assumption in some studies that there are no edge effect on ant communities comes generally from the fact richness could not be affect by the predictor. However, this result stems from the fact that human-mediated environments shelter exotics and open area ant species. In this sense, the response of species composition to the distance from the edge is key to understanding how ant communities change along the ecotone. We conclude that the type of response that ant communities show to edge distance are correlated to the type of matrix, especially because matrixes shelter exotic and generalist species. Once ants not only play a key role in several ecological process, but can also pose a potential a threat to natural environments as an invasive organism, the type of matrix that surround the patches must be explicitly consider in conservation and restoration strategies.

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CAPÍTULO 4: HOMOGENIZATION AND IMPOVERISHMENT OF TAXONOMIC AND FUNCTIONAL DIVERSITY OF ANTS IN EUCALYPTUS PLANTATIONS

Homogenization and impoverishment of taxonomic and functional diversity of ants in eucalyptus plantations

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4.1 Abstract

Eucalyptus is one of the uses that has experienced the greatest increases in extension in last decades, in which Brazil is the country with the biggest area of *Eucalyptus* plantations in the worland the largest exporter of eucalyptus cellulose. Due to its forest-vegetation phytophysionomy, eucalyptus plantations have been on the focus of a vigorous debate about their implications for conservation, especially when they are located in heterogeneous landscapes composed by patches of native forest and others anthropic land uses that do not have a forest-vegetation phytophysionomy. In this study we assess how eucalyptus plantations affect the taxonomic and functional diversities of ant communities. Sampling ant in abandoned and managed eucalyptus plantations with different ages and native rain forest we expected that abandoned eucalyptus plantationswould have higher functional and taxonomic diversities than those of managed plantations but lower located communities located in atlantic forest. Comparing taxonomic and functional diversities between sites, we expected that ant communities located in eucalyptus plantations, regardless of age and management should me more similar to each other than with forest ant communities. We assessed ant functional diversity using eight functional trais, which we also used to calculated three functional diversity indeces and the components of functional beta diversity. In three of eight functional traits communities located in native rain forest had higher values comparing to eucalyptus forest plantation. While managed eucalyptus had the lowest values of both taxonomical and functional indeces, abbandoned eucalyptus plantation had the same values of species richness and two functional indeces of communities than communities located native rain forest, but lower for functional richness. In addition, communities in abandoned eucalyptus plantations where more taxonomical and functional similar with those located in managed eucalyptus than with native rain forest communities. Our results indicate that eucalyptus plantations severely affected and had long-term impact on ant communities. On the other hand the unmanagement of these plantation approximate taxonomical and functionally ant communities from those located in native rain forests.

4.2 Introduction

The conversion of native habitat into human-modified land use reduces and fragments native habitats in small remnants, and it is expected to be one of the main drivers of biodiversity loss (Fahrig et al 2001, Foley et al. 2005). Among these conversions, plantation of trees (specially *Eucalyptus, Acacia* and *Pinus*) is one of the uses that has experienced the greatest increases in extension in last decades, reflecting the growing demand for timber and cellulose (Brockerhoff et al. 2008). Since 1980, the area of *Eucalyptus* plantations in Brazil has increased 17-fold (FAO 2006). Consequently, Brazil is the country with the biggest area of *Eucalyptus* plantations in the world, as well as the largest exporter of eucalyptus cellulose (FAO 2006). These plantations, which are mostly located in areas originally covered by rain Forest, are large monocultures that are managed with the use of ploughing, fertilizers, herbicides and are clear-cut harvested after 5-10 years of planting (FAO 2006). Due to its forest-vegetation phytophysionomy, eucalyptus plantations have been on the focus of a vigorous debate about their implications for conservation, especially when they are located in heterogeneous landscapes composed by patches of native forest and others anthropic land uses that do not have a forest-vegetation phytophysionomy (Brockerhoff 2008, Lindenmayer 2004). *Eucalyptus* plantations can be more effective than non-forest anthropic land uses in harbour native species (Borsboom et al. 2002, Klomp and Grabham 2002), increasing connectivity, i.e. the dispersion and the movement of native species (Lindenmayer and Hobbs 2004). Besides its commercial use, tree plantations with less intense management are also established to reduce erosion, combat global warming trough carbon sequestration, and facilitate land and vegetation rehabilitation (Lugo 1997, Brockerhoff et al. 2008). On the other hand, the high fertilizer and water demands, the release of allelopatic substances, as well as the intensively management characteristics of industrial-scale plantations of eucalyptus, cause severe impacts on soil structure and water supply, and reduce stability and biodiversity compared to native forests (Lugo 1997).

In the face of the duality of the value of eucalyptus plantations to conservation, it is necessary to go beyond the patterns of species richness, assessing their impact in ecological processes and species interactions. For instance, compared to native forest, tree monocultures have lower allocation and decomposition of organic matter (Lungo 1997), different species interactions - promoting the outbreak of some species, and different community structure (Suguituru et al. 2011). In this context, recent studies have shown that functional trait diversity is more strongly related to biotic interactions, abiotic filters and ecological processes than taxonomic patterns (Diaz e Cabido 2001). Thus, researchers have assessed functional diversity throughout several indexes, reflecting, for instance, the dominant trait values, the phenotypic space occupied, the distribution of abundances in this space, or the ecological resilience and resistance to environmental disturbance or invasion of communities (Garnier 2004, Villieger et al. 2008). Although most of these indices are based on the average trait values of species, ,recently some methods are starting to integrate intraspecific trait variation, better reflecting its effects on ecosystem functioning and species responses to environmental changes (Cianciaruso et al. 2009, de Bello et al. 2010, Violle et al. 2012).

In this study we assess how eucalyptus plantations affect the taxonomic and functional diversities of ant communities. Ants are key in a myriad of essential ecological processes, such as soil cycling and aeration, seed dispersion and decomposition of organic matter. In addition, ants are reasonably easy to collect and identify, have a good response to environment disturbances and reflect the impact of others invertebrates (Majer 2007), which makes them a good biodindicator of anthropic disturbances. These features makes ants a good model to study the effect of eucalyptus plantation on functional diversity, since in these agricultural areas ant communities can have both the same or lower values of taxonomic diversity, but with different composition that ant communities located in native forest (Mentone et al. 2011, Lapola & Fowler 2008). In this study we assess how eucalyptus plantations affect the taxonomic and functional diversities of ant communities. We sampled ants in eucalyptus plantations with different ages of management, as well as in abandoned eucalyptus plantations and a native rain forest. By comparing forests with different management regimes, we assessed the hypothesis that abandoned eucalyptus plantations, where natural regeneration of the vegetation is starting to take place, would have higher functional and taxonomic diversities than those of managed plantations, but still lower than those of Atlantic Forest. Comparing taxonomic and functional diversities between sites, we expected that ant communities located in eucalyptus plantations, regardless of age and management (active or abandoned) should me more similar to each other than with forest ant communities (homogenization due to management).

4.3 Material and Methods

4.3.1 Study area & sampling design

The study was conducted at the Alto Tietê and Itatinga River basins, in São Paulo, Brazil. Climate in the area is subtropical, with warm summers and mild winters. Mean annual temperature is approximately 20ºC and a precipitation of near 1500 mm evenly distributed throughout the year. The landscape consists in a mosaic of agricultural, urban areas, eucalyptus plantations under different management regimes, and native rain forest remnants. Even though eucalyptus plantations are usually cut every seven years, there are variations in management practices in the studied area, resulting in a mosaic of plantations of different ages, including abandoned ones evolving into native rainforest. Remnants of native rain forest of this region are categorized as Ombrophylous Dense Forest, which is characteristic from high precipitation regions. They are composed by evergreen phanerophytes, with an average height of 15 m, and a dense shrub vegetation of palms, lianas, epiphytes and ferns.

We selected randomly 25 sites distributed along four type of forest stands: a) recent eucalyptus cultivation, with seven years of *Eucalyptus grandis* monoculture uncut (n = 5); b) *Eucalyptus grandis* monocultures with an age of 28 years, already cut 3 times (n = 5); c) abandoned *Eucalyptus grandis* cultivations, left without management for the last 28 years prior this study (n = 5); and d) original native rain forest (n=10). The minimum distance between plots with the same treatment was 264m. In each site, we established a 250 m transect, where we systematically established six sampling sites, 50 m apart from each other.

In each sampling site we collected 1-m² of leaf litter and transferred it to mini-Winkler extractors (Belstemeyer et al. 2000) for 7 days. During that time, the ants dropped out of the mini-Winkler mesh sack and we collected them live in plastic cups with a humid sponge that was afterwards transferred to vials with 80% ethanol. All specimens were identified to morphospecies or species level (whenever possible) and deposited in the Mirmecological Laboratory of University of Mogi das Cruzes. Each sampling site was sampled once in the rainy season between Spetember 2010 and December 2011

4.3.2 Functional traits

We measured functional traits, selecting up to five individual of each species in each transect, depending on their abundance, for a total of 1395 individuals of 78 species. We selected eight morphological traits related to species ecological role to calculate functional diversity (Silva & Brandão 2014): head width, scape length, distance of compound eye to mandible insertion, eye length, minimum inter-eye distance, Weber's length, petiole height and hind femur length (Table 1). Weber's length is a surrogate of body size. All others traits were standardized with respect to this trait to avoid strong correlation with body size (this was done by diving each trait by Weber’s length). Afterwards, we log-transformed trait-values to reach normality, and standardized the values to mean of 0 and unit variance.

Table 4.1. Ant morphological traits used to calculate functional diversity and its functional significance.

Trait	Functional significance
Head width	Size of spaces through which ant can pass; mandibular musculature
Scape Length	Mechano and chemoreception
Distance of compound eye to mandible insertion	Performance for visual predatory species
Eye length	Indicates feeding behavior; predatory ants have smaller eyes
Interocular distance	Perception of habitat complexity
Weber's length	Indicative of body size; metabolic function and habitat complexity
Hind femur length	Related to species distribution inside the leaf-litter
Petiole length	Correlated to predaceous species behavior and performance

4.3.3 Taxonomic diversity

We calculated α taxonomic diversity of the ant community (species richness) of each site. To assess the taxonomic diversity between communities we computed β taxonomic diversity for all possible pairs of ant communities, as proposed by Baselga (2010). This procedure consists on estimating total β diversity using the Soresen dissimilarity index (βsor), and then decomposing it into two components: turnover β diversity, which is estimated through the Simpson dissimilarity index (βsim), and nested β diversity, which is the difference between βsor and βsim (βnes). These two components of β diversity reflect, respectively, species replacement (turnover) and the loss of species (nestedness) between sites, and they reveal the process involved in community assembly (Baselga 2010).

4.3.4 Functional diversity

We calculated the community weighted mean (CWM) of each functional trait using the trait mean value of each species weighted according to its local abundance; CWM reflects the dominant trait value of the community (Garnier et al. 2004). Then, we performed a Principal Component Analysis (PCA) using the mean trait values of each species for the eight traits; we adopted this decision because using values from individuals might have biased this analysis because of the different number of measured individuals between species. The PCA allowed us to synthesize the major axes of variations in the functional space and reduce the number of dimensions used to calculate functional diversity indices. Afterwards, we predicted the coordinates of all the individuals in the resulting PCA axes. We retained the first four axes of this PCA, which accounted for 86.37 % of the total variance in traits, and performed all subsequent analyses using those axes as indicators of the functional differentiation between species. For each ant community, we estimated functional richness (FRic), Rao's Q and functional redundancy (FRed). FRic represents the amount of functional trait space filled by the community (Villeger et al. 2008). FRed is the saturation of the functional space of the community and reflects the potential resilience and resistance of the community (Ricotta & Moretti 2011, de Bello et al 2007). Rao's Q expresses the pairwise functional differences between species of the community, weighted by their relative abundances (Botta-Dukat 2005). FRed is the saturation of the functional space of the community and reflects the potential resilience and resistance of the community (de Bello et al 2007). Finally, we calculated functional β diversity, which expresses the functional dissimilarities between all possible pairs of ant communities, We further decomposed this index in the turnover and nested components, representing the replacement of functional traits and the loss of common functional traits between communities, respectively (Villeger et al. 2013).

All functional diversity indexes were calculated using Trait Probability Distributions (TPD), which incorporates intra-specific variation, the multidimensional nature of traits, species abundances and probabilistic trait distributions (Carmona et al. 2016). The first step to calculate functional diversity with the TPD approach is to compute the Trait Probability Distribution of each species (TPDs), which reflects the probability of observing different trait values in a given species. This approach requires constructing a multidimensional probability density function using the individuals of each species. We opted to estimate these distributions using multivariate Gaussian distributions which require the average value of each species on the multidimensional trait space, along with their standard deviation (reflecting the variability in trait values among conspecifics) for each axis. We used two different strategies to estimate standard deviations, depending on the number of measured individuals of each species: a) for species with at least six measured individuals we estimated standard deviations using the data from the individuals of that species (48 species); b) for species with less than six measured individuals we used the average of the standard deviation of all the individuals of all species pooled (32 species). In the TPD framework, TPDs are used to estimate the trait probability distribution of each community (TPDc), which is the sum of the TPDs species in the community weighted by their relative abundance (which we estimated using frequencies of occurrence).

4.3.5 Data analysis

To assess the effect of eucalyptus management on ant diversity, we first conducted an one-way-ANOVA followed by a Tukey's post hoc analysis for α taxonomic and functional diversity indices (richness, FRic, FRed and RAO's Q). However, in the case of Rao, and because it presented non-normal residuals (Shapiro-Wilk test), we used the Kruskall-Wallis test followed by a non-parametric multiple comparison test (Siegel & Castellan 1988). We assessed the effect of eucalyptus managed on taxonomic and functional β diversity using PERMANOVA (Anderson 2001) for the total and components of beta diversity between sites, i.e. turnover and nestedness.

4.4 Results

There were significant differences in CWM between environments for only three of eight functional traits. Ant communities in rain forest had higher distance of compound eye to mandible insertion than those located in any eucalyptus plantations. Ant communities located in forests had greater interocular distances than ant communities located in unmanaged and 7 years old eucalyptus. For petiole length the only differences were between communities of managed eucalyptus with different ages, wherein the older ones had a smaller petiole on average (Figure 1).

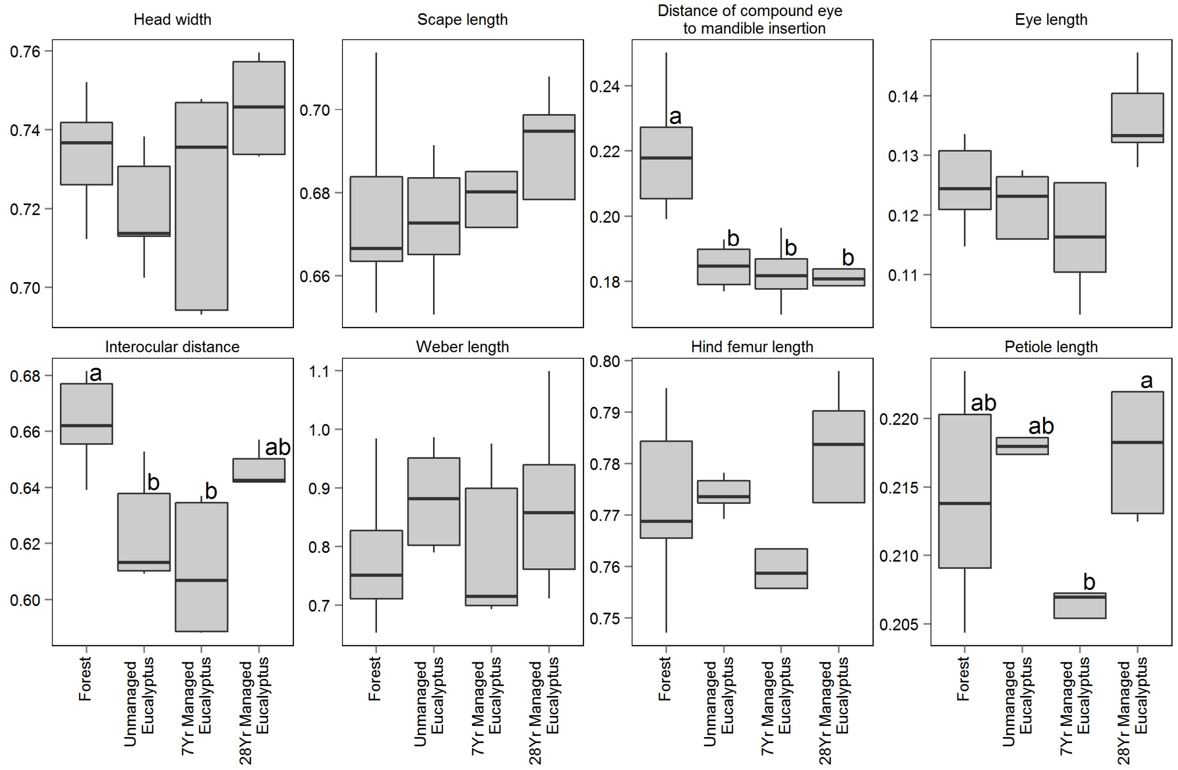

Figure 4.1. Mean and standard deviation of community weighted means of the eight functional of ant communities located in native rain forest, 28 years abandoned eucalyptus forestry, seven years commercial eucalyptus forestry and 28 years commercial eucalyptus forestry. Different letters between environments represent significant differences in the means assessed by a ANOVA and Tukey's Post-hoc analysis

Eucalyptus environments had a significant effect on α ant diversity, by decreasing both taxonomic and functional diversity. Native rain forests and unmanaged eucalyptus plantations had higher species richness than recent and old eucalyptus cultivations (Figure 2). Accordingly, native rain forests had the highest FRic values, whereas the different types of eucalyptus plantations did not differ in this aspect, regardless of their management regime (Figure 2). The lowest values of FRed were found in managed eucalyptus plantations, in contrast with native rain forests, which presented much higher values for this variable; in this respect, unmanaged eucalyptus plantations had intermediate values of functional redundancy (Figure 2). The results for Rao reflected the same pattern of species richness, with native rain forest and unmanaged eucalyptus having higher values than managed eucalyptus plantation (Figure 2).

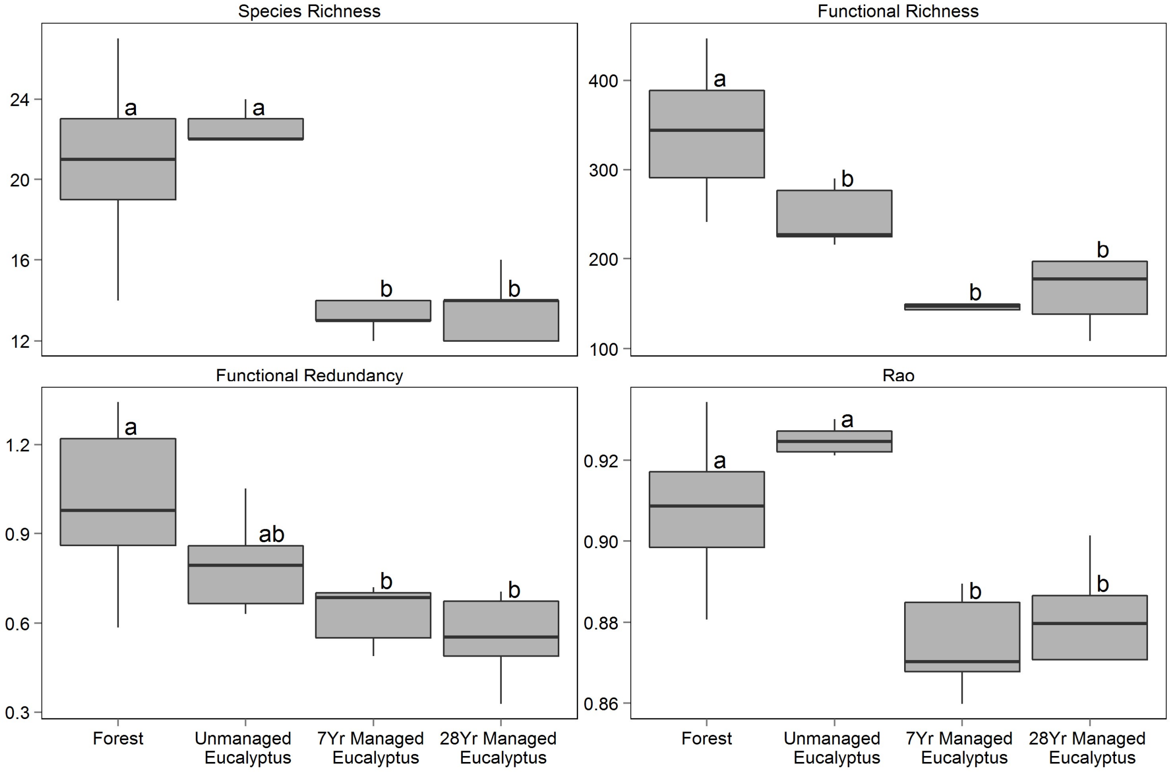

Figure 4.2 Mean and standard deviation of functional and taxonomic α diversity indexes of ant communities located in native rain forest, 28 years unmanaged eucalyptus forestry, seven years commercial eucalyptus forestry and 28 years commercial eucalyptus forestry. Different letters between environments represent significant differences in the means assessed by ANOVA and Tukey's Post-hoc analysis

PERMANOVA analyses showed that they were significant differences between environments in their taxonomic and functional β diversity, both for the total and decomposed components (table 2). Taxonomic and functional β diversities showed a similar pattern, revealing that the ant communities from native rain forest where especially different from those of eucalyptus environments, which were more similar among them (Figure 3). In taxonomic β diversity these high values were due mainly to the turnover in species composition (βsim), which accounted for the majority of the total β diversity. However, on functional β diversity this pattern was not so clear, so that the highest dissimilarities - between native rain forest and eucalyptus communities - were similarly contributed by the two β diversity components, i.e. both turnover in functional traits and nestedness.

Table 4.2 Results of PERMANOVA for total taxonomic and functional β diversities and its decomposed components

Beta diversity	Component	F model	R^2	p
Taxonomic	all	17.9	0.719	0.001
	turnover	15.219	0.685	0.001
	nested	7.626	0.521	0.001
Functional	all	17.146	0.71	0.001
	turnover	2.867	0.29	0.001
	nested	2.026	0.224	0.001

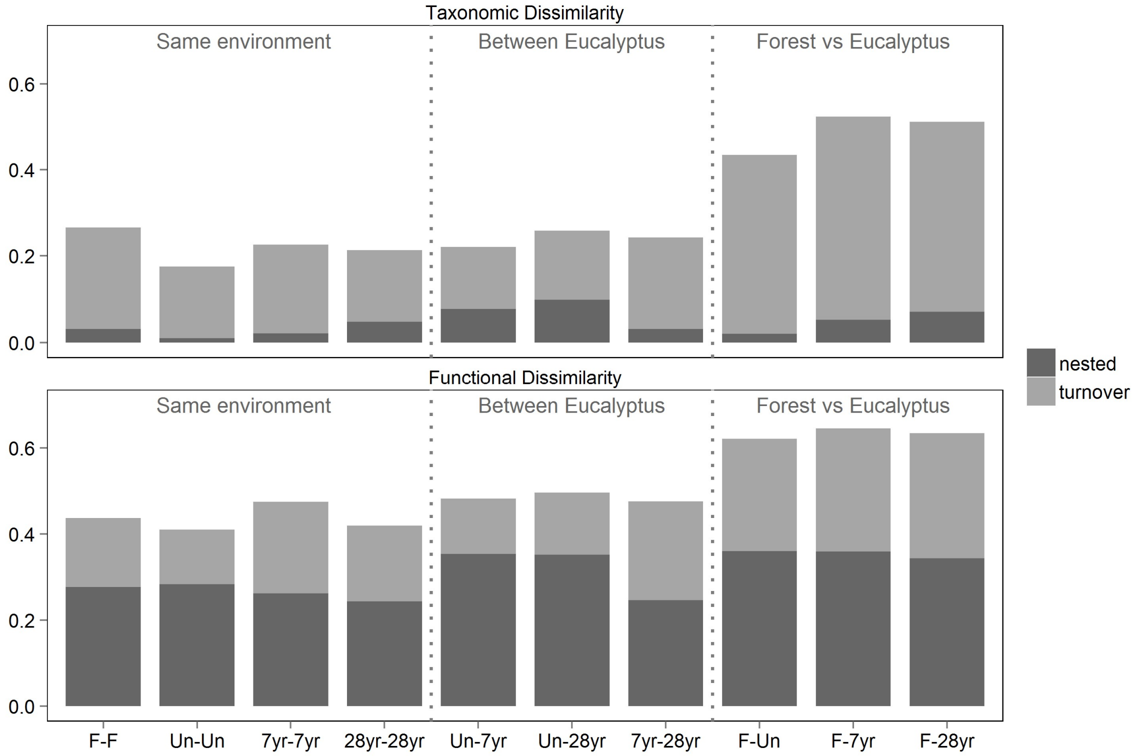

Figure 4.3. Mean of total, nested and turnover of functional and taxonomic β diversity between environments (F – native rain forest; Un - 28 years unmanaged eucalyptus plantations, 7yr – recent seven years commercial eucalyptus monoculture; 28yr – established 28 years commercial eucalyptus monoculture)

4.5 Discussion

Eucalyptus monoculture is a type of plantation that, because of its forest-like phytophysionomy, is often thought to harbour a significant portion of native species and consequently have an important value for ecosystem conservation. However, our results showed that these managed plantations reduced both taxonomic and functional diversity of ant communities (Fig. 2), and further drove to taxonomical and functional homogenization at the landscape scale (Fig. 3). On the other hand, unmanaged plantations emerged as a transition stage between managed plantations and the original forests, where values of alpha diversity were similar to those of native forests but a taxonomic and functional composition that were more similar to those of managed eucalyptus plantations. This results suggest that although ant communities from unmanaged eucalyptus plantations could eventually recover the original structure of native forests, the effect of management has a long-term impact in these communities.

We found that ants in native rain forest had longer distance of compound eyes to mandible insertion than in eucalyptus plantations. This trait is frequently considered to be related to foraging activities, with predator ants having higher values of both traits . This result reflects the low diversity of predator ants in eucalyptus plantations, which suggests a decrease in the abundance of small invertebrates that compose the soil mesofauna, the main food resource of these ants. Soil mesofauna is extremely sensitive to litter leaf structure, soil structure and composition (Goudin et al. 2010). Therefore, the application of fertilizers and pesticides that occur in eucalyptus plantations, as well as the impoverishment of litter leaf, the dryness and high concentration of substance allelopathic characteristic of these monocultures might affect the availability of this resource for ants. This result is in line with the interpretation of Majer (2007), who point ants as the best indicator of invertebrate assemblage composition in disturbed environments. Moreover, the simplification of the vegetation and litter leaf characteristics of eucalyptus monocultures, can also reduce substantially the diversity of arthropods and hinder ants coexistence (Sarty et al. 2006).

Compared to unmanaged plantations, managed eucalyptus plantations had much higher negative effect on the taxonomic and functional diversity of ant communities, as reflected by their low values for all of alpha-diversity indices. Managed eucalyptus plantations had approximately half of ant species than the native rain forest, which was reflected in a similar decrease in functional richness. At the same time, functional redundancy in managed eucalyptus plantations was lower than in the native rainforest, which suggests that the functional diversity of ant communities in plantations might be less resistant to species loss (de Bello et al. 2007; Mouillot et al 2014). Ant communities located in highly disturbed environments generally have a reduced number of species, with few species dominating the communities. These dominant species are better adapted to these special conditions, which allows them to find resources faster than other species and dominate these assemblages by numerical advantage, finally driving competing species to local extinction (Andersen 1997, Human & Gordon 1998). Hence, more than simply reducing species richness and the amount of functional trait space occupied by ant communities, managed eucalyptus plantations also changed the functional structure of the community. This interpretation is also supported by the low values of Rao in communities located in managed eucalyptus. According to Leps et al. (2006) this index represents the probability of two individuals of the community to be functionally different (Leps et al. 2006). Thus, its low values in managed eucalyptus plantations is an evidence that these communities are dominated by few species, since even with reduced similarity (functional redundancy) between species, the probability of finding two individuals with different functional traits is lower than in native rain forest.

In terms of functional diversity indices, unmanaged eucalyptus plantations rose as an intermediate type of forest. Ant communities in unmanaged eucalyptus had similar species richness and Rao values than communities in native rain forest, but occupied a smaller functional space (functional richness). This reduction in functional richness could be a consequence of the absence of some resources in the unmanaged eucalyptus, especially considering that although the recovery of the richness of vegetation communities in tropical forest can take up to 40 years, recovery of species composition can take longer than this (Dunn et al. 2004). Furthermore, the presence of eucalyptus trees could still be inhibiting, by allelopathy, the development of some plant species reducing the complexity of the environment, which might in turn reduce the availability of resources for ants, and the amount of functional space occupied by ant communities (Zhang et al. 2010).

Indicators of diversity at the local scale (alpha diversity) of ant communities from unmanaged eucalyptus plantations resembled those located in native rain forest, which suggests that the natural regeneration of rain forest in unmanaged eucalyptus plantations can attenuate the dominance that some species presented in managed eucalyptus plantations. However, ant communities in unmanaged eucalyptus plantations were taxonomically and functionally more similar to managed eucalyptus plantations as revealed by the patterns of beta diversity. This result highlights the importance that considering different aspects of diversity at different scales has for understanding the impacts of human disturbance on ecosystems (Mouillot et al 2013, McGill et al. 2015). Biologically, our results reveal that the simple abandonment of management of eucalyptus forests for almost 28 years was not enough for the ant communities to attain the characteristics of native rain forest. This results agrees with Bihn et al (2010), who suggested that the high functional diversity of ant communities in tropical forest is driven primarily by rare species, which are often more sensitive to habitat disturbance. Consequently, the taxonomic and functional structure of these communities can only be attained in primary forest. Lapola & Fowler (2006) also find that ant communities in forest fragments were more similar among themselves than to ant communities from eucalyptus plantations with restoration purposes with almost 100 years, which reinforces the idea that eucalyptus plantations have a long lasting impact in ant communities.

Our results suggest that the value of eucalyptus plantation for conservation is not in its forest-like phytophysionomy, but in how this plantation are (not) managed. The process of natural forest regeneration, known as "passive restoration", is actually one of the most frequent methods for ecosystem restoration, and it is cheaper than the artificial establishment of trees ("active restoration") (FAO 2006, Benayas et al 2008). Natural forest regeneration allows the natural colonization and secondary succession by any organisms that can disperse and establish in abandoned agricultural areas (Benayas et al 200). Although passive restoration can be faster and as efficient as active restoration , especially in tropical and humid temperate ecosystems, it is highly stochastic and dependent of organisms dispersal abilities, as well as biotic and abiotic conditions (Bullock et al. 2002, Benayas et al. 2008). In this sense, ceasing extracting activities in eucalyptus plantations may accelerate the restoration process because of the positive microclimatic effect of its canopy and the attraction of seed-dispersing fauna (Geldenhuys 1997, Neri et al. 2005). In this study, we found that after abandonment, ant communities in eucalyptus plantations started to recover the functional structure of native rain forest. This functional restructuring of ant community are probably a consequence of changes in trophic interactions involving ants. Most importantly, considering the key role of ants in ecological process such as soil ciclage and seed harvest and dispersion (Folgarait 1998), this restructuration might further accelerate the rate of recovery of the conditions of the whole system. In addition, the increase of ant diversity and vegetation complexity in unmanaged eucalyptus plantation (due to the presence of understory) can also control the direct and indirect damages that some ant species cause in restoration projects, such as the herbivory of leaf-cutting ants and the outbreak of homopterans that are protected by some generalist ant species (Philplot et al. 2010). This functional structure similarity that ant communities in unmanaged eucalyptus plantation had with communities located in rain forest offsets its lower functional richness as well as its similarity with ant communities in managed eucalyptus. In this sense, the implementation of restoration strategies such as the applied nucleation of native vegetation patches in unmanaged eucalyptus plantation may increase the diversity of resources for ants communities and consequently its functional richness (Corbin & Holl 2012).

In summary, we showed that the cultivation of eucalyptus can severely affect the taxonomic and functional diversity of ant communities, and that these impacts persisted to some degree after 28 years of unmanagement. On the other hand the passive restoration of native rain forest in unmanaged eucalyptus changed the functional structure of ant communities, increasing their functional diversity and redundancy of ant communities, approximating them to ant communities from native rain forests. Our findings suggest that although the establishment of eucalyptus plantations decrease the diversity of ants, long-term abandonment may help to restore their original properties as well as the role of these communities in essential ecological process.

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