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**Programa de Pós-Graduação em Ecologia e Conservação de Recursos
Naturais**

**RESPOSTAS DE BESOUROS SCARABAEINAE E FORMIGAS A
DISTÚRBIOS EM SAVANAS TROPICAIS**

Raquel Luiza de Carvalho

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**RESPOSTAS DE BESOUROS SCARABAEINAE E FORMIGAS A
DISTÚRBIOS EM SAVANAS TROPICAIS**

Tese apresentada à Universidade Federal de
Uberlândia, como parte das exigências para
obtenção do título de Doutora em Ecologia e
Conservação de Recursos Naturais.

Orientador

Prof. Dr. Heraldo L. Vasconcelos

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Carvalho, R.L. 2020. Respostas de besouros Scarabaeinae e formigas a distúrbios em savanas tropicais. Tese de doutorado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 133p

Os distúrbios antrópicos são um dos principais agentes de degradação dos ecossistemas, resultando em perdas da biodiversidade, funções ecológicas e serviços ecossistêmicos. Esses distúrbios ocorrem principalmente nos trópicos, por isso as savanas estão entre os ambientes mais ameaçados. O objetivo dessa tese foi compreender o efeito de diferentes distúrbios antrópicos sobre a fauna na savana brasileira e australiana, utilizando os besouros Scarabaeinae e/ou formigas como organismos de estudo. No primeiro capítulo, realizado na savana Brasileira, eu avaliei como a conversão de áreas de savana ou florestais em habitats manejados pelo homem (plantações de eucalipto, pastagens e monocultura de soja) afeta a estrutura funcional da comunidade dos besouros Scarabaeinae. Meus resultados demonstraram que para quase todas as métricas funcionais analisadas, foi encontrado diferenças entre os habitats naturais e os sistemas manejados. Entretanto essas diferenças foram muito mais acentuadas nas comparações que envolveram pastagens e plantações de soja, do que aquelas com as plantações de eucalipto. As comunidades de besouros tanto de savanas quanto de florestas apresentaram respostas bem similares à conversão para áreas de agricultura ou pastagens. Por outro lado, meus resultados indicam que a conversão das áreas naturais em plantações de eucalipto, teve um impacto maior para a comunidade de besouros da floresta, do que para a de savana. No segundo capítulo, realizado em pastagens no Brasil, eu avaliei como besouros, formigas e seus grupos funcionais respondem ao manejo da terra nas pastagens. Também verifiquei quais variáveis ambientais e de manejo melhor predizem as diferentes respostas desses grupos. Meus resultados demonstraram que besouros e formigas apresentaram respostas contrastantes ao manejo das pastagens. A estrutura da vegetação foi o principal direcionador na variação da comunidade de formigas, enquanto a comunidade de besouros respondeu principalmente a frequência no uso de parasitoides. No terceiro capítulo, eu realizei o primeiro estudo com besouros Scarabaeinae na savana tropical da Austrália, descrevendo a composição de espécies, preferência alimentar e a resposta da comunidade a diferentes regimes de fogo. A fauna amostrada compreendeu somente espécies do gênero *Onthophagus*, sendo que as fezes de cachorros foi a mais atrativa. A abundância dos besouros foi maior no tratamento com alta severidade do fogo, e foi negativamente correlacionada com a cobertura da vegetação arbórea. De forma geral, os resultados dessa tese sugerem que as mudanças do uso da terra afetam a estrutura funcional dos besouros, especialmente quando as florestas são substituídas por habitats manejados pelo homem. Também verifiquei que besouros e formigas forneceram diferentes indicações do impacto do manejo das pastagens sobre a biodiversidade. Por último, eu evidenciei que o fogo frequente promoveu a abundância de besouros através da manutenção de um ambiente mais aberto. Concluindo, os resultados dessa tese contribuíram para um melhor entendimento de como as comunidades de besouros e formigas são estruturadas e como elas respondem a diferentes impactos antrópicos em regiões tropicais de savanas.

Palavras-chave: distúrbios antrópicos, mudanças do uso da terra, pastagem, fogo, traços funcionais

Carvalho, R.L. 2020. Responses of dung beetles and ants to disturbances in tropical savannas. Tese de doutorado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 133p

Anthropogenic disturbances are one the main agents of ecosystem degradation, resulting in losses of biodiversity, ecological functions and ecosystem services. These disturbances occur mainly in the tropics; therefore, savannas are among the most threatened environments. The aim of this thesis was to understand the effect of different anthropogenic disturbances on the fauna of the Brazilian and Australian savannas, using dung beetles and/or ants as study organisms. In the first chapter, carried out in the Brazilian savanna, I evaluated the extent to which the conversion of savanna and forest areas into other land uses affects the functional structure of dung beetle assemblages. I found that for almost all functional metrics analyzed, there were significant differences between natural and man-managed habitats. However, these differences were much more marked in the comparisons involving pastures and soy plantations than those involving the eucalyptus plantations. Forest and savanna communities showed very similar responses to conversion to agriculture or pastoral lands. In contrast, my results indicate that conversion to tree plantations has a much greater effect on the forest than on the savanna community. In the second chapter, carried out on Brazilian pastures, I evaluated how the responses to pastoral land management vary between dung beetles and ants, and among functional groups within them. Then I evaluated what environmental and management variables best predict different responses. I found that beetles and ants show contrasting responses to pastoral land management. Ant communities are indicating the importance of vegetation structure, while beetles are indicating the impact of frequency of parasiticide use. In the third chapter, I reported on the first ecological study of dung beetles in the Australian tropical savanna, documenting species composition, food preferences and responses to different fire regimes. My samples were comprised entirely of nine native species of *Onthophagus*, and dog dung was the most attractive bait. Dung beetle abundance was highest under high fire severity and was negatively correlated with the cover of woody vegetation. Overall, the results of this thesis suggest that land-use changes affect the functional structure of beetle assemblages, and are more pronounced when forests are replaced by man-managed habitats. I also found that beetles and ants provide very different indications of the impact of pastoral land management on biodiversity. Finally, I highlighted that frequent fire promoted dung-beetle abundance through the maintenance of an open habitat structure. In conclusion, the results of this thesis contributed to a better understanding of how the communities of beetles and ants are structured and how they respond to different anthropogenic impacts in tropical savanna regions.

Key-words: Anthropogenic disturbances, land use changes, pastures, fire, functional traits

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Introdução geral

O distúrbio é considerado um fator chave para estruturar as comunidades biológicas (Rockström et al. 2009), e ele pode ser tanto de origem natural quanto antrópica. Os distúrbios naturais estão presentes em todas as comunidades (Souza 1984), o que significa que muitos ecossistemas estão em um estado de recuperação de distúrbios anteriores (Wu & Loucks 1995). Esses distúrbios são causados por agentes físicos (queimadas, inundações, secas, ventos) ou biológicos (pastoreio por animais, construção de ninhos), e afetam as comunidades por meio de mudanças na biomassa e na estrutura do habitat, assim como alteram a estrutura da comunidade (Scatena et al. 1996; Yamamoto 2000).

Os distúrbios antrópicos ocorrem quando partes pequenas do sistema original são removidas de maneira frequente (Singh 1998), ou quando quase ou toda a cobertura original de uma área é removida (Singh 1998). Alguns exemplos são a exploração de recursos madeireiros (França et al. 2017), a caça (Singh 1998), e a conversão de áreas florestais em áreas agrossilvipastoris (Gibb et al. 2010). Dessa forma, o efeito dos distúrbios antrópicos nos ecossistemas vai depender do tipo e da intensidade do distúrbio (Chazdon 2003), assim como da resiliência do ecossistema afetado (Holling 1973). Entretanto, de maneira geral, esses distúrbios alteram a estrutura trófica e a produtividade dos ecossistemas e ocasionam redução da biodiversidade e dos serviços ecossistêmicos (Villagra et al. 2009; Mitchell et al. 2015).

Os distúrbios antrópicos ocorrem principalmente nos trópicos (Romdal et al. 2013), e por isso as savanas estão entre os ambientes mais ameaçados, já que estas originalmente ocuparam 65% da África, 60% da Austrália e 45% da América do Sul (Huntley & Walker 1982). Por isso entender como as comunidades das savanas são estruturadas e como elas respondem aos distúrbios, é fundamental para estabelecer estratégias de conservação (Bengtsson et al. 2000).

Em grande parte da América do Sul, o bioma savana é conhecido como Cerrado, o qual ocupa uma extensão de cerca de 1.8 milhões de km² na região central do Brasil (Alho 2005). O Cerrado abriga diferentes fitofisionomias, compreendendo desde áreas abertas, com predomínio de vegetação herbácea, passando pelo campo sujo e cerrado sensu stricto, até formações florestais (Oliveira-Filho & Ratter 2002). Esse bioma é considerado um dos *hotspots* mundiais de biodiversidade, por possuir grande endemismo e diversidade de espécies vegetais e animais, além de alto grau de ameaça (Myers et al. 2000), já que mais de dois terços do bioma foi convertido, e a maioria dos seus remanescentes vegetais possui menos de 100 hectares (Bond & Parr, 2010). Embora o cerrado esteja passando por rápidas e drásticas transformações, esse ecossistema ainda é pouco estudado (Lehmann et al. 2009), principalmente se comparado às florestas tropicais (Braga et al. 2013; Carvalho et al. 2020).

A existência de áreas abertas no Cerrado facilitou a conversão desse bioma em áreas de monocultura (principalmente de grãos de soja) e pecuária (Silva 2000). Isso ocorreu principalmente a partir da década de 60, com a construção de Brasília, sendo que metade das pastagens brasileiras estão localizadas em áreas ocupadas originalmente pela vegetação do Cerrado (Silva et al. 2006). Nas últimas décadas, houve a intensificação na produção de bovinos nessas pastagens. Por exemplo, ocorreu a substituição de gramíneas nativas por gramíneas exóticas (Pivello et al. 1999) e isso resultou em sistemas mais intensivos de criação (Mapa 2003). Houve também aumento do uso de produtos médicos veterinários nos animais, o que pode afetar ainda mais a fauna de invertebrados que vivem nas pastagens (Lumaret & Errouissi 2002; Almeida & Louzada 2009; Imura et al. 2014; Verdú et al. 2015; Verdú et al. 2018). Nos dias atuais também já é comum a conversão da vegetação do Cerrado em plantações de eucalipto (Fernandes et al. 2016).

Em contrapartida, na savana Australiana, a pecuária se desenvolveu pouco. Porém existem planos para intensificar a produção de bovinos nessa região, incluindo a introdução de espécies forrageiras exóticas (Australian Government Department of the Prime Minister and Cabinet 2015). A savana ocupa principalmente a região norte da Austrália, e sua vegetação é dominada por espécies nativas de eucaliptos e arbustos (Scott et al. 2009). Embora as savanas experimentem incêndios frequentes ao longo de sua história evolutiva (Kershaw et al. 2002), portanto, fogo é considerado o principal distúrbio nesse ecossistema (Andersen et al. 2003), sendo que mudanças nos regimes de fogo, podem afetar a vegetação e a fauna (Andersen et al. 2003).

Uma das maneiras de avaliar os impactos antrópicos e suas consequências sobre a biodiversidade é com a utilização de bioindicadores (Heink & Kowarik 2010), já que utilizar toda a fauna não é logisticamente viável. Por isso, muitos estudos tem utilizado invertebrados como bioindicadores devido a rápida resposta desses organismos a mudanças ambientais, associado com a fácil amostragem e baixo custo de coleta (Gardner 2010). Dentre os invertebrados terrestres, besouros Scarabaeinae (Coleoptera: Scarabaeidae) e formigas (Hymenoptera: Formicidae) são amplamente utilizados como indicadores ecológicos para avaliar os impactos de distúrbios antrópicos. Eles são sensíveis às mudanças na estrutura do habitat (Braga et al. 2013; Philpot et al. 2010), e podem ser separados em grupos funcionais, o que facilita o entendimento de suas respostas aos distúrbios (Majer et al. 1983; Andersen 1995; Hallfater and Emonds 1982; Buse et al. 2015). Além disso, eles são diversos (7000 e 11700 espécies de besouros e formigas, respectivamente) (Schoolmeesters et al. 2010; Bolton 2003), e encontrados em quase todas as regiões, com exceção dos polos (Tarasov & Genier 2015; Wilson 1997). Os besouros apesar da ampla distribuição são particularmente abundantes nos trópicos,

especialmente em florestas e savanas (Hanski & Cambefort 1991). Esses organismos possuem várias características que são importantes para o funcionamento do ecossistema, e consequentemente realizam várias funções ecológicas, como a bioturbação do solo, a ciclagem de nutrientes, a dispersão secundária de sementes e o controle de moscas e parasitas intestinais (Nichols et al. 2008). Já as formigas são dominantes na maioria dos ecossistemas terrestres (Hölldobler & Wilson 1990) e estão envolvidas com a ciclagem de nutrientes, a regulação da população de insetos e o recrutamento de plantas (Wardle et al. 2011/ Del Toro et al. 2015; Kendrick et al. 2015).

Diante disso, essa tese visa compreender o efeito de diferentes distúrbios antrópicos sobre a fauna na savana brasileira e australiana, usando os besouros Scarabaeinae e/ou formigas como organismos de estudo. Por isso, essa tese foi dividida em três capítulos: no primeiro capítulo, realizado na savana brasileira, eu avaliei como a conversão de áreas de savana ou floresta em habitats manejados pelo homem (plantações de eucalipto, pastagens e monocultura de soja) afeta a estrutura funcional da comunidade dos besouros Scarabaeinae. No segundo capítulo, realizado em pastagens no Brasil, eu avaliei como besouros, formigas e seus grupos funcionais respondem ao manejo da terra nas pastagens. Também verifiquei quais variáveis ambientais e de manejo melhor predizem as diferentes respostas desses grupos. No terceiro capítulo, que foi realizado na savana australiana, eu documentei a composição de espécies, a preferência alimentar e as respostas da comunidade de besouros a diferentes regimes de fogo, utilizando plots experimentais que foram estabelecidos em 2004.

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Capítulo 1

Changes in the functional structure of dung-beetle assemblages following the conversion of forests and savannas into silvicultural, pastoral or agricultural lands in central Brazil

Formatado de acordo com a revista ‘Insect Conservation and Diversity’

Abstract

Community responses to conversion of the savanna and forest into other land-uses can vary, since these responses are often associated with the functional trait composition of each community. However, knowledge about the effect of the conversion of natural habitats on the functional structure of dung beetles (Coleoptera: Scarabaeinae) is still limited. Here, we used univariate (Community-weighted mean (CWM)) and multivariate metrics (Functional richness (FRic) and Rao's quadratic entropy (FDq) of functional diversity). Then, we evaluated the extent to which the conversion of savanna and forests into man-managed habitats (eucalyptus plantations, cattle pastures and soy plantations) affects the of dung beetle assemblages in the *Cerrado* biome of central Brazil. Dung beetles were sampled in 40 sites distributed across five-land use types: savannas (*cerrado sensu stricto*), semideciduous forest, eucalyptus plantations, pastures and soy plantations. Almost all dung beetle functional metrics varied between the natural and man-managed habitats, but these differences were more marked in the comparisons involving pastures and soy plantations than those involving the eucalyptus plantations. However, savanna and forest communities had similar responses to conversion to agriculture and pastoral lands, while the conversion into tree plantations has a much greater effect on the forest than on the savanna community. Savanna communities presented the highest functional richness and Rao's quadratic entropy, whereas forest community presented the lowest values. These metrics were positively correlated with taxonomic species. Although semideciduous forests had the smaller taxonomic richness, it presented the greatest number of exclusive species. In conclusion, our study demonstrated that the effects on the functional structure of dung-beetle assemblages it will depend on land use type and which was the original vegetation that was transformed.

Key – words: Cerrado, functional traits, functional diversity, Scarabaeinae, land-use change

Introduction

Understanding how biodiversity is influenced by changes in land use has been a long-standing issue in ecology and conservation (Lee 1985; Turner *et al.* 1995; Foley *et al.* 2005, Solar *et al.* 2015). These changes are recurrent in tropical regions where, increasingly, large natural areas have been replaced by high-intensity agriculture, pastures, or tree plantations (Romdal *et al.*, 2013; Carvalho *et al.*, 2020), resulting in severe losses of species diversity (Braga *et al.*, 2013; Queiroz *et al.*, 2017). However, the implications of such losses for ecosystem function are not always clear, because species richness and functional diversity are not always closely linked (Correa *et al.*, 2019).

Functional diversity refers to the variability of functional traits among species (Petchey & Gaston, 2006). Functional traits can be morphological, behavioral or physiological. They can be ‘response’ traits, influencing the growth, survival and reproduction of organisms (Violle *et al.*, 2007, Mouillot *et al.*, 2013), or ‘effects’ traits, influencing the ecological roles of organism (Mlambo 2014; Violle *et al.*, 2007). Functional traits can affect how organisms respond to habitat disturbances, and therefore the impacts of disturbance on ecosystem functioning (Derhé *et al.*, 2016).

Land-use changes can decrease the functional diversity of biological communities (Flynn *et al.* 2009), with this effect dependent on both the type and intensity of change and the characteristics of the original ecosystem (Flynn *et al.*, 2009). Many studies have assessed the impacts of land-use changes on forest communities, often finding that functional diversity is highly impoverished in areas that have been converted into agricultural or pastoral lands, but less so in those converted to tree plantations (Neita & Escobar, 2012; Gómez-Cifuentes *et al.*, 2017). In contrast, relatively few studies have evaluated how the conversion of open habitats such as

grasslands and savannas affects the functional diversity of plant and animal communities (but see Loiola *et al.*, 2010; Correa *et al.*, 2019), despite the prominence and threatened status of these habitats globally (Bond 2019). A better understanding on how open habitats respond to land use changes is fundamental for a more comprehensive evaluation of the resilience of these communities in the face of environmental modifications (Didham, 1996; Sterk *et al.*, 2013), and to better guide ecosystem managers (Demars *et al.*, 2002) and decision-makers (Cadotte *et al.*, 2011).

Dung beetles (Scarabaeidae: Scarabaeinae) play an important role in ecosystem functioning in both natural and managed ecosystems, as they are involved in the cycling of nutrients, in secondary seed dispersal, and in the control of dung-dwelling pests and intestinal parasites (Nichols *et al.*, 2008; Carvalho *et al.*, 2020). They are widely used as a focal taxon for assessing the effects of habitat disturbance on biodiversity (e.g. Gardner *et al.*, 2008; Braga *et al.*, 2013), given that some functional groups can be highly sensitive to habitat disturbances (Barrágan *et al.*, 2011; Nichols *et al.*, 2013; Beiroz *et al.*, 2018). For example, species that roll balls of dung ('rollers'), and diurnal species, are especially sensitive to hot and dry conditions (Escobar *et al.*, 2000; Nichols *et al.*, 2013), and thus can be more affected by the replacement of forest by agricultural systems than are species from other functional groups (Escobar *et al.*, 2000, Larsen *et al.*, 2008; Nichols *et al.*, 2013). Similarly, large-bodied species and resource specialists are particularly sensitive to the conversion of forest habitats into other land-uses (Gardner *et al.*, 2008; Nichols *et al.*, 2009). The conversion of natural habitats tends to eliminate species with disturbance- sensitive traits, while promoting the increase of species with traits that are tolerant to new conditions (Díaz *et al.*, 2013), and these changes, in turn, may have impacts on ecosystem functioning (Larsen *et al.*, 2005; Barragan *et al.*, 2011).

Several studies have investigated the impacts of changed land-use on the functional diversity of dung-beetle assemblages in tropical forest (Audino et al. 2014; Griffiths et al. 2016; Gómez-Cifuentes et al. 2017; Beiroz et al. 2018), but such impacts in savanna have received little attention. The faunal composition of dung beetle communities differs markedly between savannas and forests (Spector & Ayzama 2003; Krell *et al.*, 2003; Almeida & Louzada, 2009), which suggests that the responses of savanna dung-beetle communities to land-use changes may be different from those in forest. For example, communities in savannas have a dominance of small-sized species (Spector & Ayzama, 2003), including rollers with diurnal habits and nocturnal tunnelers (Krell *et al.*, 2003), whereas in forests tunnelers dominate numerically both during the day and the night (Krell *et al.*, 2003).

Here, we evaluate the extent to which the conversion of savanna and forest areas into other land uses affects the functional structure and diversity of dung beetle assemblages in the *Cerrado* biome of central Brazil. The Cerrado is dominated by savannas but also includes forests and grasslands (Oliveira & Marquis, 2002), and is a global hotspot for biodiversity conservation (Myers *et al.*, 2000). About two thirds of its original vegetation has already been converted to other uses, including especially pastures for cattle grow, large-scale agriculture (including especially soy plantations), and plantations of exotic trees (especially *Eucalyptus* spp.) (Cavalcanti & Joly, 2002; Bond & Parr, 2010). We used univariate and multivariate metrics of functional diversity, to evaluate the changes in the functional structure of dung-beetle communities when their native, savanna and forest habitats are converted into silvicultural, pastoral or agricultural lands.

Materials and Methods

Study area

The study was conducted in the rural region of Uberlândia, Minas Gerais state, in southeastern Brazil. According to the Köppen classification (Kottek *et al.*, 2006), the regional climate is Aw, with a dry winter (May to September) and a rainy summer (October to April). The annual mean temperature and precipitation are 22°C and 1,600 mm, respectively (Rosa *et al.*, 1991). The average elevation of the region is approximately 800 meters above sea level.

We sampled dung beetles at 40 sites, that were separated from each other by at least 2 km, comprising eight replicates each of the five major land-use systems in the region (Fig. 1): 1) Savannas. Locally known as *cerrado sensu stricto*, which is the dominant vegetation physiognomy in our study area, characterized by two distinct layers: an open woody layer composed of large shrubs and trees up to 8 m in height, and a ground layer composed of small shrubs, herbs and grasses (Oliveira-Filho & Ratter, 2002); 2) Semi-deciduous forest. A type of seasonal forest with a high diversity of trees (Oliveira-Filho & Ratter, 2002), occurring predominantly on nutrient-rich soils (Oliveira-Filho & Fontes, 2000); 3) Eucalyptus plantations. Plantations of approximately five years of age, and trees between 15-17 meters in height; 4) Pastures. Cattle pastures, planted with *Urochloa* spp. grasses and with the presence of scattered trees (ca. 5 trees > 1m in height per ha); 5) Soy beans. Extensive, high-input agricultural areas used for soy production with no-tillage (i.e., no soil manipulation is performed prior to planting). Soy plants were one month old and approximately 15 cm in height at the time of our sampling. The different land uses were highly interspersed (Fig. 1).

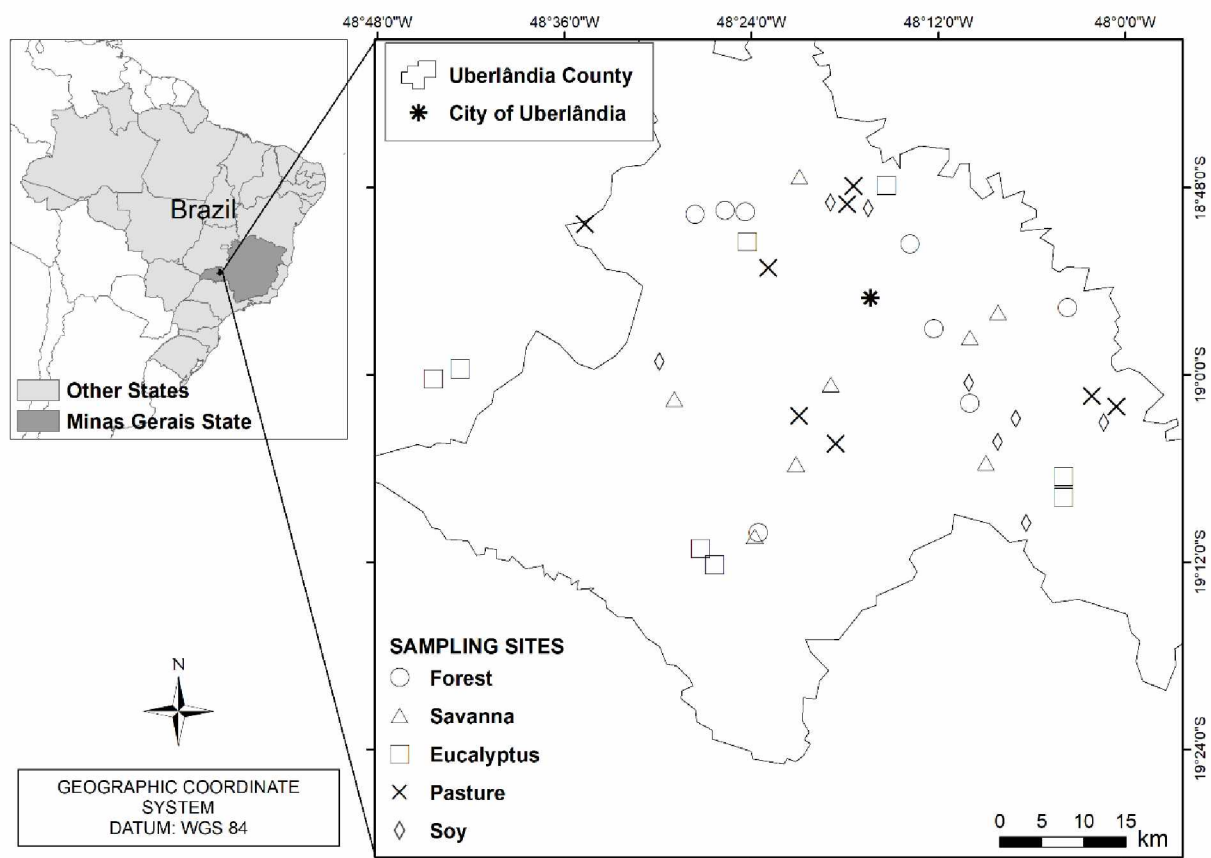


Figure 1 – Map of the study region, showing the location of the sampling sites in different land uses.

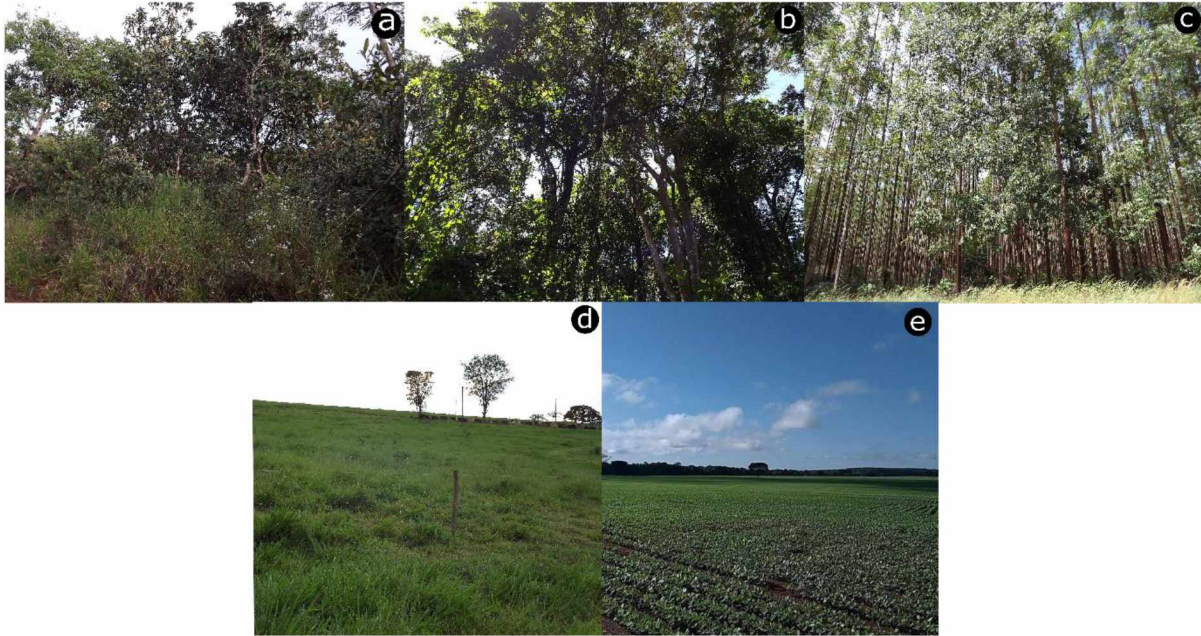


Fig. 2 – A-E. View of sites according to land-use type: (a) Savannas; (b) Semi-deciduous forest; (c) Eucalyptus plantations; (d) Pastures; (e) Soy.

Field sampling

Sampling was conducted in December 2017, during the local rainy season, within a 1-ha plot established in each site located at least 75 m from any other land use. We sampled dung beetles using baited pitfall traps. The traps consisted of plastic containers (19 cm wide, 11 cm in height), filled with 250 ml of a saline solution and detergent, and baited with 40 g of a mixture of pig dung and human feces (4:1 proportion, Marsh *et al.*, 2013). The bait was suspended in the center of the trap, and a 20 cm diameter plastic cover was suspended above ground to protect the trap from rain and direct sun. The traps remained in the field for 48 hours. We placed eight traps in each plot, at the corners and midpoints of the sides of each 100 x 100 m plot.

Trap catches were transported to the laboratory where all dung beetles were counted and identified to the lowest taxonomic level using the key of Vaz-De-Mello *et al.*, (2011), and with assistance from a dung-beetle expertise. Voucher specimens have been deposited at the Zoological Collections from Federal University of Uberlândia (UFU) and Federal University of Mato Grosso (UFMT).

Dung beetle traits

For each species, we measured four traits that are known to be sensitive to habitat modifications and of importance for the ecosystem services provided by dung beetles (Slade *et al.*, 2007; Nichols *et al.*, 2013; Griffiths *et al.*, 2016). These were: 1) Feeding strategy: species were classified as rollers (species that make a dung ball, that is rolled away from the dung pile), tunnelers (species that take a small portion of the dung and bury it directly below the dung pile) or dwellers (species that nest inside dung). 2) Body mass: We determined the mean body mass of each species by weighing up to 30 individuals of each species (when possible, the same proportion of males and females). The specimens were dried at 40 °C for 72 h (or until they reached a constant weight) and weighted in a 0.001 mg precision balance. The mean mass of each species was multiplied by its abundance in each pasture. 3) Dietary preference: Species were classified as coprophagous, necrophagous, frugivorous or predatory, as those using predominantly (>80%) or exclusively dung, carcass, fruits or insect prey as food resources, respectively. Species not falling in any of these four categories were classified as generalists. 4) Period of activity: The species were classified as crepuscular (active primarily at dawn or dusk), diurnal, nocturnal or active all day long. (Table S2). We obtained information about these traits from the data base of the Zoological Collection of the Federal University of Mato Grosso

(UFMT), under supervision from the dung-beetle specialist, Dr. Fernando Vaz de Mello. Information on feeding strategy was also based on Hanski & Cambefort (1991). Trait data were not available for all species (Feeding strategy: 10 species; Dietary preference: 10 species; Diel activity: 15 species; see Table S2).

Data analysis

Data from the eight traps were summed to obtain one value per sampling site. To calculate the functional metrics, we removed species for which we had no information for more than two traits; this was the case for 10% of the species, representing 0.57% of all the individuals collected. We calculated three different functional metrics — Community-weighted mean (CWM), Functional richness (FRic) and Rao's quadratic entropy (FDq) — that describe complementary aspects of the community (Ricotta & Moretti, 2011). CWM gives the mean value of a trait in a community, weighted by the relative abundance of each species carrying that trait (Violle *et al.*, 2007). The traits of dominant species exert large effects on many ecosystem services (Lin *et al.*, 2016; Prado-Junior *et al.*, 2016), such as dung removal and seed dispersal (Griffiths *et al.*, 2016). FRic is based on the total range of traits in a biological community (Mouchet *et al.*, 2010) and represents the amount of the functional space occupied by the species in a community (Villéger *et al.*, 2008). It acts as an indicator of multiple ecosystem services (Manning *et al.*, 2016). Rao's quadratic entropy calculates the mean dissimilarity of all individual pairs of species based on their functional traits, therefore representing a measure of functional dispersion, which is the probability of finding functionally different species in a community by chance. More functionally diverse communities have wider niche widths, and use resources more efficiently (Schnitzer *et al.*, 2011; Zhang *et al.* 2012). We used the “dbFD”

function in the “FD” package (Lliberté *et al.*, 2014) for calculation of the CWM and FRic metrics, and the “mpd” function in the “Picante” package (Kembel *et al.*, 2010) for the FDq. The CWM was calculated only for the most frequent traits, namely those that occurred in at least 30 sites.

We evaluated if each of the functional metrics of the dung-beetle communities found in the Eucalyptus plantations, cattle pastures, or soy plantations, differed for that found in the natural habitats (savanna or semideciduous forest) using generalized linear models (GLMs). The models were built using a Gaussian error distribution and identity linking function, except for those in which overdispersion of the residuals was detected and a Quasi-Poisson error distribution and a log-linking function was used. The significance of the models was evaluated using Type II sum of squares using the ‘car’ package (Fox *et al.*, 2011). Posteriorly, we performed contrast analyses test to determine which man-managed habitats were significantly different from each of the two natural areas. All the statistical analyses were conducted in R (R Core Team, 2018).

Results

We captured a total of 89 species and 46,479 individuals of dung-beetles. Fifty species (and 8,683 individuals) were found in forests, 57 (6,938 individuals) in savannas, 49 (4,047 individuals) in the eucalyptus plantations, 46 (12,012 individuals) in pastures and 54 (14,799 individuals) in soy plantations (Table S1) (Fig. 3). We obtained trait information for 80 species (90% species of the 89 species sampled), which represented 99.4% of the individuals sampled. Most (58%) species were classified as tunnelers, followed by rollers (20%), and dwellers (13%). The majority of the species were classified as coprophagous (65%), followed by necrophagous

(9%) and generalists (7%). The period of activity was determined for 74 species, of which most were nocturnal (50%), followed by diurnal (42%) (Fig.4).

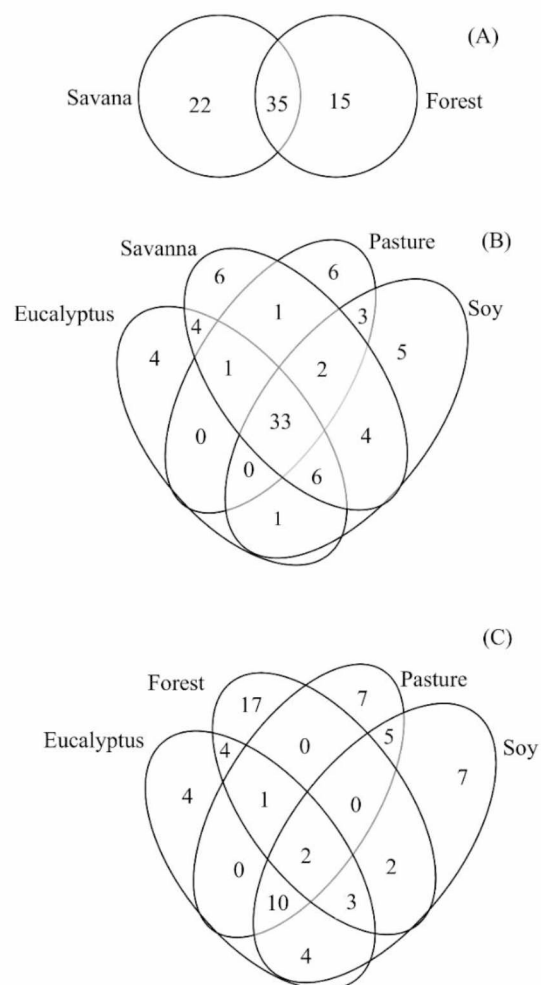


Figure 3- Venn-diagram showing the number of unique species found in each land use type and the number of species shared among each other. (A) Between savanna and forest only; (B) between savanna and Eucalyptus, pastoral or soy lands (C) between forest and eucalyptus, pastoral or soy lands

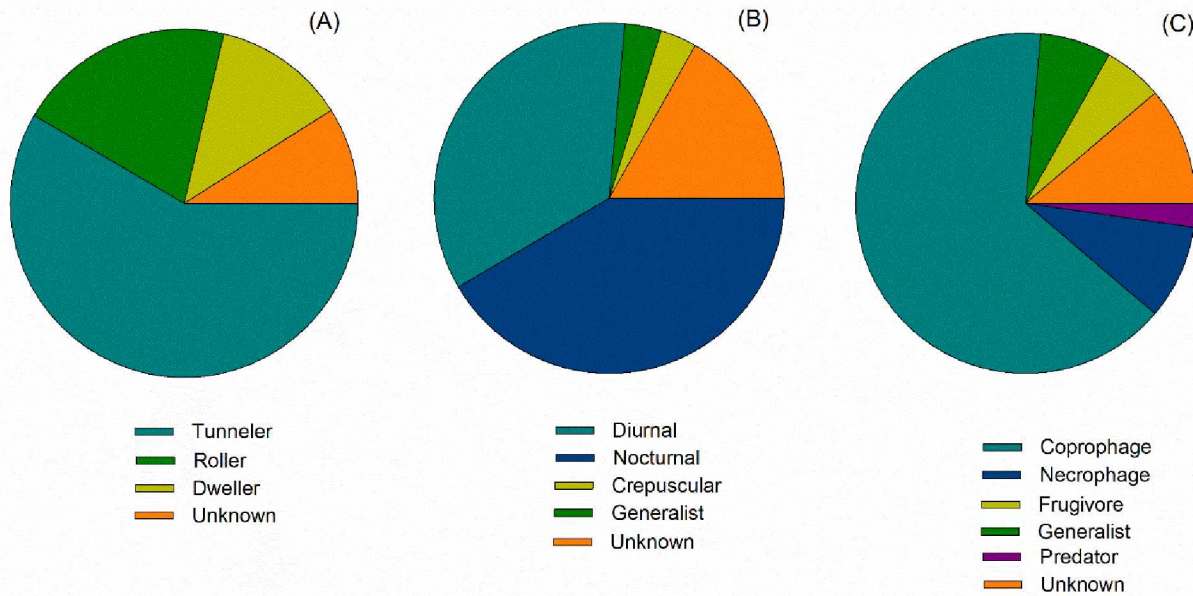


Figure 4 – Percentage of the total number of beetle species in relation to: (A) the feeding strategy, (B) the period of activity and (C) the dietary preference.

Functional metrics

Analysis of the community-weighted means (CWM) indicated that the dung-beetle communities sampled in the man-managed habitats (and most notably those in pastures or soy plantations) differed from those in natural habitats in terms of body mass ($F_{4,35} = 5.04$, $p < 0.01$), feeding strategies (Tunneler: $F_{4,35} = 5.04$, $p < 0.01$; Roller: $F_{4,35} = 9.11$, $p < 0.01$; Dweller: $F_{4,35} = 9.11$, $p < 0.01$), dietary preferences (Coprophagous: $F_{4,35} = 25.02$, $p < 0.01$; Necrophagous: $F_{4,35} = 2.85$, $p = 0.04$; Generalists: $F_{4,35} = 29.75$, $p < 0.01$) and diel period of activity (Diurnal: $F_{4,35} = 6.86$, $p < 0.01$; Nocturnal: $F_{4,35} = 3.06$, $p = 0.03$). Compared to savannas, dung beetle communities in pastures and soy plantations had significantly less body mass, and more dwellers and coprophagous individuals. In addition, communities in pastures and soy plantations had

significantly less tunnellers, generalists and necrophagous individuals than those in the savannas (Fig. 5A-I).

The same differences were detected when we compared the semideciduous forests to pastures and soy plantations, except that forests had less rollers and less diurnal beetles, whereas no significant difference was detected in regard to the CWM of necrophagous beetles (Fig. 5C, E, H). Beetle communities in the Eucalyptus plantations only differed from those in savannas in that it had significantly more generalists. Beetle communities in the Eucalyptus plantations differed from those in semideciduous forests by having significantly more rollers, dwellers and coprophagous, and less generalists and nocturnal beetles (Fig. 5C, D, F, G, L).

The conversion of natural areas into man-managed habitats affected both the functional richness (FRic) ($F_{4,35} = 7.83$, $p < 0.01$) and the Rao's quadratic entropy (FDq) ($F_{4,35} = 4.13$, $p < 0.01$) of the beetle communities. Savanna dung-beetle communities had a significantly greater FRic, whereas communities in forests a significantly smaller FRic than those in pastures, soy or eucalyptus plantations (Fig 6A). Communities in forests also presented a significantly smaller Rao's quadratic entropy (FDq) than did the communities in all the three man-managed habitats. The FDq of the savanna communities did not differ from those in Eucalyptus plantations and soy.

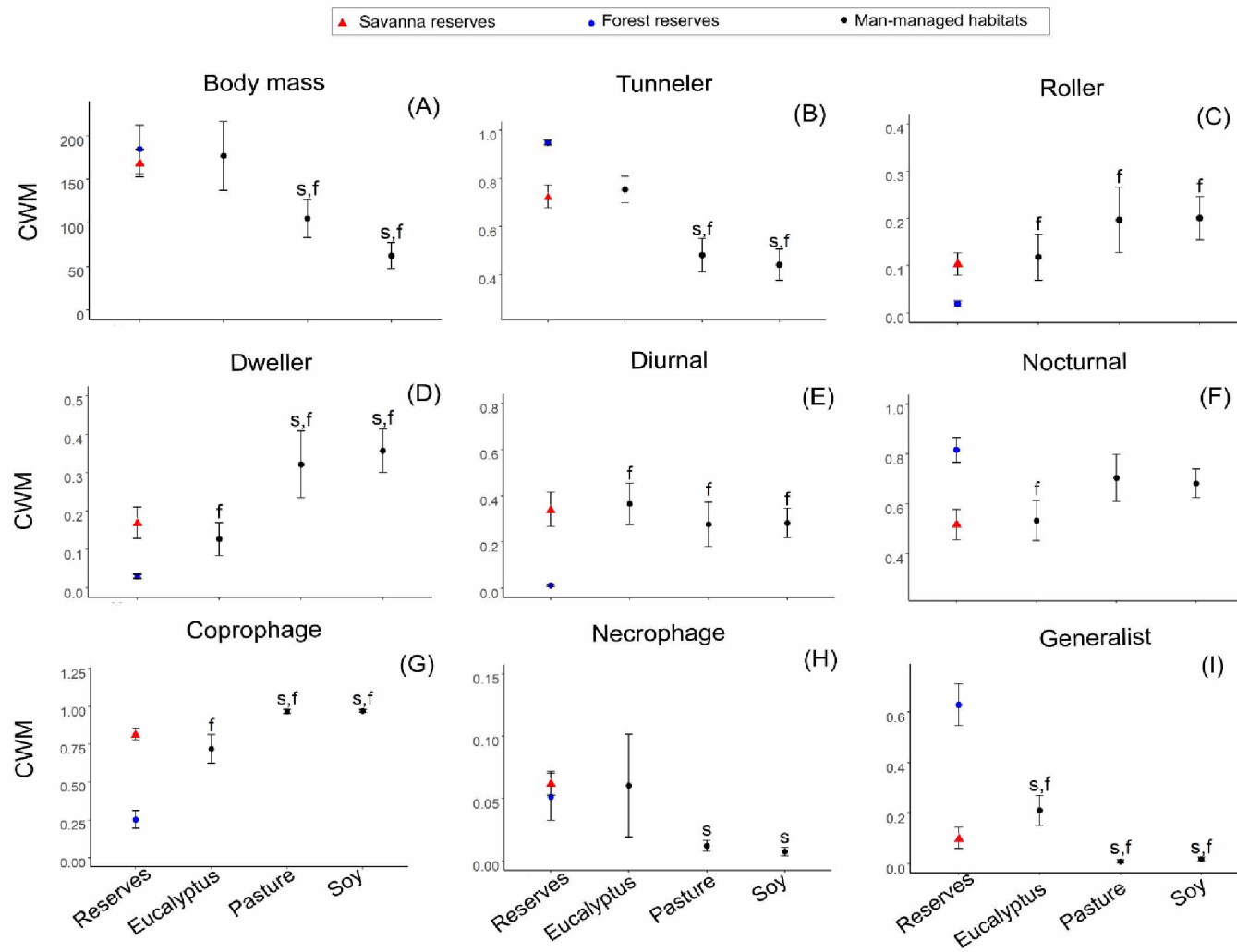


Figure 5 - Community weighted means of different functional traits of dung beetles in different land-use types: “Reserves” (savanna: red triangles or semideciduous forest patches: blue circles) , eucalyptus plantations, cattle pastures and soy plantations in central Brazil. Shown are mean values and their standard errors. The letters “s” and “f” are depicted when mean trait values in the silvicultural, pastoral or agricultural lands are significantly different from those found in the savanna and/or forest reserves, respectively.

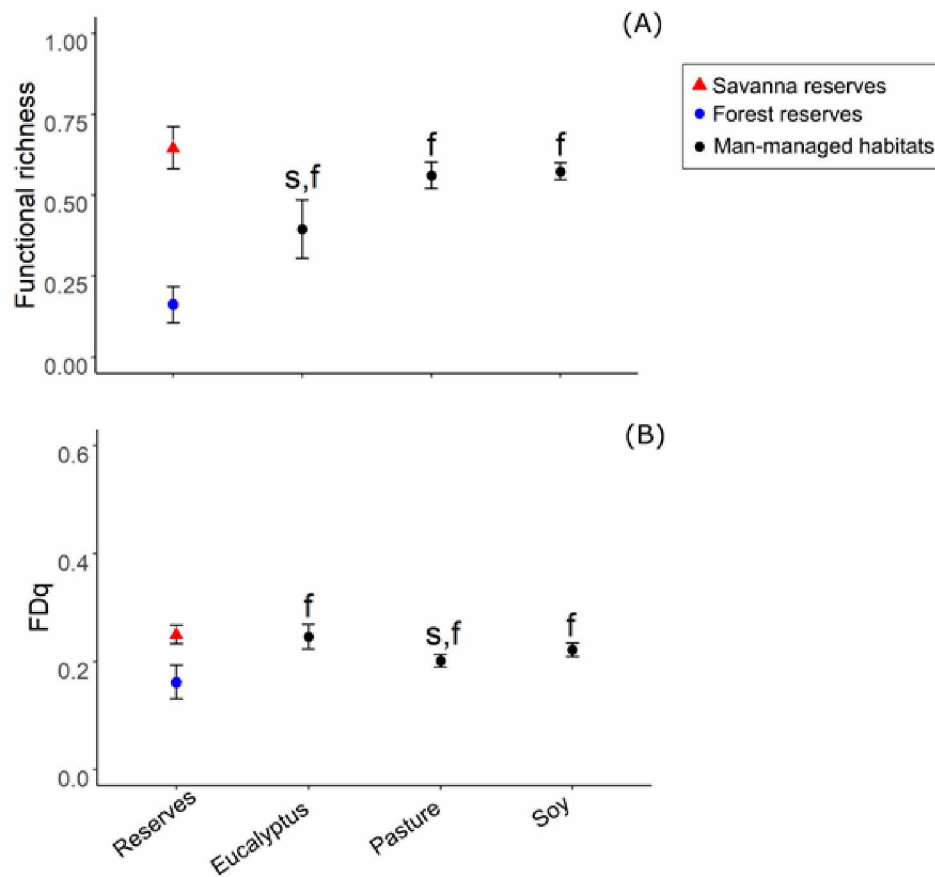


Figure 6- Functional richness (A) and Rao's quadratic entropy (FDq) (B) metrics of dung beetle assemblages in different land-uses: "Reserves" (savanna: red triangles or semideciduous forest patches: blue circles), eucalyptus plantations, cattle pastures and soy plantation. Shown are mean values and their standard errors. The letters "s" and "f" are depicted when mean trait values in the silvicultural, pastoral or agricultural lands are significantly different from those found in the savanna and/or forest reserves, respectively.

Discussion

Our study is the first study to compare how the conversion of savanna and forest into different man-managed habitats affects the functional structure of dung-beetle assemblages in a Brazilian savanna-dominated landscape. Our results demonstrate that, for almost all functional metrics analyzed, there were significant differences between the natural and man-managed habitats. However, these differences were much more marked in the comparisons involving pastures and soy plantations than those involving the Eucalyptus plantations. Surprisingly, forest and savanna communities showed some similar responses to conversion to pastoral or agriculture lands. In contrast, our results indicate that conversion to tree plantations has a much greater effect on the forest than on the savanna community.

The replacement of savanna and forests into pastoral or agricultural lands negatively affected the total body mass and that are tunnelers, perhaps as result of changes in temperature, humidity, and light (Davis *et al.*, 2001; Van Klink *et al.*, 2014), which seem to make species with these traits sensitive to habitat modification and extinction prone (Larsen *et al.*, 2005; Quintero & Haffter, 2009). The loss of large bodied and tunneler species resulted in a hyper-abundance of small-bodied and dweller species in the pastoral and areas agricultural, as also noted in previous studies (Nichols *et al.* 2007). Small-sized species have higher thermal tolerances than large-sized ones (Verdú *et al.*, 2006; Barragán *et al.*, 2011), whereas dwellers are considered competitively inferior to tunnelers (Krell *et al.*, 2003), since that dwellers do not moving dung. The replacement of large-sized, tunneller species by small-sized, dweller species may affect some of the ecosystem services provided by dung-beetles (Slade *et al.*, 2007; Nichols *et al.*, 2008), since that there is no functional compensation for all functions (Carvalho *et al.*, 2020). For example, small beetles, if sufficiently abundant, may be able to remove dung efficiently but, given their

small body size, they will excavate less soil (Braga *et al.*, 2013) and disperse fewer seeds (Andresen, 2002; Andresen & Feer, 2005; but see Nichols *et al.*, 2013) than large-bodied species. Dweller species nest inside the dung piles, and thus not dig tunnels (Halffter & Edmonds, 1982). Consequently, their contribution to soil excavation and seed dispersal is much less compared to the tunneller species.

Roller and diurnal species were not affected by the conversion of the savanna into agricultural areas; however, unlike some previous studies conducted in tropical forests (Larsen *et al.*, 2008, Nichols *et al.*, 2013), we found that roller and diurnal beetles were much more common in the man-managed habitats than in semideciduous forests. Similarly, Krell *et al.* (2003), reported that roller and diurnal species are relatively rare in forests of Africa. This is perhaps because roller species optimize their locomotor activity by external heating (Bartholomew & Heinrich, 1978), and thus may have a preference for more open habitats (even if anthropogenic), and a day-light activity (Bartholomew & Heinrich, 1978). Although rollers tend to be more effective than dwellers in performing ecological functions, they are less effective than tunnelers (Andresen, 2001; Slade *et al.*, 2007).

As also observed in forests elsewhere (Halffter *et al.*, 1992; Navarrete & Halffter, 2008), most dung beetles found in the semideciduous forests were nocturnal. However, nocturnal beetles were also abundant in pastures and soy plantations, indicating that the climatic conditions prevailing in these open areas at night are not limiting. Nocturnal beetles are recognized to be more important in playing ecological functions than diurnal beetles; however, their activities are complementary (Slade *et al.*, 2007). In all habitats we studied, the most common nocturnal species were tunnelers or dwellers (Table S1 and S2) (see also Krell *et al.*, 2003; Escobar, 2004; Slade *et al.*, 2007), perhaps because at night, rollers are virtually missing, enabling tunneler

and/or dweller species, which are competitively inferior to rollers, to use the available resources (Krell *et al.*, 2003).

Beetles with a generalist diet were much more common in forests than in savannas or any of the three man-managed habitats where coprophagous beetles dominate. Generalist species utilize a wide range of food resources, including dung, carrion, rotting fruits, and fungi (Hanski & Cambefort, 1991. Scholtz *et al.*, 2009), and thus the higher abundance of these species in forests may be related with differences in the availability of some of these resources, notably rotting fruits and fungi. The high abundance of coprophagous beetles – which are considered dietary generalists in relation to the dung type utilized (Frank *et al.*, 2018) – in the man-managed habitats, and especially in the soy plantations, is somewhat surprising. However, it may well reflect the fact that some of the species from the Cerrado mammal fauna (with approximately 194 species in total) actually thrive in agricultural lands (Garshelis, 2000; Gehring & Swihart, 2003).

The functional trait composition parameters of the dung-beetle community in eucalyptus plantation was much more similar to the savanna than to the forest community (Fig. 5A-I), which may well reflect the fact that eucalyptus plantations shared more species with the savanna than with the forest community (Fig. 2). These results contrast with those presented previously, and which suggest that eucalyptus plantations have higher a conservation value for forest than for open-habitat species (Gries *et al.*, 2012). However, meta-analysis performed by Nichols *et al.*, 2007 demonstrated that landscape context is important for understanding the responses of dung-beetles to habitat conversion. In particular, it has been shown that the spatial arrangement of the elements that make up the landscape can affect the persistence of dung-beetle populations in man-managed habitats (Shahabuddin *et al.*, 2005; Costa *et al.*, 2017). We suggest that as

savannas are much more important elements in the studied landscape than seasonal forests (in terms of the area originally and currently occupied by these types of vegetation) it has a greater potential to influence the composition of dung-beetle assemblages in eucalyptus plantations.

At the site level, both the functional richness and the Rao's quadratic entropy of dung-beetle communities was strongly and positively correlated with taxonomic richness (Figure S1). Not surprisingly thus, savanna communities, which presented the highest species richness, also had the functional richness of all the habitats we sampled, whereas the comparatively species-poor forest community presented a comparatively low functional richness. Similarly, inter-habitat variation in taxonomic richness may also help to explain why Rao's quadratic entropy (which measures the probability of finding functionally different species in a community by chance) was lower in forests than in the remaining habitats. In the Cerrado, seasonal forests occur only on soils of higher fertility or near to watercourses, and consequently they have a much smaller and sparser spatial distribution than do the savanna habitats (Oliveira-Filho & Ratter, 2002). Thus, the observed differences in taxonomic (and functional) richness between savannas and forests seems to be in agreement with the habitat amount hypothesis which predicts that taxonomic richness will increase with increasing habitat amount (Bailey *et al.*, 2010; Puttker *et al.*, 2011). This is not to say that semideciduous forests have a low conservation value, as in spite of the smaller taxonomic richness it presented the greatest number of exclusive species.

Overall, our results clearly indicate that land-use changes in the Cerrado have significant effects on the functional structure of dung-beetle assemblages. They also indicate that some of these effects are more pronounced when forests – rather than savannas – are replaced by cattle pastures or by soy or tree plantations, likely because fewer forest species are able to colonize the man-managed habitats. There is evidence that variation in the functional structure of

communities, including its functional richness, Rao's quadratic entropy, and range of existing traits, can affect the rate at which the ecosystem services provided by the organism embedded in these communities are delivered (Slade *et al.*, 2007; Manning *et al.*, 2016; Beiroz *et al.*, 2019). Dung-beetles provide many ecosystem services (Nichols *et al.*, 2008; Carvalho *et al.*, 2020), and in this sense future studies should evaluate the extent to which the differences observed in here between natural and man- managed habitats translate into differences in the functioning of these ecosystems.

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Supplementary information

Statistical Analyses

Linear models (assuming a Gaussian error distribution) were performed to determine the relationship between species richness and functional richness and between species richness.

Rao's quadratic entropy

Results

There was a positive relation between the species richness and the functional richness ($F_{1, 38} = 60.33$, $p < 0.01$, $r^2=0.61$), and between species richness and Rao's quadratic entropy ($F_{1, 38} = 12.88$, $p < 0.01$, $r^2 = 0.26$) (Figure S1 A-B).

Figure S1 – Scatterplot of the relationship between species richness and (A) functional richness, and (B) the Rao's quadratic entropy.

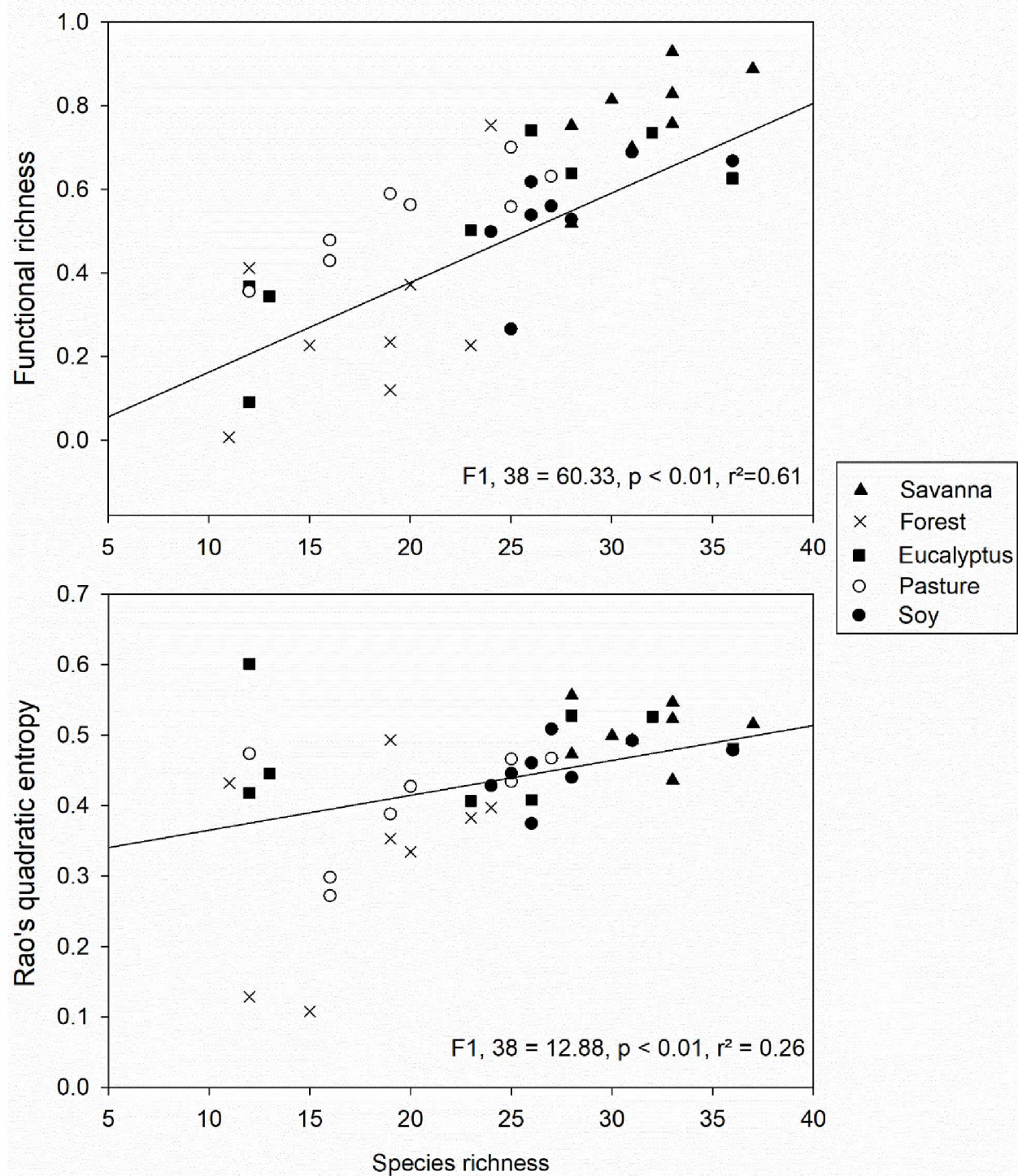


Table S1 - Number of individuals per species in different land-use types in the Brazilian Cerrado

(SA = savanna, FO = forest, EU = eucalyptus, PA = pasture, SO = soy).

Species	SA	FO	EU	PA	SO	Total number of individuals
<i>Agamopus viridis</i> Boucomont, 1928	273	0	15	612	2785	3685
<i>Anomiopus</i> sp.1	0	1	0	0	0	1
<i>Ateuchus</i> aff. <i>ovalis</i> (Boucomont, 1928)	3	9	0	0	0	12
<i>Ateuchus striatus</i> (Preudhomme de Borre, 1886)	10	9	34	23	83	159
<i>Ateuchus vividus</i> (Germar, 1823)	34	0	12	8	6	60
<i>Ateuchus volxemi</i> Borre, 1886	0	1	0	0	0	1
<i>Ateuchus</i> sp.1	57	0	19	0	27	103
<i>Ateuchus</i> sp.4	50	0	0	0	2	52
<i>Besourengea</i> sp.1	0	0	2	0	0	2
<i>Canthidium barbaticum</i> Preudhomme de Borre, 1886	523	0	0	19	0	542
<i>Canthidium decoratum</i> (Perty, 1830)	0	0	0	18	0	18
<i>Canthidium prasinum</i> Blanchard, 1846	0	0	0	1	0	1
<i>Canthidium refugens</i> Boucomont, 1928	594	1	28	84	27	734
<i>Canthidium</i> sp.1	0	1522	0	0	0	1522
<i>Canthidium</i> sp.2	6	1	51	14	22	94
<i>Canthidium</i> sp.3	0	0	0	2	0	2
<i>Canthidium</i> sp.4	0	1	0	0	0	1
<i>Canthidium</i> sp.5	0	1	0	0	0	1
<i>Canthidium</i> sp.6	10	0	0	2	9	21
<i>Canthidium</i> sp.7	33	0	20	21	203	277
<i>Canthon conformis</i> Harold, 1868	1	2	1	0	7	11
<i>Canthon dives</i> Harold, 1868	0	0	0	0	1	1
<i>Canthon histrio</i> (Lepelletier de Saint-Fargeau & Audinet-Serville, 1828)	0	0	0	1	0	1
<i>Canthon lituratus</i> (Germar, 1824)	18	0	3	3293	813	4127

<i>Canthon muticus</i> Harold, 1867	0	0	0	0	1	1
<i>Canthon ornatus</i> Redtenbacher, 1867	0	0	0	0	6	6
<i>Canthon piluliformis</i> Blanchard, 1843	94	0	5	178	12	289
<i>Canthon tristis</i> Harold, 1862	18	0	0	0	1	19
<i>Canthon virens</i> (Mannerheim, 1829)	99	0	15	2	7	123
<i>Canthonella</i> aff <i>barrerae</i> (Halfiter & Martínez, 1968)	0	1	0	0	0	1
<i>Chalcocopris inexpectatus</i> Rossini & Vaz-de-Mello, 2015	1	0	0	0	0	1
<i>Coprophanaeus cyanescens</i> Olsoufieff, 1924	114	169	52	18	0	353
<i>Coprophanaeus ensifer</i> (Germar, 1824)	94	21	32	6	1	154
<i>Coprophanaeus horus</i> (Waterhouse, 1891)	3	1	0	0	4	8
<i>Coprophanaeus pessoai</i> (Pereira, 1949)	15	0	0	0	12	27
<i>Coprophanaeus spitzii</i> (Pessôa 1935)	136	15	26	30	36	243
<i>Deltochilum Enceladus</i> Kolbe, 1893	3	63	8	0	0	74
<i>Deltochilum icariforme</i> Paulian, 1938	0	9	0	0	0	9
<i>Deltochilum pseudoicarus</i> Balthasar, 1939	32	0	25	0	1	58
<i>Deltochilum</i> aff <i>guyanenses</i> Paulian, 1933	0	8	0	0	0	8
<i>Deltochilum</i> aff <i>komareki</i> Balthasar, 1939	148	27	152	0	5	332
<i>Deltochilum</i> aff <i>sextuberculatum</i> Bates, 1870	0	22	0	0	0	22
<i>Dendropaemon convexus</i> Harold, 1869	2	3	0	0	0	5
<i>Dendropaemon flechtmani</i> <u>Génier & Arnaud, 2016</u>	0	1	0	0	0	1
<i>Dendropaemon nitidicollis</i> Olsoufieff, 1924	0	0	0	4	0	4
<i>Diabroctis mimas</i> Linnaeus, 1758	1	0	1	9	6	17
<i>Diabroctis mirabilis</i> (Harold, 1877)	149	0	20	0	6	175
<i>Dichotomius angeloi</i> (Nunes, Carvalho & Vaz-de-Mello, 2016)	0	4	0	0	0	4
<i>Dichotomius bicuspidis</i> (Germar, 1824)	6	108	2	0	10	126
<i>Dichotomius bos</i> (Blanchard, 1843)	121	9	191	228	402	951
<i>Dichotomius</i> aff <i>carbonarius</i> (Mannerheim 1829)	181	5354	207	25	4	5771
<i>Dichotomius cuprinus</i> (Felsche, 1901)	40	0	98	163	5	306
<i>Dichotomius glaucus</i> (Harold, 1869)	482	12	106	572	72	1244

<i>Dichotomius aff interstitialis</i> Luederwaldt, 1931	0	0	0	3	0	3
<i>Dichotomius nisus</i> (Olivier, 1789)	42	1	112	998	453	1606
<i>Dichotomius semianeus</i> (Germar, 1824)	0	0	0	5	78	83
<i>Dichotomius sexdentatus</i> (Luederwaldt, 1925)	0	0	2	0	0	2
<i>Dichotomius smaragdinus</i> (Perty, 1830)	13	3	22	110	2	150
<i>Dichotomius transiens</i> Lued, 1928	16	206	4	0	0	226
<i>Dichotomius aff zikani</i> (Luederwaldt 1922)	9	313	8	0	0	330
<i>Digitonthophagus gazella</i> (Fabricius, 1787)	0	0	0	1	2	3
<i>Eurysternus caribaeus</i> (Herbst, 1789)	0	218	2	0	0	220
<i>Eurysternus nigrovirens</i> Génier, 2009	3	0	1	0	0	4
<i>Eurysternus parallelus</i> Castelnau, 1840	0	7	0	0	0	7
<i>Eutrichillum hirsutum</i> Boucomont, 1928	72	1	2	1	3	79
<i>Eutrichillum</i> sp.1	0	1	0	0	2	3
<i>Genieridium bidens</i> (Balthasar, 1938)	407	5	326	981	3225	4944
<i>Genieridium cryptops</i> (Arrow, 1913)	537	9	28	18	732	1324
<i>Isocoprís foveolatus</i> (Luederwaldt, 1931)	9	0	0	0	0	9
<i>Isocoprís inhatus</i> (Germar, 1824)	2	1	206	34	207	450
<i>Malagoniella aenicollis</i> (Waterhouse, 1890)	0	0	5	0	6	11
<i>Ontherus apendiculatus</i> (Mannerheim, 1829)	151	9	161	241	286	848
<i>Ontherus azteca</i> Harold, 1869	186	83	189	9	182	649
<i>Ontherus ulcopygus</i> Génier, 1996	176	181	178	5	152	692
<i>Onthophagus buculus</i> Mannerheim, 1829	61	1	16	1734	721	2533
<i>Onthophagus hircus</i> Billberg, 1815	155	13	616	251	1710	2745
<i>Onthophagus haematopus</i> Harold 1875	0	35	0	0	0	35
<i>Onthophagus ptax</i> Erichson, 1842	143	0	69	685	1223	2120
<i>Oxysternon palaemon</i> (Castelnau, 1840)	892	7	379	63	105	1446
<i>Phanaeus kyrbyi</i> Vígors, 1825	183	2	94	9	6	294
<i>Phanaeus palaeno</i> Blanchard 1846	416	11	80	11	57	575
<i>Phanaeus splendidulus</i> (Fabricius, 1781)	0	0	2	0	0	2
<i>Sulcophanaeus menelas</i> (Castelnau, 1840)	0	0	0	0	55	55
<i>Trichillum adjunctum</i> Martínez, 1967	1	0	0	6	36	43

<i>Trichillum externepunctatum</i> Borre, 1886	48	0	12	1383	890	2333
<i>Trichillum heydeni</i> Harold, 1868	20	5	408	127	79	639
<i>Uroxys thoracalis</i> Balthasar, 1940	41	187	0	0	0	228
<i>Uroxys</i> sp.1	4	9	0	0	0	13
<i>Vulcanocanthon</i> sp.1	0	0	0	4	11	55
Species total	57	50	49	46	53	89
Total abundance	6938	8683	4047	12012	14799	46479

Table S2 – Traits of the 89 dung beetle species sampled in the Brazilian Cerrado.: body mass (mg), nesting behavior (dweller, tunneler and roller), diel activity (crepuscular, diurnal, nocturnal or all day) and dietary preferences (coprophage, necrophage, frugivore, predator or generalist). -- indicates unknown.

Species	Mean body mass (mg)	Nesting behavior	Diel activity	Dietary preferences
<i>Agamopus viridis</i>	2.77	roller	nocturnal	coprophage
<i>Anomiopus</i> sp.1	8.12	--	--	--
<i>Ateuchus</i> aff. <i>ovalis</i>	11.53	--	nocturnal	coprophage
<i>Ateuchus striatus</i>	12.91	tunneler	--	coprophage
<i>Ateuchus vividus</i>	17.22	tunneler	nocturnal	coprophage
<i>Ateuchus volxemi</i>	21.81	tunneler	nocturnal	coprophage
<i>Ateuchus</i> sp.1	16.63	tunneler	--	coprophage
<i>Ateuchus</i> sp.4	10.25	tunneler	--	coprophage
<i>Besourengea</i> sp.1	2.89	dweller	--	coprophage
<i>Canthidium barbaticum</i>	6.52	tunneler	nocturnal	coprophage
<i>Canthidium decoratum</i>	14.50	tunneler	diurnal	frugivore
<i>Canthidium prasinum</i>	8.13	tunneler	diurnal	coprophage
<i>Canthidium refugens</i>	5.65	tunneler	--	coprophage
<i>Canthidium</i> sp.1	3.15	tunneler	--	coprophage
<i>Canthidium</i> sp.2	43.11	tunneler	--	coprophage
<i>Canthidium</i> sp.3	28.23	tunneler	--	--
<i>Canthidium</i> sp.4	39.43	tunneler	--	--
<i>Canthidium</i> sp.5	21.81	tunneler	--	--
<i>Canthidium</i> sp.6	31.02	tunneler	--	--
<i>Canthidium</i> sp.7	31.49	tunneler	--	coprophage
<i>Canthon conformis</i>	24.20	roller	diurnal	generalist
<i>Canthon dives</i>	65.88	roller	diurnal	coprophage
<i>Canthon histrio</i>	78.96	roller	diurnal	coprophage

<i>Canthon lituratus</i>	4.48	roller	diurnal	coprophage
<i>Canthon muticus</i>	8.96	roller	diurnal	coprophage
<i>Canthon ornatus</i>	74.06	roller	diurnal	coprophage
<i>Canthon piluliformis</i>	5.21	roller	diurnal	coprophage
<i>Canthon tristis</i>	101.35	roller	diurnal	coprophage
<i>Canthon virens</i>	41.86	roller	diurnal	predator
<i>Canthonella aff barrerae</i>	11.70	--	--	coprophage
<i>Chalcocopris inexpectatus</i>	94.11	tunneler	nocturnal	--
<i>Coprophanaeus cyanescens</i>	719.26	tunneler	crepuscular	necrophage
<i>Coprophanaeus ensifer</i>	3534.71	tunneler	crepuscular	necrophage
<i>Coprophanaeus horus</i>	289.50	tunneler	diurnal	necrophage
<i>Coprophanaeus pessoai</i>	387.73	tunneler	diurnal	necrophage
<i>Coprophanaeus spitzzi</i>	593.09	tunneler	crepuscular	necrophage
<i>Deltochilum enceladus</i>	1047.87	roller	nocturnal	coprophage
<i>Deltochilum icariforme</i>	124.20	roller	diurnal	predator
<i>Deltochilum pseudoicarus</i>	490.39	roller	diurnal	coprophage
<i>Deltochilum aff guyanenses</i>	122.57	roller	diurnal	generalist
<i>Deltochilum aff komareki</i>	103.34	roller	nocturnal	generalist
<i>Deltochilum aff sextuberculatum</i>	80.61	roller	diurnal	generalist
<i>Dendropaemon convexus</i>	92.41	--	diurnal	--
<i>Dendropaemon flechtmanni</i>	227.31	--	diurnal	--
<i>Dendropaemon nitidicollis</i>	49.75	--	diurnal	--
<i>Diabroctis mimas</i>	528.16	tunneler	diurnal	coprophage
<i>Diabroctis mirabilis</i>	388.85	tunneler	diurnal	coprophage
<i>Dichotomius angeloi</i>	277.93	tunneler	nocturnal	coprophage
<i>Dichotomius bicuspis</i>	195.02	tunneler	nocturnal	frugivore
<i>Dichotomius bos</i>	420.39	tunneler	nocturnal	coprophage
<i>Dichotomius aff carbonarius</i>	132.13	tunneler	nocturnal	generalist
<i>Dichotomius cuprinus</i>	182.69	tunneler	nocturnal	coprophage
<i>Dichotomius glaucus</i>	179.93	tunneler	nocturnal	coprophage
<i>Dichotomius aff interstitialis</i>	168.33	tunneler	nocturnal	coprophage

<i>Dichotomius nesus</i>	295.55	tunneler	nocturnal	coprophage
<i>Dichotomius semianeus</i>	79.18	tunneler	nocturnal	coprophage
<i>Dichotomius sexdentatus</i>	327.45	tunneler	nocturnal	frugivore
<i>Dichotomius smaragdinus</i>	53.28	tunneler	nocturnal	frugivore
<i>Dichotomius transiens</i>	220.34	tunneler	nocturnal	frugivore
<i>Dichotomius aff zikani</i>	379.39	tunneler	nocturnal	coprophage
<i>Digitonthophagus gazella</i>	21.15	tunneler	nocturnal	coprophage
<i>Eurysternus caribaeus</i>	108.24	dweller	generalist	coprophage
<i>Eurysternus nigrovirens</i>	18.83	dweller	generalist	coprophage
<i>Eurysternus parallelus</i>	51.01	dweller	generalist	coprophage
<i>Eutrichillum hirsutum</i>	3.19	dweller	nocturnal	necrophage
<i>Eutrichillum sp.1</i>	6.21	dweller	nocturnal	necrophage
<i>Genieridium bidens</i>	6.33	dweller	nocturnal	coprophage
<i>Genieridium cryptops</i>	5.04	dweller	nocturnal	coprophage
<i>Isocopris foveolatus</i>	150.62	tunneler	nocturnal	coprophage
<i>Isocopris inhatus</i>	740.61	tunneler	nocturnal	coprophage
<i>Malagoniella aenicollis</i>	174.39	roller	nocturnal	necrophage
<i>Ontherus apendiculatus</i>	25.18	tunneler	nocturnal	coprophage
<i>Ontherus azteca</i>	61.52	tunneler	nocturnal	generalist
<i>Ontherus ulcopygus</i>	62.54	tunneler	nocturnal	coprophage
<i>Onthophagus bucus</i>	9.14	tunneler	diurnal	coprophage
<i>Onthophagus hircus</i>	7.04	tunneler	diurnal	coprophage
<i>Onthophagus haematopus</i>	6.69	tunneler	nocturnal	coprophage
<i>Onthophagus ptox</i>	4.67	tunneler	diurnal	coprophage
<i>Oxysternon palaemon</i>	200.41	tunneler	diurnal	coprophage
<i>Phanaeus kyrbyi</i>	294.68	tunneler	diurnal	coprophage
<i>Phanaeus palaeno</i>	225.46	tunneler	diurnal	coprophage
<i>Phanaeus splendidulus</i>	246.75	tunneler	diurnal	coprophage
<i>Sulcophanaeus menelas</i>	196.84	tunneler	diurnal	coprophage
<i>Trichillum adjunctum</i>	3.66	dweller	nocturnal	coprophage
<i>Trichillum externepunctatum</i>	2.91	dweller	nocturnal	coprophage

<i>Trichillum heydeni</i>	5.54	dweller	nocturnal	coprophage
<i>Uroxys thoracalis</i>	5.33	--	--	--
<i>Uroxys</i> sp.1	6.20	--	nocturnal	coprophage
<i>Vulcanocanthos</i> sp.1	2.28	roller	diurnal	coprophage

Capítulo 2

Understanding what bioindicators are actually indicating: linking disturbance responses to ecological traits of dung beetles and ants

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Abstract

Biological responses to a disturbance can vary among taxa, which challenges the use of bioindicators for representing biodiversity responses more broadly. Linking ecological traits to disturbance response helps clarify what different bioindicator groups are actually indicating, providing a mechanistic basis for predicting the responses of other taxa. Dung beetles and ants are ecologically contrasting but widely used bioindicator taxa. Here we link variation in dung beetle assemblages to body size and dung-feeding behavior, and variation in ant communities to habitat preferences, foraging behaviour and competitive dynamics, to clarify what dung-beetles and ants are indicating in terms of biodiversity responses to pastoral land management in a Brazilian savanna landscape. Dung beetles and ants were sampled at 24 pastoral sites that varied in grass cover, tree density, pasture age, cattle density, and frequency of parasiticide use. Community metrics (abundance, richness, composition, functional group composition) of both dung beetles and ants varied markedly with pastoral land management, but this variation was not correlated, or only weakly, between taxa. For dung beetles, abundance, biomass and richness were all best predicted by frequency of parasiticide use, whereas species composition was best predicted by cattle density. Tree density was the most important variable for explaining ant abundance (both total and of several functional groups) and was also significantly related to ant species composition. Dung beetles and ants provided different indications of the impacts of

pastoral management on biodiversity. However, by linking responses to ecological traits we were able to clarify what they were actually indicating. Leaf-cutter ants showed a similar response to dung beetles; collectively they are indicating an impact of parasiticide use on dung-feeders. The abundance of small-sized roller beetles was negatively related to grass cover; along with ants they are indicating the importance of vegetation structure. Such a linking of disturbance responses to ecological traits allows for more-robust predictions of likely responses of other faunal groups. We believe that such an approach provides a substantially improved foundation for the use of bioindicators in land management.

Key words: Brazilian savanna, functional groups, ivermectin, tree density, Scarabaeinae, Formicidae

Introduction

Biological responses to a disturbance can vary markedly among taxa (Barlow et al., 2007; Filgueiras et al., 2019), and this severely challenges the use of bioindicators (sensu McGeoch, 1998) for representing broader biodiversity responses (Lawton et al., 1998; Barlow et al., 2007). Given highly idiosyncratic responses, the extent to which any bioindication can be generalized is unclear. Moreover, bioindicator responses are often assessed using univariate metrics such as species richness, which often provides little insight into the ecological processes that drive biodiversity responses (Lawton et al., 1998).

An understanding of the relationship between ecological traits of species and environmental factors can reveal important insights into community dynamics and can substantially increase the predictive power of ecology (Neilly et al., 2018; Wong et al., 2018). A trait-based approach is therefore increasingly being applied to assessments of biodiversity

responses to disturbance (Wong et al., 2018). The variability of biodiversity responses to disturbance reflects differences in key ecological traits that mediate these responses. For example, terrestrial and arboreal reptiles have contrasting ecological drivers, which relate to ground-layer complexity in the former, and tree characteristics such as hollows in the latter (Bryant et al., 2012). As a consequence, terrestrial species are sensitive to the impact of livestock grazing, whereas arboreal species are not (Neilly et al., 2018). Similarly, among birds, ground-nesting or feeding species are most detrimentally affected by livestock (Bonnaud et al., 2009), whereas the abundance of birds can remain unaffected or even be promoted by pastoralism if trees are not cleared (Lusk and Koper, 2013). Terrestrial vs arboreal reptiles, and ground-active vs arboreal birds, thus provide very different indicators of biodiversity responses to grazing. However, linking of ecological traits to disturbance response provides a mechanistic basis for understanding what the bioindicator is actually indicating, and therefore what other taxa are likely to show similar responses to those of a bioindicator taxon.

Here we take the novel approach of linking the disturbance responses of two widely used bioindicator taxa, dung beetles (Coleoptera: Scarabaeinae) and ants (Hymenoptera: Formicidae), to their ecological traits in order to clarify what the bioindicators are actually indicating in terms of ecological responses to disturbance. Dung beetles are broadly distributed across the tropics (Hanski and Cambefort, 1991), where they play a key role in nutrient cycling through the removal and burial of vertebrate (mostly mammalian) dung (Nichols et al., 2008). The consumption and relocation of dung by Scarabaeinae beetles can also play other important ecological roles, such as soil excavation, secondary seed dispersal, and the control of dung dwelling pests and intestinal parasites (Nichols et al., 2008). Ants are an ecologically dominant faunal group in most terrestrial ecosystems (Hölldobler and Wilson, 1990), contributing a

substantial proportion to total terrestrial faunal biomass and playing fundamental roles in soil development, nutrient cycling, the regulation of insect populations, and plant growth and recruitment (Del Toro et al., 2015). Dung beetles and ants have very different environmental drivers and consequently show very different responses to disturbance (Filgueiras et al., 2019). They therefore can be expected to indicate very different things when used to assess the ecological impacts of disturbance, which they frequently are (Andersen and Majer, 2004; França et al., 2017).

Both dung beetles and ants are frequently classified into functional groups based on ecological traits that facilitate an understanding of their responses to disturbance (Andersen, 1995; Buse et al., 2015). This provides a basis for linking ecological traits to disturbance responses *within* both taxa, thus gaining a more-refined understanding of what they are actually indicating. Dung beetles are commonly classified into functional groups based on body size and their feeding and nesting behavior, traits that have important implications for ecosystem functioning (Hanski and Cambefort, 1991; Barragán et al., 2011). These groups can have markedly different environmental associations. For example, small-sized species tend to have higher thermal tolerances and lower humidity tolerances than large-sized species (Barragán et al., 2011). Similarly, roller species are typically more sensitive to changes in vegetation cover than are other feeding groups (Escobar, 2004). The different dung-beetle groups can, therefore, be expected to provide different indications of disturbance responses.

Ants are frequently classified into functional groups based on their responses to environmental stress and disturbance, and these groups also have markedly different environmental associations (Andersen, 1995, 1997). For example, Dominant Dolichoderinae and

Hot-climate specialists strongly prefer open habitats, Cryptic species, Subordinate Camponotini and Specialist predators have specialized habitat and resource requirements, and Epigaeic generalists and Opportunists occur in a wide range of environments (Hoffmann and Andersen, 2003). These different functional groups likewise can be expected to provide very different indications of disturbance responses (Escobar, 2004; Andersen, 2018).

In this study we link environmental responses of dung beetles and ants to their ecological traits for clarifying what they are actually indicating in the context of pastoral land management in a Brazilian savanna. Grazing by livestock is a dominant land-use throughout the world (Reid et al., 2008), and can have a marked impact on the structure of faunal habitat (Eldridge et al., 2011). In addition, intensive pastoral management often involves the use of veterinary medical products (VMPs; especially ivermectin) for parasite control (Lumaret et al., 1993), and these products are highly toxic if consumed by non-target insects (Floate et al., 2005; González-Tokman et al., 2017). Our study addresses two specific questions: (1) How do responses to pastoral land management vary between dung beetles and ants, and among functional groups within them?; and (2) What environmental and management variables best predict different responses? The results will allow disturbance responses to be linked to ecological traits, and thus enable a better-informed assessment of how other taxa are likely to respond.

Material and methods

Study area

The study was conducted on cattle farms located in the rural outskirts of Uberlândia (18° 56' 38" S 48° 18' 39" W; approximately 900 meters above sea level), Minas Gerais, in the Brazilian cerrado (savanna; Araújo and Haridasan, 1997). The region is characterized by a

tropical climate with a cooler dry season (May to September) and a warmer wet season (October to April). The mean annual temperature and precipitation are 22°C and 1,600 mm respectively (Rosa et al., 1991). The Cerrado is considered a biodiversity hotspot (Myers et al., 2000), and has been extensively converted to agricultural use, including cattle ranching (Sano et al., 2010), which is the dominant land use in the region (INDI network data, 2017). Throughout the study region, native grasses have been largely replaced by exotic species (primarily *Urochloa* spp.) to increase carrying capacity (Pivello et al., 1999), but the taller trees and those of economic importance have generally been retained (Frizzo and Vasconcelos, 2013). More recently, there has been a progressive replacement of traditional extensive grazing in favour of intensive systems (MAPA, 2003), such that the region now has some of the largest cattle herds in Brazil. Intensification has involved an increase in the use of veterinary medical products, mainly based on ivermectin, doramectin and abamectin, which are highly toxic to non-target invertebrates (González-Tokman et al., 2017).

Sampling was conducted within a 4-ha plot in each of 24 pastures (Fig. 1) representing variation in grass cover (43 - 100%), tree density (0 - 40.8/ha), pasture age (3 - 100 yrs), cattle density (0.4 - 389 head/ha), and frequency of VMP use (2 - 18 times/yr) (Table S1). All pastures were dominated by exotic grasses (*Urochloa decumbens*), and they were separated from each other by at least 3 km. They were located on farms ranging in size from 14 to 950 ha, which represents the size range of farms in the region (IBGE, 2018).

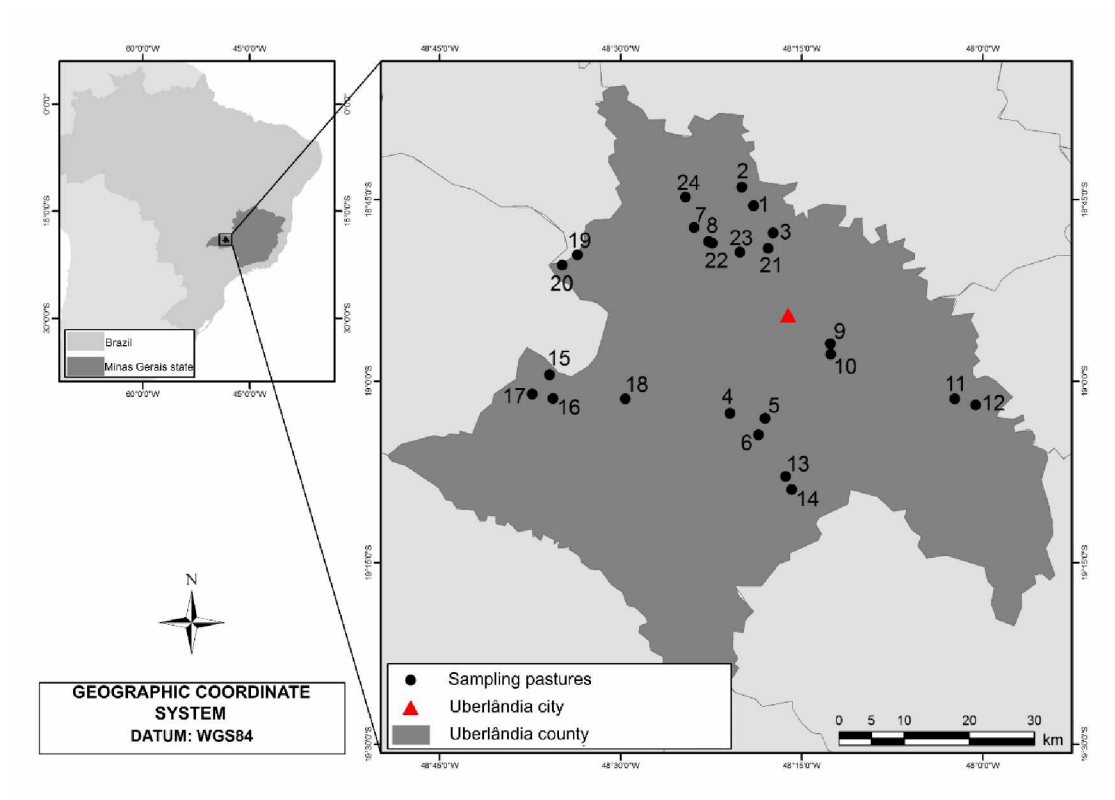


Figure 1. – Map of the study region, showing the location of the sampling pastures.

Dung-beetle and ant sampling

Sampling occurred in the rainy season (months of December 2016 and January 2017), the optimal period of the year to sample both dung beetles and ants in the tropics (Milhomem et al., 2003; Rabello et al., 2015). The same pitfall traps were used to sample both dung beetles and ants. Eight traps were established in each pasture, with traps located at the corners of a 200 x 200 m square, and at the mid-points of the sides of the square. All traps were at least 100 m distant from the pasture edge. Traps were plastic containers (19 cm diam, 11 cm height) filled with 150 ml of a saline solution and detergent. Each trap had a wire hoop suspended over it to accommodate a small (4 cm diam, 4 cm height) plastic container for holding a dung bait. We

used a 20 cm diameter plastic cover supported by three sticks to protect traps from rain. Traps were baited with cow dung and left in the field for a 48-hr period in each pasture.

Collected specimens were transported to the laboratory for processing and identification. Dung beetles were identified to genera using the key provided in Vaz-de- Mello et al. (2011) and specialist assistance from Dr. Fernando Vaz de Mello. Ant species were identified to genus using keys in Baccaro et al. (2015) and where possible to species by comparison with named species in the Zoological Collection at the Federal University of Uberlândia (UFU). For species that could not be confidently named we assigned a morphospecies code. Vouchers of all ant and beetle species were deposited at UFU's Zoological Collection.

Response variables and functional group classification

For both dung beetles and ants we analysed variation in abundance, species richness and functional-group composition among pastures. We also body mass as a response variable for dung beetles. To obtain an estimate of the total biomass of dung beetles we first weighed up to 30 individuals of each species (and where possible, a similar proportion of males and females), drying all specimens in a constant temperature oven at 40 °C for 4 days before weighing them on a precision scale (0.0001 g). The average mass of each species was then multiplied by its abundance in each pasture.

Based on the distribution of body masses (as a measure of size; Barragan et al., 2011; Carvalho et al., 2018 (Fig. S2), we classified the species as small (<100 mg) or large (>100 mg). We also classified dung beetle species based on feeding/nesting behavior as: rollers (species that make a dung ball and roll it away for burial), tunnelers (species that store dung in tunnels dug immediately below the dung source) or dwellers (species living within or immediately below the

dung, without moving it) (Hanski and Cambefort, 1991) (Table S3). Such classification was based on leg morphology (roller species have curved and elongated posterior tibiae, tunnelers have well-developed anterior tibiae, and dwellers have developed medium legs (Halffter and Edmonds, 1982)), behavioural observations of some species (*Canthon lituratus*, *Dichotomius bos*, *Onthophagus hircus*, *Trichillum heydeni* and *Trichillum externepunctatum*), published information (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Koller et al., 2007; Almeida and Louzada, 2009; Filgueiras et al., 2011), or with the assistance of a dung-beetle specialist (Dr. Fernando Vaz-de-Mello). We chose to classify species based on body size and feeding/nesting behavior because these traits are especially sensitive to habitat disturbance (Escobar, 2004; Imura et al., 2014). Food preference was not considered because the vast majority (>90%) of dung beetles in our pastures are coprophagous (F. Vaz-de-Mello, unpublished data). We also did not consider diel activity because it is not directly relevant to responses to land use (see Slade et al., 2011). However, we note that diurnal activity is often associated with smaller body size (Slade et al., 2007), while nocturnal species are often larger (Chown and Klok, 2011), and we already have incorporated body size into our classification.

Ant species were classified into functional groups based on their responses to environmental stress and disturbance. Such functional group classification was originally proposed by Andersen (1995), and then adapted for the Neotropics by Leal et al. (2012): (1) Arboreal specialists, comprising tree-nesting species of *Cephalotes* and *Pseudomyrmex*; (2) Cryptic species, comprising specialist cryptobiotic taxa that nest and forage exclusively in soil and litter; (3) Dominant Dolichoderinae, comprising mass-recruiting, behaviourally dominant species of *Dorymyrmex* and *Forelius*; (4) Epigaeic generalists, comprising a range of

generalized, ground-nesting taxa; (5) Hot climate specialists, comprising a single species, the specialist granivore *Pogonomyrmex naegelii*; (6) Higher Attini, comprising species of the leaf-cutting genera *Atta* and *Acromyrmex*, which are functionally herbivorous; (7) Lower Attini, which grow their fungus on dead organic material and are functionally detritivorous; (8) Opportunists, comprising species of the disturbance-tolerant genera *Ectatomma*, *Brachymyrmex* and *Nylanderia*; (9) Specialist predators, comprising species that feed primarily on live prey (Ponerinae, Dorylinae and *Gnamptogenys*; (10) Subordinate Camponotini, comprising species of *Camponotus*, whose submissive 236 behaviour allows them to co-exist with behaviourally dominant species (Table S4). Voucher specimens of all dung beetle and ant species have been deposited in the Zoological Collection at the Federal University of Uberlândia.

Predictor variables

A range of predictor variables relating to vegetation structure and cattle management (collectively referred to as pastoral land management variables) were quantified. Grass cover and tree density were used as measures of vegetation structure. Grass cover was visually estimated within a 1 x 1 m quadrat centred on each pitfall trap, and tree density was calculated by counting the number of trees (height >1 m) in each 4- ha plot. Three variables associated with cattle management were quantified based on interviews with farmers: time since the pasture had been established (pasture age), cattle density, and frequency of application (number per year) of veterinary medical products– VMP. Cattle density reported by farmers (cows per unit of area) represented the average value over the three years prior to our interview.

Data analysis

All analyses were performed on plot-level data ($n = 24$). We used Spearman rank correlation (due to the absence of normality and homoscedasticity) to test for associations between dung beetles and ants in terms of overall abundance and species richness. We also conducted Spearman rank correlation analysis for the abundances of each pair of functional groups that occurred at more than half of the sites. This excluded three ant functional groups, Arboreal specialists, Cryptic species and Hot-climate specialists. To compare compositional responses of dung beetles and ants, we first constructed Bray-Curtis similarity matrices, based on abundance data. We then conducted Mantel tests to assess the correlation between the matrices within and between taxa in the “vegan” package in R (Oksanen et al., 2016; R Core Team, 2018). We repeated this for each pair of functional groups that occurred in at least 23 sites: Small and large tunneler dung beetles, and Dominant Dolichoderinae, Generalist epigaeic, Opportunist, Specialist predator and Subordinate Camponotini ants.

We built generalized linear models (GLMs) using the R package “MASS” (Venables and Ripley, 2002) to evaluate the effect of the pastoral land management variables on the abundance and richness of dung beetles and ants, the biomass of dung beetles, and the abundance of each dung-beetle and ant functional group. To improve the linearity of our models we log10-transformed the variables tree density, pasture age, cattle density and frequency of VMP use, and logit-transformed percentage of grass cover prior to the analyses. For analyses of species richness we used the Poisson distribution (Hilbe, 2007), whereas the negative binomial distribution was used for analyses involving abundance and biomass. We used the logarithmic link function in all cases, except for non-count data (namely, beetle biomass) and for data on

abundance of Generalist and Opportunist ants as in these cases the identity link function provided a better model fitting. The residuals of all models were analysed to verify the adequacy of the models (Crawley, 2013).

We assessed collinearity among our predictor variables using the Variance Inflation Factor (VIF). Predictors holding VIF values > 10 are considered multicollinear and should be removed from the model (Kutner et al., 2004). As none of our predictors achieved $VIF > 2.37$ (Table S2), all were maintained in our analyses. We selected our models based on the Akaike criterion corrected for small sample size (AICc). Most of the best models had a low support value (as indicated by the Akaike weight; w_i), and so we implemented a model averaging procedure (Burnham and Anderson, 2002). For each response variable, we used standardized coefficients of the weighted model to compare the effect size across predictor variables (Burnham and Anderson, 2002). We established the individual contribution of each variable by the sum of the values of w_i of all the models that included the variable. Multimodel selection and model averaging were conducted in R (R Core Team, 2018), using the “MuMIN” package (Barton, 2016).

We tested the importance of pastoral land management variables as predictors of variation in species composition (as shown by our Bray-Curtis matrices), by building Distance-based Linear Models (DistLM) (Legendre and Anderson, 1999). DistLM uses a “best method” AIC-model selection procedure (Burnham and Anderson, 1999) considering the value of the selection criterion for all possible combinations of predictor variables. Marginal tests, evaluating the relationship between species composition and each predictor variable individually, were also carried out and the results compared with the “best solution” models derived from the

conditional tests above. All P-values were generated by permutation ($n = 999$). Analyses using DistLM were conducted in PRIMER V.7 with PERMANOVA (Clarck and Gorley, 2015).

Results

The dung-beetle and ant faunas

We collected a total of 2,047 individuals (range of 7 - 464 per pasture) of 40 species (4 - 23) of dung beetles. *Dichotomius* was the most diverse genus with seven species, and the most common species were *D. bos* and *Trichillum externepunctatum*, which both occurred in 20 pastures. Small-sized tunnelers was the most abundant (44.5 % individuals) and richest (40% species) functional group. All the roller and dweller species we collected were of small size (Table S3). A total of 11,583 ants (range 312-738 per 311 pasture) from 98 species (17-39) and 39 genera was recorded (Table S4). *Pheidole* was the most diverse genus, with 16 species, followed by *Camponotus*, *Solenopsis* and *Trachymyrmex* with 8 species each. *Pheidole subarmata* occurred in all pastures, and *P. oxyops* and *P. radoszkowskii* were each found in 23 of the 24 pastures. The richest functional groups were Epigaeic generalists (30 species), Lower Attini (16), Specialist predators (13) and Dominant Dolichoderinae (10).

Cross-taxon congruence

There was no correlation between dung beetles and ants for either total abundance ($r_s = 0.063$, $p = 0.768$) or species richness ($r_s = 0.318$, $p = 0.129$) per site. Most (74.5%) of the 55 functional-group pairs analysed were not significantly correlated. The significant correlations ranged from weakly negative (Dominant Dolichoderinae and Opportunists: $r_s = -0.445$, $p < 0.05$) to strongly positive (Subordinate Camponotini and Higher Attini: $r_s = 0.707$, $p < 0.001$;

Lower Attini and small-sized rollers: $r_s = 0.615$, $p < 0.001$; Table 1). Similarity matrices for dung beetles and ants were not correlated (Mantel test: $r = 0.045$; $p = 0.281$), indicating that site variation in species composition was markedly different for the two taxa. Correlations among functional groups were either weak or not significant (Table 1), indicating that patterns of species composition were markedly different among functional groups within each taxon.

Table 1. Spearman correlation values for abundances of dung-beetle and ant functional groups that occurred in more than half of the sites (below the diagonal) and Mantel test statistic (above) of functional groups that were diverse enough for analysis. Statistical significance * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Functional Group	Small-sized rollers	Small-sized tunnelers	Large-sized tunnelers	Small-sized dwellers	Dominant Dolichoderinae	Epigaeic generalists	Higher Attini	Lower Attini	Opportunists	Specialist predators	Subordinate Camponotini
Small-sized rollers	-										
Small-sized tunnelers	0.290	-	-0.096		-0.015	-0.008			0.088	0.104	0.157
Large-sized tunnelers	0.206	0.445*	-		-0.068	0.145			-0.002	-0.039	-0.106
Small-sized dwellers	0.382	0.482*	0.368	-							
Dominant Dolichoderinae	0.167	0.073	-0.102	-0.057	-	0.107			0.128	-0.084	0.071
Epigaeic generalists	0.001	-0.097	0.130	0.366	-0.026	-			0.095	-0.025	-0.008
Higher Attini	0.400	-0.393	-0.007	-0.271	0.019	-0.082	-				
Lower Attini	0.615***	-0.122	0.259	0.020	-0.038	0.492*	0.395*	-			
Opportunists	0.450*	-0.155	0.201	-0.028	-0.445*	-0.033	0.026	0.490*	-	0.074	0.462**
Specialist predators	0.081	-0.450*	-0.025	-0.379	0.375	0.218	0.230	0.466*	0.617	-	0.061
Subordinate Camponotini	0.487*	-0.268	0.130	-0.125	-0.048	0.115	0.707***	0.580**	0.407*	0.067	-

Response to pastoral land management variables

VMP use was by far the most important factor explaining variation in the abundance and diversity of dung beetles. VPM use was negatively related to overall beetle abundance, biomass and species richness, and to the abundances of large-sized tunnelers, small-sized rollers, and small-sized dwellers (Table 2; Fig. 2). The only other significant variable in any of the dung-beetle GLMs was grass cover, which was negatively related to the abundance of small-sized rollers. In contrast to univariate responses, VMP use was not a significant factor explaining variation in species composition of dung beetles, where cattle density was the only significant predictor variable (Table 3).

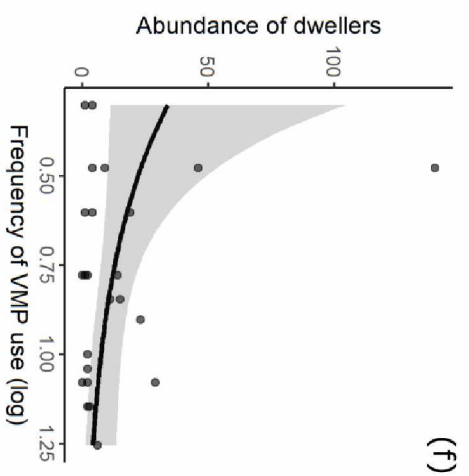
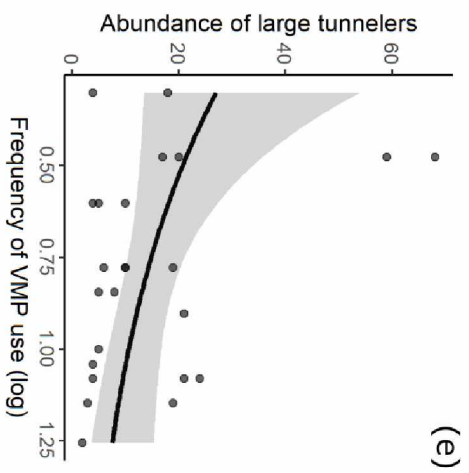
The most important variable for explaining ant abundance was tree density, which was significant in the GLMs for total abundance and for the abundances of Higher Attini, Specialist predators and Subordinate Camponotini (the relationship was positive in all cases; Table 2). VMP use was a significant variable only for Higher Attini. The only other significant variables in ant GLMs were pasture age, which was positively related to ant species richness, and grass cover, which was negatively related to the abundance of Arboreal and Hot-climate specialists (Table 2; Fig. 3). Grass cover and tree density were the only significant variables explaining variation in ant species composition (Table 3).

Table 2. Model averaged coefficients and relative importance (within parentheses) of environmental (grass cover and tree density) and management variables (pasture age, cattle density and frequency of application (number per year) of veterinary medical products – VMP) used to model the community attributes and functional groups of dung beetles and ants in the pastures of southeastern Brazil. Also shown are the variables included in the minimum adequate model ($\Delta AICc = 0$), the relative weight (w_i) of the model and the amount of variance explained. Significant predictor variables are marked in bold.

Minimum adequate model				Averaged coefficients (relative importance)					71
Dung beetles	Model	w _i	PseudoR ²	Grass cover	Tree density	Pasture age	Cattle density	VMP	
Richness	VMP	0.30	0.27	-0.076 (0.23)	0.021 (0.17)	0.034 (0.16)	-0.113 (0.28)	- 0.210 (0.82)	
Abundance	VMP	0.30	0.24	-0.043 (0.16)	0.118 (0.19)	0.072 (0.18)	0.437 (0.39)	- 0.579 (0.96)	
Biomass	TD+VMP	0.36	0.32	0.068 (0.18)	0.430 (0.69)	-0.077 (0.15)	-0.036 (0.22)	- 0.627 (0.81)	
Small- sized roller	GC+VMP	0.27	0.31	-0.771 (0.83)	0.492 (0.24)	0.208 (0.16)	0.649 (0.29)	- 0.785 (0.83)	
Small-sized tunneler	TD	0.16	0.15	0.166 (0.18)	-0.427 (0.45)	-0.115 (0.17)	0.492 (0.32)	-0.524 (0.55)	
Large-small tunneler	TD+VMP	0.18	0.26	0.123 (0.19)	-0.286 (0.21)	0.172 (0.22)	-0.246 (0.27)	- 0.438 (0.69)	
Small-sized dwellers	VMP	0.19	0.14	-0.055 (0.15)	-0.438 (0.28)	0.473 (0.23)	0.830 (0.46)	- 0.901 (0.82)	
Ants									
Richness	TD+PA	0.16	0.31	-0.070 (0.51)	0.076 (0.55)	0.116 (0.88)	-0.003 (0.18)	0.003 (0.17)	
Abundance	TD+VMP	0.29	0.39	-0.074 (0.23)	0.284 (1.00)	-0.062 (0.19)	-0.018 (0.19)	-0.165 (0.51)	
Arboreal specialists	GC+PA	0.2	0.45	-0.607 (0.87)	-0.091 (0.16)	0.527 (0.53)	-0.224 (0.23)	0.325 (0.34)	
Cryptic species	Null	0.23		0.559 (0.30)	0.032 (0.17)	-0.123 (0.16)	0.490 (0.24)	0.471 (0.23)	
Dominant Dolichoderinae	Null	0.22		-0.318 (0.34)	0.063 (0.18)	-0.215 (0.27)	-0.149 (0.23)	-0.001 (0.16)	
Epigeic generalists	TD+CD	0.13	0.28	0.277 (0.34)	0.367 (0.50)	0.317 (0.36)	0.401 (0.61)	-0.099 (0.21)	
Hot-climate specialists	GC	0.32	0.39	-0.484 (1.00)	-0.014 (0.17)	0.266 (0.38)	0.042 (0.17)	0.078 (0.18)	
Higher Attini	TD+VMP	0.25	0.36	-0.473 (0.39)	0.841 (0.88)	0.252 (0.22)	-0.397 (0.24)	- 0.842 (0.79)	
Lower Attini	PA	0.16	0.10	-0.162 (0.22)	0.270 (0.31)	0.419 (0.51)	0.230 (0.24)	-0.212 (0.24)	
Opportunists	TD+ VMP	0.14	0.25	-0.119 (0.15)	0.659 (0.66)	0.235 (0.16)	-0.312 (0.32)	-0.470 (0.52)	
Specialist predators	TD + CD	0.20	0.41	0.008 (0.14)	0.464 (0.79)	0.486 (0.56)	-0.324 (0.50)	0.174 (0.21)	
Subordinate Camponotini	TD	0.30	0.27	-0.035 (0.16)	0.568 (0.90)	-0.131 (0.19)	-0.036 (0.17)	-0.321 (0.31)	

Table 3. Distance-based linear modelling (DistLM) of dung beetle and ant species composition with environmental (grass cover and tree density) and management variables (pasture age, cattle density and frequency of application (number per year) of veterinary medical products (VMP). Statistical significance * $P < 0.05$.

Variable	AICc	SS (trace)	Pseudo-F	P	Prop	res.df
Marginal tests – Dung beetles						
Grass cover	-	1053.1	0.681	0.705	0.030	22
Tree density	-	1148.1	0.745	0.685	0.033	22
Pasture age	-	1169	1.100	0.387	0.047	22
Cattle density	-	2904.3	1.998	0.040*	0.088	22
VMP	-	2374.3	1.598	0.127	0.067	22
<i>Sequential tests - Best solution</i>						
Cattle density	176.8	-	-	-	0.088	-
Marginal tests – Ants						
Grass cover	-	2551.3	1.947	0.010*	0.081	22
Tree density	-	2179.4	1.793	0.010*	0.075	22
Pasture age	-	1644.9	1.327	0.171	0.056	22
Cattle density	-	965.15	0.759	0.759	0.033	22
VMP	-	1423.1	1.139	0.340	0.049	22
<i>Sequential tests - Best solution</i>						
Grass cover +Tree density	172.14	-	-	-	0.157	-



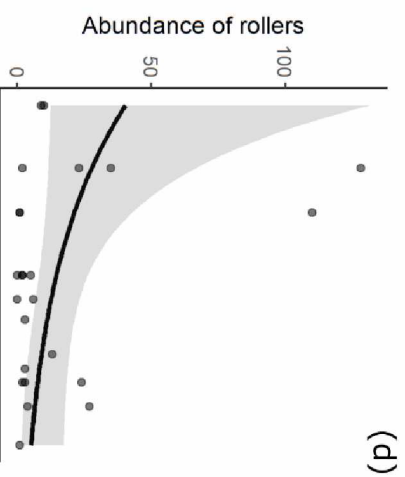
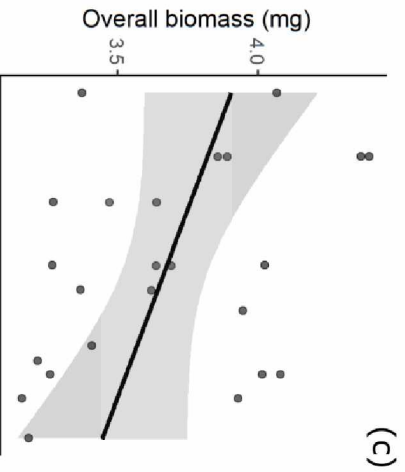
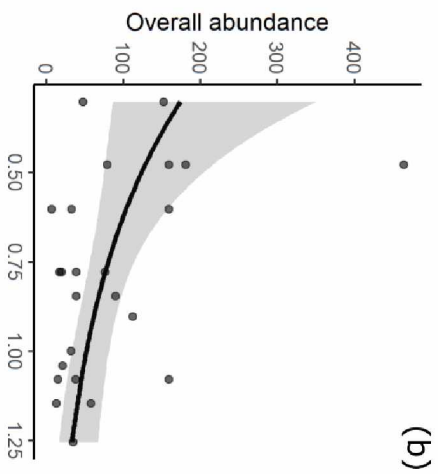
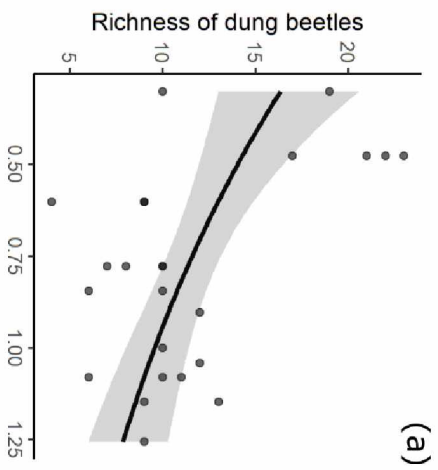


Figure 2. Effect of the frequency of application (number per year) of Veterinary Medical Products (VMP) on various attributes of the community of dung beetles: (a) species richness, (b) overall abundance, (c) biomass, (d) abundance of small-sized rollers, (e) large-sized tunnelers, and (f) small-sized dwellers. The shaded area shows the 95% confidence interval of the best-fit generalized linear model. Analyses were performed using log-transformed VMP frequency data to improve model fit.

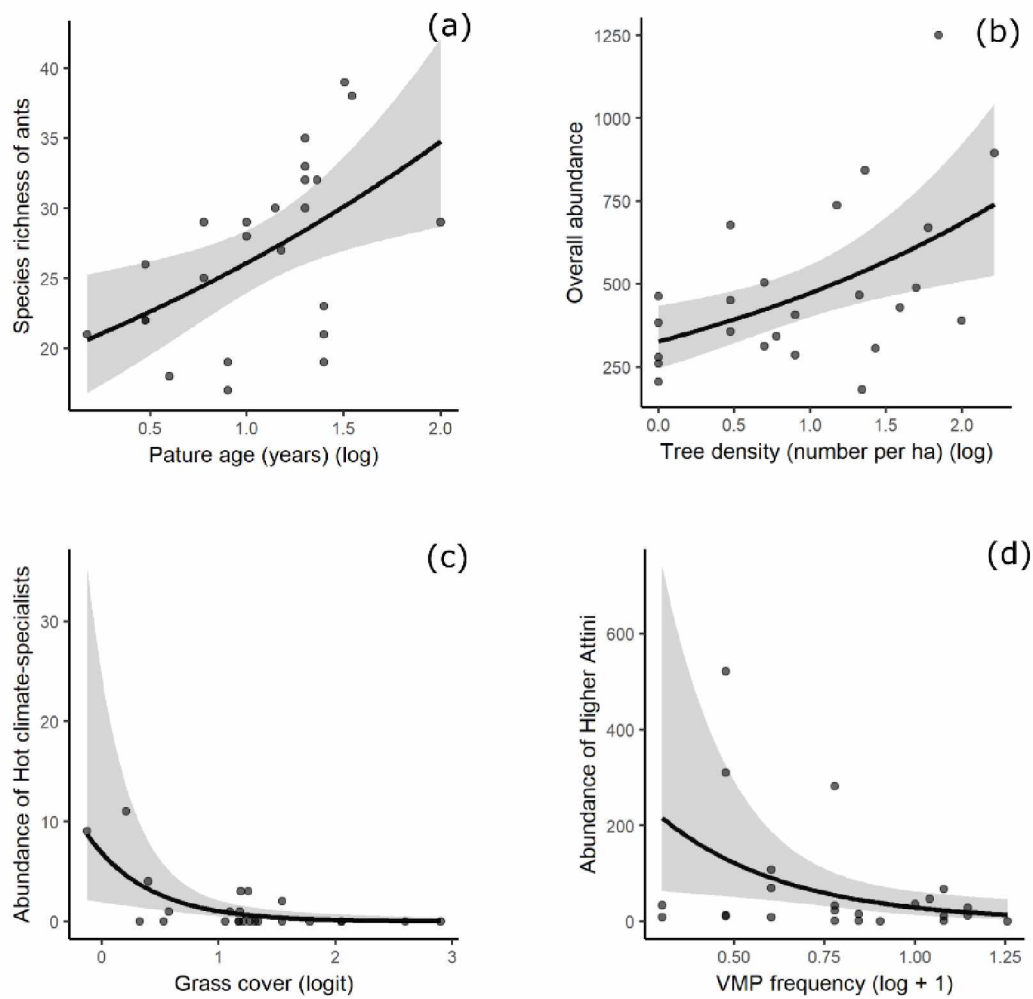


Figure 3. Effect of the environmental and pasture management variables on some attributes of the ant community: (a) species richness, (b) overall abundance, (c) Abundance of hot-climate specialists (d) Abundance of higher attini. The shaded area shows the 95% confidence interval of the best-fit generalized linear model. Data on pasture age, tree density and VMP frequency of use were log-transformed, whereas data on grass cover was logit transformed to improve model fit.

Discussion

The highly idiosyncratic responses of different taxa to disturbance pose a major challenge to the use of bioindicators for representing biodiversity more generally. An ecological trait approach can help provide a mechanistic understanding of disturbance responses of bioindicator taxa, and thereby clarify what they are actually indicating. We have taken the novel approach of linking environmental responses of dung beetles and ants to their ecological traits in order to clarify what they are indicating in the context of pastoral land management in a Brazilian savanna.

We first asked how responses to pastoral land management vary between dung beetles and ants, and among functional groups within them. We found that the abundance, richness and composition of both dung beetles and ants varied markedly among pastures with different management histories, as has been previously demonstrated (e.g. dung beetles: Imura et al., 2014; Tonelli et al., 2017; ants: Arcoverde et al., 2017; both groups: Verdú et al., 2011). However, dung beetles and ants showed no congruent spatial patterns of abundance and diversity, such that dung beetles and ants provided very different indications of the impacts of pastoral land management on biodiversity. We classified both dung beetles and ants into functional groups in order to provide a clearer perspective on their disturbance responses. Responses varied markedly among functional groups within both taxa, as illustrated by generally weak or no correlations in abundance or species composition. This further highlights the lack of generality of biodiversity responses, and the need for a mechanistic understanding to allow for an interpretation of the responses.

We sought such a mechanistic understanding by examining which environmental variables best predicted dung-beetle and ant responses. We found that significant environmental predictors varied markedly between dung beetles and ants, and often

among their component functional groups, consistent with their contrasting responses to pastoral land management. The major driver of variation in dung beetle communities was VMP use, with overall abundance, biomass and species richness, and the abundances of most functional groups, all negatively related to the frequency of VMP use. VMP residue within dung retains insecticidal activity (Schmidt, 1983) and can negatively affect larval and adult survival, along with the reproductive, sensorial and locomotor activity of dung beetles (Lumaret et al., 1993; Verdú et al., 2015). Among ants, VMP use was related only to leaf-cutter ants (Higher 386 Attini). In our study area, leaf-cutter ants were frequently seen removing large amounts of bovine dung, presumably for fungus-culturing. We are not aware of any study that has directly analyzed the effect of VMPs on the fungus cultivated by leaf-cutter ants, but long-term exposure to ivermectin is known to decrease the formation and germination of spores in some types of fungi (Kollmann et al., 2003). High concentrations of VMPs have been shown to affect the reproduction and survival of leaf-cutter ant queens (Antunes et al., 2000). The parallel responses of dung beetles and leaf-cutter ants suggest that VMP use would be a major driver of the diversity of insects and other invertebrates more generally that feed on cattle dung.

Species composition of dung beetles was not related to VMP use, suggesting that most species were similarly affected. The major predictor of species composition was cattle density, which also had a near-significant relationship with total abundance of dung beetles. Variation in cattle density is likely to have both direct and indirect effects on dung beetles. More cattle means more dung and thus more food resources for beetles, and previous studies show that dung availability can affect both the abundance (Tonelli et al., 2017) and species composition of dung beetles (Lobo et al., 2006). The abundances of *Dichotomius glaucus*, *Oxysternon palaemon* and *Sulcophaneus menelas*

(large-sized tunnelers) were all negatively related to cattle density, whereas that of *Onthophagus appendiculatus* (small-sized tunneler) was positively related. All these species are coprophagous (Almeida and Louzada, 2009; Vaz-de-Mello, personal observation), and so their different responses to cattle density do not appear to be related to diet. Rather, we suggest that such responses are due to soil compaction, given that soil compaction can also increase with cattle density (Negro et al. 2011; R. Carvalho unpublished data). Soil compaction is an important factor influencing the composition of dung beetles, having a particularly detrimental effect on large-sized tunnelers (Jankielsohn et al. 2001; Negro et al. 2011). Large tunnelers are known to be more sensitive to cattle disturbance through soil compaction than other functional groups (Jankielsohn et al. 2001; Negro et al. 2011).

In contrast to dung beetles, vegetation structure (tree density and grass cover) was the main driver of variation in ant communities in our pastoral system. Total ant abundance was positively related to tree density, which reflects the importance of trees in providing ant nesting sites (Frizzo and Vasconcelos, 2013) and food resources (Arnan et al., 2007), and in ameliorating the microclimate (Perfecto and Vandermeer, 1996). Tree density was also a predictor of the abundance of the ant functional groups Higher Attini, Subordinate Camponotini and Specialist predators, which is consistent with their ecological traits. Trees provide Higher Attini with their favoured leaf resources (Leal et al., 2012), and many species of Subordinate Camponotini nest and forage in trees for honeydew or extra-floral nectar (Camarota et al., 2015). The response of Specialist predators suggests that trees provide important prey resources for ants.

Another vegetation attribute, grass cover, was negatively related to the abundance of Arboreal specialists and Hot-climate specialists. The latter strongly prefer open environments (Andersen, 1995), and often benefit from moderate disturbance

(Andersen, 2018). The abundance of small-sized roller dung beetles was also negatively related to grass cover, as also found by Louzada et al. (2010). This is presumably because high grass cover impedes the rolling of dung balls. The responses of Hot climate specialist ants and small-sized roller dung beetles are likely to reflect those of other arthropod groups that favour open environments. Both grass cover and tree density were significant predictors of variation in ant species composition, which is consistent with the known sensitivity of ant communities to variation in vegetation structure, and particularly the effects of habitat openness on microclimate and locomotory activity (Andersen, 1995, 2018).

In conclusion, we have found that two commonly used bioindicator groups show contrasting responses to pastoral land management in a Brazilian savanna, and therefore provide very different indications of the impact of pastoral land management on biodiversity. However, by linking responses to ecological traits we have been able to clarify what the bioindicators are actually indicating. Dung beetles and leaf-cutter ants are indicating an impact of VMPs on dung-feeding invertebrates (Floate et al., 2005) and other invertebrates relying on food derived from dung (Puniamoorthy et al., 2014). Ant communities are indicating the importance of vegetation structure, and particularly the role of trees in providing nesting and food resources for fauna (Frizzo and Vasconcelos, 2013; Neilly et al., 2018). Ants and small-sized roller beetles are indicating the effects of ground-layer openness on microclimate and locomotory activity. We believe that such a linking of disturbance responses to ecological traits provides a substantially improved foundation for the use of individual taxa as bioindicators in land management.

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Supplementary information

Table S1 – Geographic coordinates of the 24 cattle pastures studied in southeastern Brazil, and data on their size, grass cover, tree density, age, cattle density, and the frequency of use of VPMs.

Pasture	Coordinates	Area (ha)	Grass cover (%)	Tree density (ha)	Pasture age (years)	Cattle density ²	VMP use ³
1	-18.887222 S -48.573889 W	95	77.2	1.75	20	6.25	10
2	-18.980833 S -48.582778 W	100	43.0	0.5	32	0.83	3
3	-18.990833 S -48.383056 W	40	71.5	24.5	20	10.50	14
4	-19.044072 S -48.349058 W	105	93.7	6.5	3	28.50	12
5	-19.051411 S -48.300231 W	48	97.3	5.0	14	17.50	14
6	-19.073872 S -48.309758 W	225	94.0	17.25	20	1.93	3
7	-18.864444 S -48.632778 W	65	99.7	9.5	100	2.68	6
8	-18.930278 S -48.569167 W	26	92.0	1	6	159.72	4
9	-19.185000 S -48.370000 W	80	99.13	0	25	20	6
10	-19.168611 S -48.365833 W	350	95.6	40.75	35	2.73	6
11	-19.142778 S -48.116389 W	950	93.8	5.5	10	4	7
12	-19.281389 S -48.158333 W	26	94.7	14.75	20	40	12
13	-19.358611 S -48.355556 W	800	97.3	0	23	0.94	6
14	-19.398333 S -48.478889 W	830	95.6	0	25	0.95	3
15	-19.111111 S -48.834444 W	28	92.6	5.25	8	40	18
16	-19.140000 S -48.751667 W	14	98.4	0	1.5	9	2
17	-19.033889 S -48.705000 W	165	94.3	12.25	25	0.41	4
18	-19.144167 S -48.650833 W	10	99.8	1.25	4	50	8
19	-18.970556 S -48.712500 W	180	94.9	0.5	3	1.85	2
20	-18.948611 S -48.800000 W	1450	61.8	0	8	30	7
21	-18.820556 S -48.502778 W	30	93.7	0.5	15	7	3
22	-18.964.722 S -48.473.889 W	12	99.3	3.5	6	388.88	12
23	-18.914.444 S -48.365.000 W	30	68.1	1	3	16.8	4
24	-18.954.444 S -48.570.278 W	32	79.1	1.75	10	6.66	11

¹ 1 hectare² livestock/ha³annual frequency

Table S2 – Variance inflation factor (VIF) and Pearson correlation among predictor variables of the species richness and abundance of dung beetles and ants in pastoral lands (Grass cover – GR and Tree density – TD, and pastures management (Pasture age – PA, Cattle density – CD, Frequency of VMP'S use – VMP'S))

	GR	TD	PA	CD	VMP'S	VIF
GR	1.00					1.08
TD	0.02	1.00				1.38
PA	0.01	0.30	1.00			1.73
CD	0.18	0.02	-0.48	1.00		2.37
VMP's	0.02	0.45	0.09	0.51	1.00	2.09

Table S3 – List of the species of dung beetles collected, body mass (mg), overall abundance, mass category and functional group.

Species	Mean mass $\pm$ SE	Abundance	Category	Functional group	Number of farms
<i>Agamopus viridis</i> Boucomont, 1928	2,751 $\pm$ 0,137	134	Small	rollers	15
<i>Ateuchus puncticollis</i> (Harold, 1867)	25,556	1	Small	tunnelers	1
<i>Ateuchus striatulus</i> (Preudhomme de Borre, 1886)	12,951 $\pm$ 0,682	198	Small	tunnelers	14
<i>Ateuchus vividus</i> (Germar, 1823)	13,533 $\pm$ 0,765	2	Small	tunnelers	2
<i>Ateuchus</i> sp.1	14,738 $\pm$ 0,727	43	Small	tunnelers	7
<i>Canthidium decoratum</i> (Perty, 1830)	14,499 $\pm$ 0,928	7	Small	tunnelers	3
<i>Canthidium impressum</i> Boucomont, 1928	9,500	1	Small	tunnelers	1
<i>Canthidium refulgens</i> Boucomont, 1928	10,668 $\pm$ 1,783	9	Small	tunnelers	7
<i>Canthidium</i> sp.1	9,200	1	Small	tunnelers	1
<i>Canthidium</i> sp.2	28,256 $\pm$ 1,939	33	Small	tunnelers	11
<i>Genieridium bidens</i> (Balthasar, 1938)	6,327 $\pm$	97	Small	dwellers	12
<i>Canthon conformis</i> Harold, 1868	37,384	1	Small	rollers	1
<i>Canthon lituratus</i> (Germar, 1824)	4,486 $\pm$ 0,387	270	Small	rollers	16
<i>Canthon muticus</i> Harold, 1867	10,767 $\pm$ 4,249	4	Small	rollers	2
<i>Canthon virens</i> (Mannerheim, 1829)	23,460 $\pm$ 5,595	5	Small	rollers	3
<i>Pseudocanthon</i> sp.1	1,948 $\pm$ 0,023	5	Small	unknown	3
<i>Vulcanocanthon</i> sp.1	1,819 $\pm$ 0,237	7	Small	rollers	2
<i>Dichotomius</i> aff. <i>bicuspis</i> (Germar, 1824)	106,330 $\pm$ 5,659	2	Large	tunnelers	2
<i>Dichotomius</i> aff. <i>carbonarius</i> (Mannerheim 1829)	181,228 $\pm$ 1,376	3	Large	tunnelers	3
<i>Dichotomius bos</i> (Blanchard, 1843)	420,388 $\pm$ 26,683	174	Large	tunnelers	20
<i>Dichotomius glaucus</i> (Harold, 1869)	179,930 $\pm$ 5,458	49	Large	tunnelers	4
<i>Dichotomius nisus</i> (Olivier, 1789)	279,167 $\pm$ 19,273	22	Large	tunnelers	14
<i>Dichotomius semiaeneus</i> (Germar, 1824)	79,180 $\pm$ 2,679	46	Small	tunnelers	7
<i>Dichotomius smaragdinus</i> (Perty, 1830)	46,049 $\pm$ 2,719	18	Small	tunnelers	3
<i>Digitonthophagus gazella</i> (Fabricius, 1787)	21,147 $\pm$ 2,169	11	Small	tunnelers	6
<i>Eutrichillum hirsutum</i> Boucomont, 1928	2,969 $\pm$ 0,510	20	Small	dwellers	8

<i>Isocoprís inhiatus</i> (Germar, 1824)	484,372 ± 58,598	6	Large	tunnelers	4
<i>Ontherus appendiculatus</i> (Mannerheim, 1829)	25,180 ± 1,112	229	Small	tunnelers	18
<i>Trichillum heydeni</i> Harold, 1868	5,493 ± 0,168	34	Small	dwellers	3
<i>Trichillum externepunctatum</i> Borre, 1886	2,911 ± 0,102	189	Small	dwellers	20
<i>Onthophagus</i> aff. <i>hircus</i> Billberg, 1815	7,208 ± 0,402	86	Small	tunnelers	12
<i>Onthophagus ptox</i> Erichson, 1842	4,805 ± 0,311	213	Small	tunnelers	17
<i>Onthophagus</i> sp. 1	8,874 ± 0,834	14	Small	tunnelers	5
<i>Coprophanaeus cyanescens</i> Olsoufieff, 1924	621,980 ± 38,018	14	Large	tunnelers	4
<i>Coprophanaeus spitzii</i> (Pessôa 1935)	593,094 ± 28,997	69	Large	tunnelers	13
<i>Coprophanaeus pessoai</i> (Pereira, 1949)	387,733	1	Large	tunnelers	1
<i>Dendropaemon denticollis</i> Felsche, 1909	49,749 ± 9,010	3	Small	unknown	3
<i>Diabroctis mimas</i> Linnaeus, 1758	431,723	1	Large	tunnelers	1
<i>Oxysternon palaemo</i> (Castelnau, 1840)	200, 407 ± 17,749	4	Large	tunnelers	6
<i>Sulcophanaeus menelas</i> (Castelnau, 1840)	196, 841 ± 15,949	9	Large	tunnelers	3
Total abundance		2047			

Table S4 - List of the species of ants collected, their functional group and overall abundance.

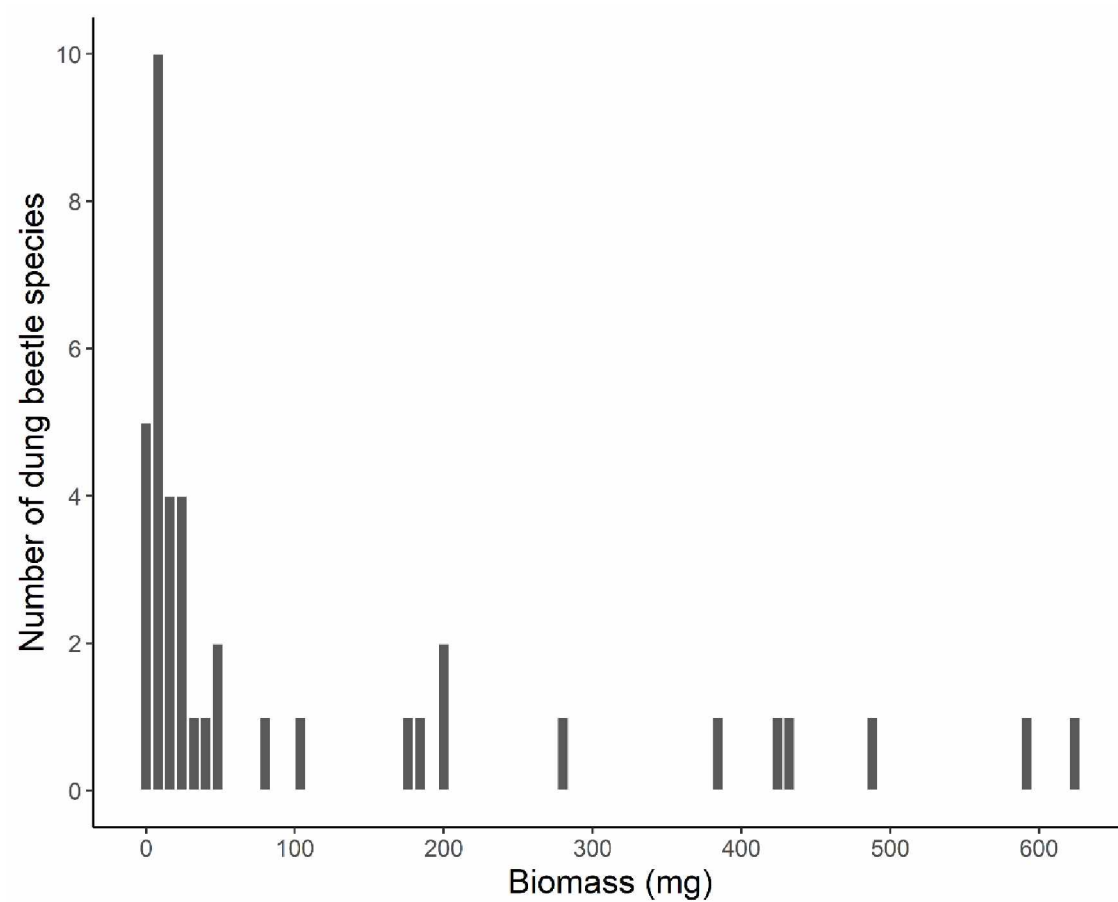
Subfamily/Species	Occurences	Functional Group	Number of farms
Dolichoderinae			
<i>Azteca</i> sp.1	1	Arboreal specialist	1
<i>Dorymyrmex bruneus</i> Forel, 1908	64	Dominant Dolichoderinae	22
<i>Dorymyrmex goeldii</i> Forel, 1904	75	Dominant Dolichoderinae	21
<i>Dorymyrmex pyramicus</i> Roger, 1863	34	Dominant Dolichoderinae	13
<i>Dorymyrmex</i> sp.21	7	Dominant Dolichoderinae	7
<i>Forelius albiventris</i> Forel, 1912	2	Dominant Dolichoderinae	2
<i>Forelius brasiliensi</i> , Forel, 1908	34	Dominant Dolichoderinae	13
<i>Forelius</i> sp.12	7	Dominant Dolichoderinae	2
<i>Gracilidris pombero</i> Wild & Cuezco, 2006	2	Dominant Dolichoderinae	2
<i>Linepithema angulatum</i> Emery, 1894	3	Dominant Dolichoderinae	2
<i>Linepithema cerradense</i> Wil, 2007	2	Dominant Dolichoderinae	2
<i>Tapinoma</i> sp.3	7	Oportunist	6
<i>Tapinoma</i> sp.7	11	Oportunist	6
Dorylinae			
<i>Eciton burchellii</i> Westwood, 1842	1	Specialist predator	1
<i>Labidus praedator</i> Smith, 1858	1	Specialist predator	1
Ectatomminae			
<i>Ectatomma brunneum</i> Smith, 1858	90	Oportunist	21
<i>Ectatomma edentatum</i> Roger, 1863	24	Oportunist	13
<i>Ectatomma opaciventre</i> Roger, 1861	33	Oportunist	13
<i>Ectatomma tuberculatum</i> Olivier, 1792	17	Oportunist	7
<i>Gnamptogenys acuminata</i> Emery, 1896	3	Specialist predator	2
<i>Gnamptogenys</i> sp. 9	36	Specialist predator	16
<i>Gnamptogenys</i> sp.10	1	Specialist predator	1
<i>Gnamptogenys sulcata</i> Smith, 1858	27	Specialist predator	15
Formicinae			
<i>Brachymyrmex</i> sp.5	52	Oportunist	21
<i>Camponotus blandus</i> Smith, 1858	57	Subordinate	22
<i>Camponotus leydigi</i> Forel, 1866	8	Subordinate	7

<i>Camponotus melanoticus</i> Santschi, 1839	24	Subordinate	15
<i>Camponotus personatus</i> Emery, 1894	8	Subordinate	7
<i>Camponotus renggeri</i> Emery, 1894	1	Subordinate	1
<i>Camponotus senex</i> Smith, 1858	5	Subordinate	4
<i>Camponotus</i> sp.10	1	Subordinate	1
<i>Camponotus</i> sp.35	14	Subordinate	8
<i>Myrmelachista</i> sp.5	1	Arboreal specialist	1
Myrmecinae			
<i>Acromyrmex crassispinus</i> Forel, 1909	16	Higher Attini	11
<i>Acromyrmex landolti</i> Forel, 1885	38	Higher Attini	15
<i>Apterostigma</i> sp.1	1	Lower Attini	1
<i>Atta laevigatta</i> Smith 1858	48	Higher Attini	17
<i>Cardiocondyla emeryi</i> Forel, 1881	32	Opportunist	16
<i>Cephalotes borgmeieri</i> Kempf, 1951	1	Arboreal specialist	1
<i>Cephalotes depressus</i> Klug, 1824	1	Arboreal specialist	1
<i>Crematogaster</i> sp. nr. <i>obscurata</i> Smith, 1857	7	Epigaeic generalist	5
<i>Crematogaster</i> sp. 13	2	Epigaeic generalist	1
<i>Crematogaster</i> sp. 28	1	Epigaeic generalist	1
<i>Cyphomyrmex rimosus</i> (Spinola, 1851)	22	Lower Attini	14
<i>Cyphomyrmex</i> sp. 26	4	Lower Attini	3
<i>Hypoponera</i> sp. 16	1	Cryptic species	1
<i>Mycetarotes parallelus</i> Emery, 1906	8	Lower Attini	5
<i>Mycocepurus goeldii</i> (Forel, 1893)	70	Lower Attini	20
<i>Mycocepurus smithii</i> (Forel, 1893)	1	Lower Attini	1
<i>Myrmicocrypta squamosa</i> Smith, 1860	2	Lower Attini	1
<i>Ochetomyrmex neopolitus</i> Fernández, 2003	1	Epigaeic generalist	1
<i>Oxyepoecus inquilinus</i> Kusnezov, 1952	1	Cryptic species	1
<i>Pheidole fractipes</i> Wilson, 2003	12	Epigaeic generalist	6
<i>Pheidole gertrudae</i> Forel, 1886	4	Epigaeic generalist	3
<i>Pheidole oxyops</i> Forel, 1908	125	Epigaeic generalist	23
<i>Pheidole radoszkowskii</i> Mayr, 1884	93	Epigaeic generalist	23
<i>Pheidole rufipilis</i> Forel, 1908	8	Epigaeic generalist	7
<i>Pheidole scolioiceps</i> Wilson, 2003	1	Epigaeic generalist	1

<i>Pheidole subarmata</i> Mayr, 1884	103	Epigaeic generalist	24
<i>Pheidole susannae</i> Forel, 1886	1	Epigaeic generalist	1
<i>Pheidole tetrica</i> Forel, 1913	1	Epigaeic generalist	1
<i>Pheidole triconstricta</i> Forel, 1886	15	Epigaeic generalist	9
<i>Pheidole vafra</i> Santschi, 1923	11	Epigaeic generalist	7
<i>Pheidole</i> sp. 20	1	Epigaeic generalist	1
<i>Pheidole</i> sp. 38	2	Epigaeic generalist	2
<i>Pheidole</i> sp. 70	1	Epigaeic generalist	1
<i>Pheidole</i> sp. 84	21	Epigaeic generalist	11
<i>Pheidole</i> sp. 98	1	Epigaeic generalist	1
<i>Pogonomyrmex naegelii</i> Emery 1878	17	Hot-climate specialist	9
<i>Sericomyrmex srobifer</i> Forel, 1911	2	Lower Attini	2
<i>Solenopsis germinata</i> Fabricius, 1804	4	Epigaeic generalist	2
<i>Solenopsis loretana</i> Santschi, 1936	21	Epigaeic generalist	14
<i>Solenopsis</i> sp.1	3	Epigaeic generalist	3
<i>Solenopsis</i> sp. 6	1	Epigaeic generalist	1
<i>Solenopsis</i> sp.8	22	Epigaeic generalist	14
<i>Solenopsis</i> sp.17	4	Epigaeic generalist	4
<i>Solenopsis</i> sp.30	1	Epigaeic generalist	1
<i>Solenopsis substituta</i> Santschi, 1925	25	Epigaeic generalist	12
<i>Strumigenys</i> sp.6	1	Cryptic species	1
<i>Trachymyrmex holmgreni</i> Wheeler, 1925	7	Lower Attini	7
<i>Trachymyrmex</i> sp.2	5	Lower Attini	3
<i>Trachymyrmex</i> sp.3	4	Lower Attini	4
<i>Trachymyrmex</i> sp.5	2	Lower Attini	2
<i>Trachymyrmex</i> sp.31	2	Lower Attini	2
<i>Trachymyrmex</i> sp.40	9	Lower Attini	6
<i>Trachymyrmex</i> sp.41	4	Lower Attini	2
<i>Trachymyrmex</i> sp.45	2	Lower Attini	2
<i>Wasmannia auropunctata</i> (Roger, 1863)	4	Epigaeic generalist	3
Ponerinae			
<i>Anochetus inermis</i> André, 1889	1	Specialist predator	1
<i>Centromyrmex brachycola</i> Roger, 1861	1	Cryptic species	1

<i>Neoponera marginata</i> Roger, 1861	2	Specialist predator	2
<i>Neoponera verenae</i> (Forel, 1922)	1	Specialist predator	1
<i>Odontomachus bauri</i> Emery, 1892	13	Specialist predator	10
<i>Odontomachus meinerti</i> Forel, 1905	5	Specialist predator	2
<i>Pachycondyla harpax</i> Fabricius, 1804	6	Specialist predator	4
<i>Pachycondyla striata</i> Smith, 1858	1	Specialist predator	1
Pseudomyrmecinae			
<i>Pseudomyrmex</i> sp.25	1	Arboreal specialist	1
<i>Pseudomyrmex termitarius</i> Smith, 1855	28	Epigaeic generalists	14

Figure S1. Body mass distribution of dung beetle species sampled in 24 cattle pastures in southeastern Brazil.



Capítulo 3

Dung beetles of an Australian tropical savanna: species composition, food preferences and responses to experimental fire regimes

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Abstract

Dung beetles are an ecologically important group of insects globally, but the ecology of the Australian fauna is poorly known. Here we report on the first ecological study of dung beetles in an Australian tropical savanna, documenting species composition, food preferences and responses to fire. Dung beetles were baited using dung from five types of vertebrates and using mushrooms. We sampled at nine plots subject to experimental fire regimes (three replicates each of high fire severity, moderate fire severity and unburnt over 15 years) at the Territory Wildlife Park near Darwin. Our samples were comprised entirely of nine native species of *Onthophagus*. Dog dung was the most attractive bait, recording all nine species and nearly 80% of all individuals, whereas no beetles were recorded at either wallaby or magpie goose dung. Dung beetle abundance was highest under high fire severity and was negatively correlated with the cover of woody vegetation, a result driven by the two most common species, *O. minsiculus* and *O. nr. quadripunctulatus*. Our results indicate that *Onthophagus* is the dominant genus in dung-beetle assemblages of monsoonal Australia, as it is in open habitats of the Australian wet tropics. All our species of *Onthophagus* are relatively small (≤ 10 mm body length) and are ‘tunnelers’, storing dung and other food resources in tunnels dug immediately below the food source. Such

an overwhelming dominance by small tunnelers does not occur in African savannas, and reflects the far lower availability of large mammalian dung.

Keywords: Australian monsoonal tropics; fire experiment; fire severity; *Onthophagus*; vegetation cover

Introduction

Dung beetles (Scarabaeidae: Scarabaeinae) are a highly diverse (approximately 7000 species; Schoolmeesters *et al.* 2010), globally distributed group of insects that feed on dung (mainly mammalian) and other food resources including carrion, mushrooms, fruits, and rotting plant matter (Hanski & Cambefort 1991; Martin Pierra & Lobo 1996; Salamao *et al.* 2014). They play key roles in nutrient cycling (Menendez *et al.* 2016), secondary seed dispersal (Andresen and Feer 2005), bioturbation, and the control of pests and intestinal parasites (Nichols *et al.* 2008). Dung beetles show high sensitivity to habitat disturbance and so are often used as ecological indicators in land management (Gardner *et al.* 2008; Audino *et al.* 2014).

Dung beetle species typically use dung from multiple sources (Hanski and Cambefort 1991; Frank *et al.* 2018; Ebert *et al.* 2019), enabling them to survive in the face of scarce and ephemeral resources (Estrada *et al.* 1993; Dormont *et al.* 2004). However, they often differentiate between the dung of carnivores, herbivores and omnivores (Holter & Scholtz 2007) due to differences in the amount of fiber, nutritional quality, moisture, and chemical content (Hanski & Cambefort, 1991; Dormont *et al.* 2007; Hernandez *et al.* 2012). Dung-beetle species usually have strong habitat preferences (Barbero *et al.* 1999; Dormont *et al.* 2007; Almeida & Louzada 2009; Kunz & Krell 2011), relating to soil type, vegetation structure, temperature, and humidity (Barbero *et al.* 1999; Davis *et al.* 2001; Haffter & Arellano 2002; Louzada *et al.* 2010). In particular, species composition in open habitats is usually very different to that in forests

(Galante *et al.* 1991; Lumaret and Kirk 1991), and open-habitat species tend to have smaller body sizes (Krell *et al.* 2003; Nichols *et al.* 2007; Navarrete & Halfpeter 2008).

Australia has more than 500 species of native dung beetles (Matthews 1972, 1974, 1976, T. Weir, unpublished data), along with 23 exotic species that have been introduced for the removal of cattle dung (Doubé *et al.* 1991; Edwards 2009; Edwards *et al.* 2015) because the native fauna does not adequately use this resource (Matthews 1972), as reflects the absence of native bovids from Australia (Matthews 1972; Doubé *et al.* 1991). Australia's native dung beetle species are well-known taxonomically (Matthews 1972, 1974, 1976), but little is known about the composition of native assemblages, their food preferences or their responses to habitat disturbance (Vernes *et al.* 2005; Gollan *et al.* 2011; Kenyon *et al.* 2016; Ebert *et al.* 2019), which are all foundations for their use as bioindicators (Andersen 1999). Ecological studies of native species have been conducted primarily in the wet tropics of North Queensland, where rainforest and dry sclerophyll forest have been shown to harbor distinct faunas with contrasting biogeographical origins (Vernes *et al.* 2005; Kenyon *et al.* 2016; Ebert *et al.* 2019). The former is dominated by Australian endemic genera, whereas the latter is dominated by the cosmopolitan genus *Onthophagus* (Matthews 1972, 1974; Hill 1996; Derhe *et al.* 2016; Kenyon *et al.* 2016).

Dung-beetle assemblages of the vast tropical savanna landscapes that dominate northern Australia outside the wet tropics have been virtually unstudied. In the Neotropics, dung-beetle diversity is higher in forest than savanna (Almeida & Louzada 2009), whereas the reverse is true in Africa (Davis *et al.* 2002; Kunz & Krell 2011), and large species that roll balls of dung are far more prominent in Africa than in the Neotropics (Krell *et al.* 2003). These inter-continental differences can be explained by differences in mammalian faunas, and especially the great diversity and abundance of native bovids in Africa (Hanks & Camberfort 1991). Given the

absence of native bovids in Australia, the body size of dung beetles in Australian savannas can be expected also to be smaller, and abundance of roller species far lower, than in Africa.

Fire is a major disturbance in tropical savannas (Andersen *et al.* 2003) and, at least in the Neotropics, dung-beetle assemblages are highly resilient to the direct effects of fire (Nunes *et al.* 2019). However, assemblages are sensitive to the indirect effects of fire through changes in vegetation structure (Andrade *et al.* 2011; Silveira *et al.* 2016). Australian savannas are extremely fire prone, with most sites burnt every 2-3 years (Russell-Smith & Yates 2001). Variation in fire regimes has a pronounced effect on vegetation structure, which has important implications for fauna (Andersen *et al.* 2003, 2012). However, the effects of variation in fire regimes on dung-beetle assemblages in Australian savannas is unknown.

Here we describe the first ecological study of a dung-beetle assemblage of an Australian tropical savanna. We document the (1) composition, (2) food preferences and (3) responses to variation in fire regimes, using a long-term fire experiment in the ‘Top End’ of the Northern Territory.

Methods

Study area

The study was conducted as part of the *Burning for Biodiversity* fire experiment at the Territory Wildlife Park (12°42’S 130°59’E), located at Berry Springs, 40 km south-east of Darwin. Mean annual rainfall is approximately 1,700 mm, heavily concentrated in a summer wet season, and mean daily maximum and minimum temperatures are 31°C and 23.2 °C, respectively (Australian Bureau of Meteorology; <http://www.bom.gov.au/climate/data>). The vegetation in the region is primarily savanna woodland dominated by *Eucalyptus tetradonta* and *E. miniata* in the overstorey, and the tall annual grass *Sorghum stipoides* in the grass layer. Understorey shrubs

such as *Acacia* spp., *Calytrix exstipulata*, *Exocarpus latifolius* and *Petalostigma pubescens* can also be common, especially where fire frequency is low.

The fire experiment consists of a string of 18 1-ha plots arranged in three blocks (A - C), each with six fire treatments that have been applied since 2004 (Parr *et al.* 2007; Scott *et al.* 2010; Andersen *et al.* 2014). Plots within a block were separated by 10 m, and blocks by 50-100 m. Fire had been actively excluded from the Park for 20 years prior to the beginning of the experiment. Sampling was conducted in nine of the 18 plots, representing three replicates each of high fire severity (H), moderate fire severity (M) and unburnt (U) (Fig 1). H included the annually burned plots in blocks A (plot A3) and B (plot B2), and M included plots burned every three years in blocks A (plot A1) and B (plot B4). The annually burned plot of block C (plot C3) had an unusually high density of shrubs and low cover of grass, making it highly resistant to burning. Its fires were extremely patchy and of very low intensity, and so we considered it an M plot. We used plot C2, experiencing higher-intensity, late-season fire every two years, as the third H plot. U comprised each of the unburnt plots (A6, B6 and C5) (Fig 2).

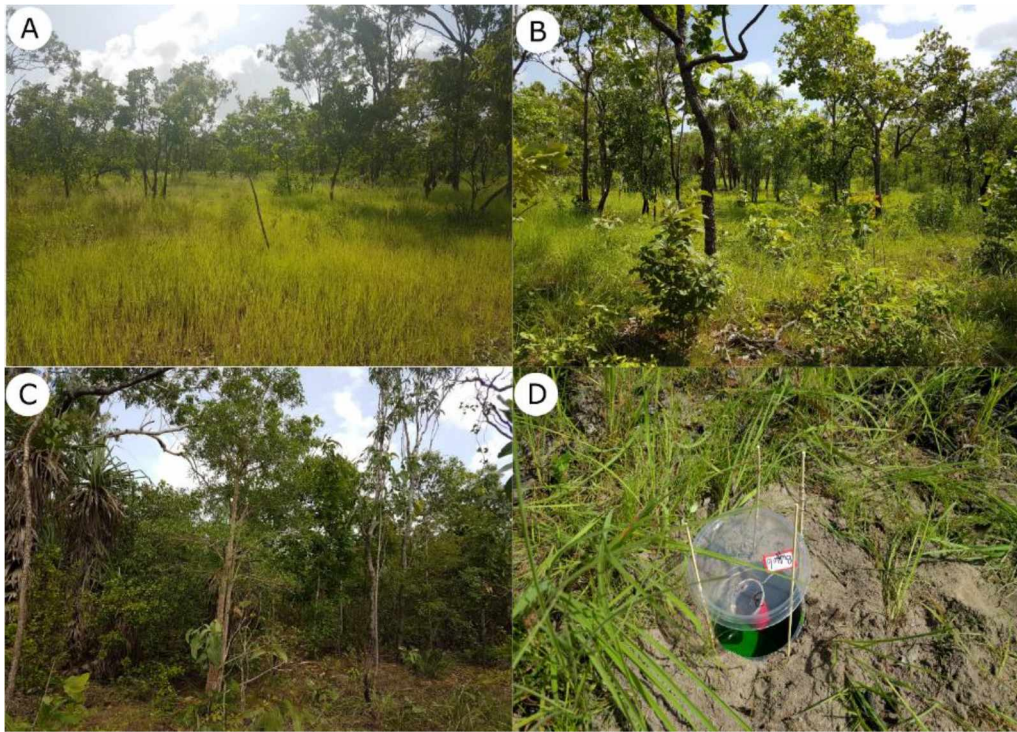


Fig. 1 – A-C. View of plots subject to different experimental fire regimes: (A) high severity; (B) moderate severity; (C) unburnt for 30 years. D. Baited trap used to sample dung beetles.

Sampling

We sampled dung-beetles using dung from five types of vertebrates:

1. Northern quoll (*Dasyurus hallucatus*), a small (0.5 - 1 kg), carnivorous marsupial occurring throughout far northern Australia;
2. Domestic dog (*Canis lupis familiaris*), a medium-sized (typically 5-40 kg) introduced and feral carnivorous placental mammal, occurring in throughout mainland Australia;
3. Agile wallaby (*Macropus agilis*), a medium-sized (16 - 27 kg), herbivorous macropod common throughout subcoastal northern Australia;

4. Asian water buffalo (*Bubalus bubalis*), a very large (up to 1,000 kg) domesticated herbivore with large feral populations in the Northern Territory;
5. Magpie goose (*Anseranas semipalmata*), a small (up to 3,2 kg), herbivorous bird that is common in wetlands throughout coastal northern Australia;

These dung types represented the dominant dung resources available in the region, both native (macropod, dasyurid and bird) and introduced (canid and bovid). As a sixth bait type, we also used cultivated mushrooms (*Agaricus bisporus*), given that mushrooms are known to be attractive to some Australian dung beetle species (Ebert *et al.* 2019).

The dung was collected fresh by Park staff during September and October 2018, and stored in a freezer prior to use. Dung beetles were sampled using baited traps during December (early wet season) 2018 and February (mid wet season) 2019. The wet season is the optimum period of the year to sample dung beetles in tropical areas (Lobo & Halffter 2000), and it is when most surveys in the wet tropics of North Queensland have been conducted (e.g. Ebert *et al.* 2019). On each occasion, six traps were established in the center of each plot, with traps located at the corners of a 10 x 5 m rectangle, and at the mid-points of the longer sides of the rectangle. Traps were plastic containers (19 cm diameter, 11 cm height) dug into the ground and filled with 150 ml of ethylene glycol as a preservative. Each trap had a wire hoop suspended over it to accommodate a small (4 cm diam, 5 cm height) plastic container for holding a dung bait (Fig. 1D). The traps were covered with plastic lids (20 cm diam) supported by three sticks to reduce drying of the bait and to protect the traps from rain. Traps within a plot were randomly assigned *ca.* 40 g of one of the six baits, and samples were collected after 48 hours. There was no rain during either sampling period. There was a total of 108 samples (6 baits x 9 plots x 2 sampling periods).

After sampling, dung beetles were sorted to morphospecies and counted. Voucher specimens were pinned and identified by the specialist Tom Weir, who is a leading expert on Australian dung beetles. A complete collection of voucher specimens is deposited at the Australian National Insect Collection, Canberra.

Woody cover

In December 2018 we quantified woody-plant cover in each plot, as a key measure of vegetation structure that is influenced by fire. Measurements were taken 5 estimates along each transect, totaling at 15 points (points within a transect separated by 15 m; transects separated by 30 m) in each plot. At each point, woody cover was visually estimated inside a 5 x 5 m quadrat according to a 6-point scale: <5%, 5-10%, 11-25%, 26-50%, 51-75%, >75% (as proposed by CNPS 2019). The mean-points of cover classes were used for statistical analysis.

Data analysis

For all statistical analyses we pooled data from the two sampling periods (December and February). To evaluate the significance of bait types and fire regime as correlates of the abundance and richness of dung beetles, we carried out two separate generalized linear models (GLMs), one for each response variable, assuming a quasi-poisson error distribution and using a log-linking function. We built a generalized linear mixed model (GLMM) to determine if woody cover varied among fire treatments, using quadrat-level data and with plot as a random factor intercept. This was performed using the lme4 package (Bates *et al.* 2015), assuming a binomial error distribution. We tested if the total abundance and richness of dung beetles (response variables) were related to woody cover (plot means; predictor variable) using GLMs with quasi-

poison error distribution. We used the *multcomp* package (Bretz *et al.* 2010) to perform all post-hoc comparisons using Tukey tests when models indicated differences in categorical variables. All analyses were performed in R version 3.5.2. (R Core Team 2018) and we checked the adequacy of each model by examining the distribution of the residuals (Crawley 2012).

To compare compositional responses of dung beetles to bait type and fire regime, we first constructed Bray-Curtis similarity matrices, based on abundance data. For fire regime we pooled all the beetles from each bait-type from each plot, and for bait type we disregard the fire regime. We ordinated sites using Non-metric Multidimensional Scaling (NMDS) and conducted permutational multivariate analysis of variance (PERMANOVA) in PRIMER V.7 (Clarke & Gorley 2015) to test for site clustering in relation to bait type and fire regime. P-values were generated by permutation (n = 999).

Results

The dung-beetle fauna

In total, 221 dung beetles (107 and 114 in the early and mid-wet seasons, respectively) were collected, belonging to nine species of *Onthophagus* (Table 1). The most commonly recorded species were *O. mimusculus* (51% of total beetles sampled) and *Onthophagus* nr. *quadripustulatus*(20%).

Table 1 – List of species of dung beetles collected and their abundance in relation to season (early and mid-wet season), bait type (no beetles were recorded at either wallaby or magpie goose dung), and fire regime (High intensity, Moderate intensity and Unburnt).

Species	Season		Bait type				Fire regime			Total
	Early	Mid	Dog	Quoll	Buffalo	Mushroom	High	Moderate	Unburnt	
<i>Onthophagus discolor</i> Hope, 1842	1	10	5	1	5			5	6	11
<i>Onthophagus erichsoni</i> Hope, 1842	9	10	18	1			2	11	6	19
<i>Onthophagus fabricii</i> Waterhouse, 1894	2	4	5		1			6		6
<i>Onthophagus glabratus</i> Hope, 1842	6	1	7				2	1	4	7
<i>Onthophagus minusculus</i> Macleay, 1888	41	71	83	11	15	3	62	33	17	112
<i>Onthophagus ocelliger</i> Harold, 1877	4		4				3		1	4
<i>Onthophagus parrumbal</i> Matthews, 1972	2	14	4	1		11	2	7	7	16
<i>Onthophagus rubescens</i> Macleay, 1888	2		2				1		1	2
<i>Onthophagus</i> nr. <i>quadripustulatus</i>	40	4	44				24	15	5	44
Number of species	9	7	9	4	3	1	7	7	8	9
Total	107	114	172	14	21	14	96	78	47	221

Food preferences

The total abundance and richness of dung beetles both varied with bait type (abundance: $F_{5,46} = 109.43$, $p < 0.001$; richness: $F_{5,46} = 40.63$, $p < 0.001$; Fig. 2). Dog dung was by far the most attractive bait, accounting for 78% of all beetles collected, and recording all nine species. Traps with wallaby and magpie-goose dung failed to capture any beetles, while baits with quoll dung, buffalo dung and mushrooms attracted four, three and two species respectively.

The composition of dung-beetle species varied significantly with bait type (Pseudo $F = 8.82$, $df = 3$, $p < 0.01$, Fig 5A). Species composition at Buffalo dung was significantly ($p < 0.01$) different from all other bait types except Quoll dung ($p = 0.17$), which was significantly ($p < 0.01$) different from dog dung, but not from mushrooms ($p = 0.09$). *Onthophagus glabratus*, *O. ocelliger*, *O. rubescens* and *O. nr. quadripustulatus* were recorded only at dog dung, and *O. erichsoni* was recorded only at dog and quoll dung. *Onthophagus minisculus* was commonly recorded at buffalo as well as dog and quoll dung (i.e. at both carnivore and herbivore dung), and *O. discolor* and *O. fabricii* were also recorded at both dog and buffalo dung. Finally, *O. parrumbal* occurred primarily at mushroom baits, but also at dog and quoll dung.

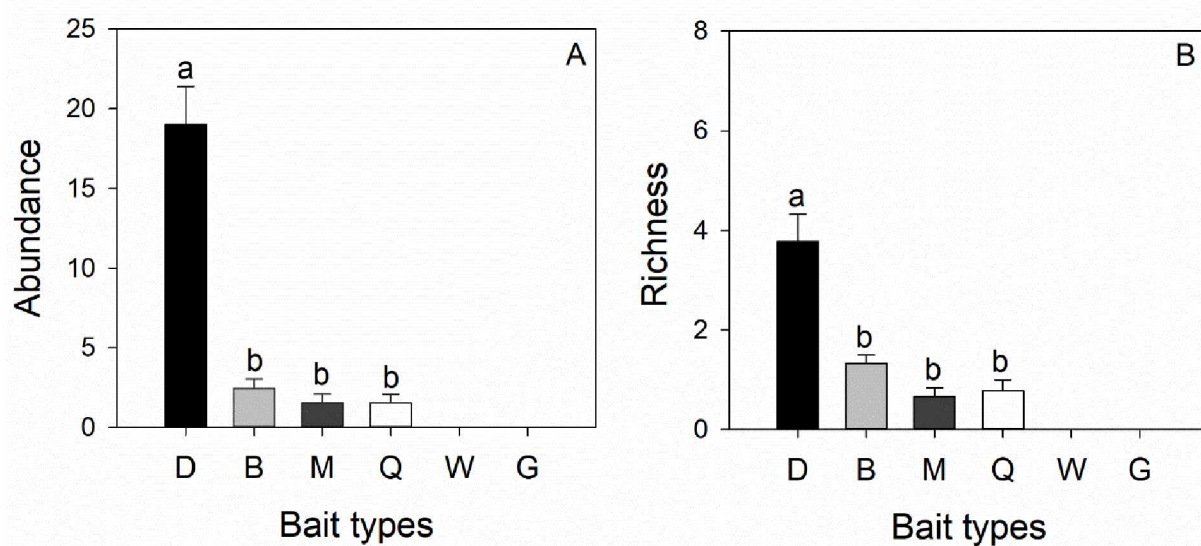


Fig. 2 – Mean and standard error of the (A) abundance and (B) species richness of dung beetles in relation to different types of baits. Different letters indicate statistical difference between bait as indicated by Tukey analyses at 5% significance. D = dog; B = buffalo; M = mushroom; Q = quoll; W = wallaby; G = mapgie goose.

Responses to fire

The total abundance of dung beetles varied significantly with fire regime ($F_{2,51} = 10.69$, $p < 0.001$), with no interaction with bait type ($F_{10,36} = 1.36$, $p = 0.23$). Abundance was higher under high (H) and moderate (M) severity fires compared with unburnt (Fig. 3A), due primarily to the two most common species, *O. minisculus* and *O. nr. quadripustulatus* (Table 1). *Onthophagus erichsoni* and *O. fabricii* were most commonly recorded in M plots, and *O. glabratus* in unburnt plots. Species richness was not related to fire regime ($F_{2,51} = 0.17$, $p = 0.84$, Fig. 3B), and there was no interaction between fire regime and dung type ($F_{10,36} = 0.36$, $p = 0.95$).

Woody cover varied among fire regimes ($\chi^2 = 33.57$, $df = 2$, $p < 0.001$), being two times higher in the unburnt than in the burnt plots, but not significantly different between the H and M regimes (Fig. 4A). Dung beetle abundance decreased with increasing woody cover ($F_{1,7} = 11.15$, $p = 0.01$, Fig. 4B), but there was no relationship between dung beetle species richness and woody cover ($F_{1,7} = 2.39$, $p = 0.17$).

There was no significant relationship between species composition and fire regime (Pseudo $F = 1.33$, $df = 2$, $p = 0.30$, Fig. 5B), and no interactive effect of bait type and fire regime on species composition (Pseudo $F = 0.61$, $df = 6$, $p = 0.83$).

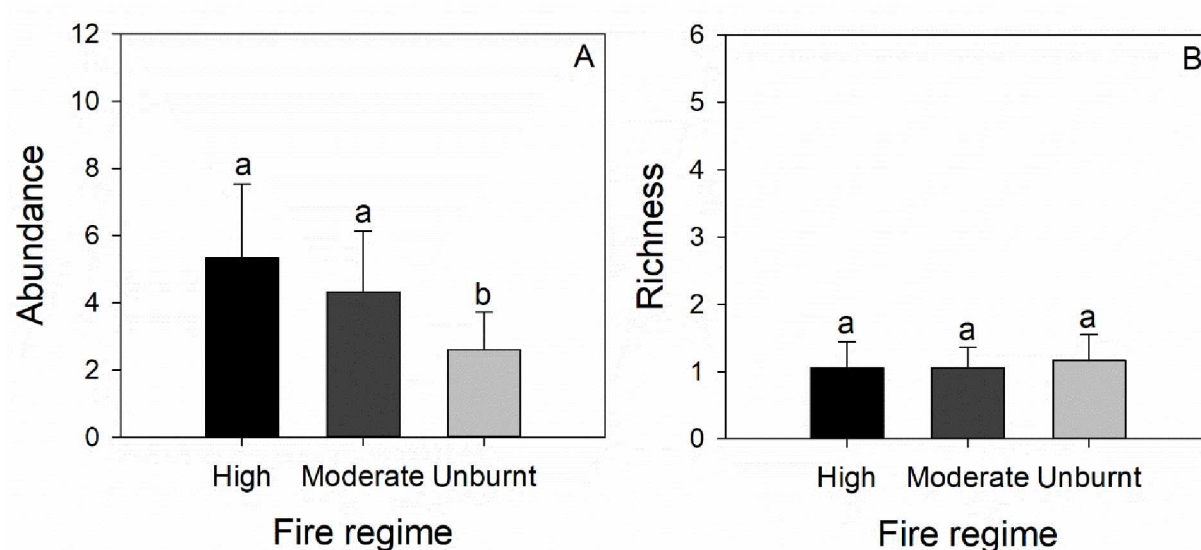


Fig. 3 – Mean and standard error of the (A) abundance and (B) species richness of dung beetles in relation to different fire regimes. Different letters indicate statistical difference between bait as indicated by Tukey analyses at 5% significance

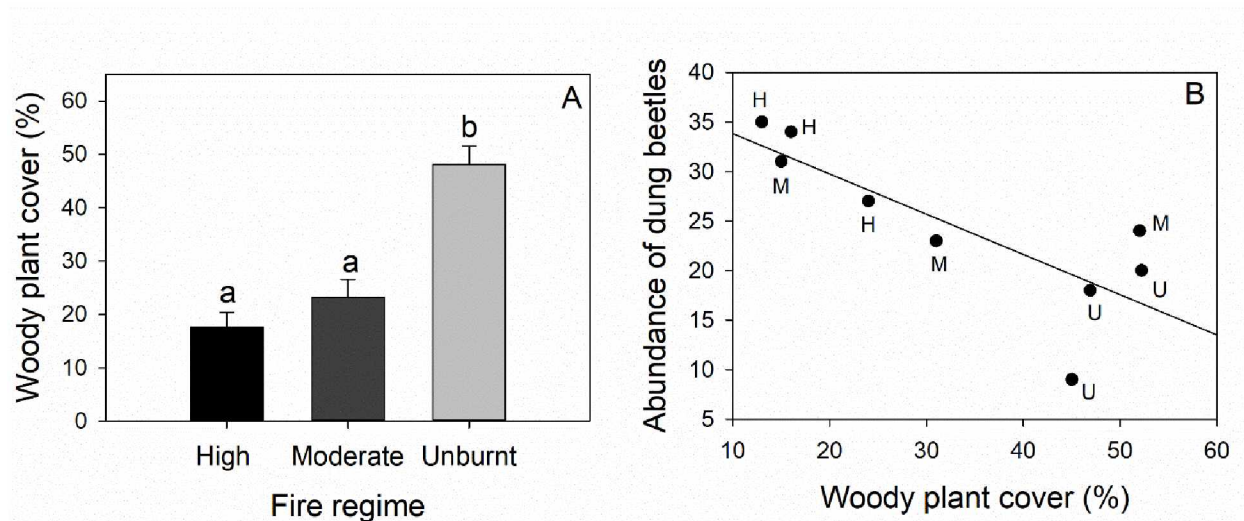


Fig. 4 – A. Mean woody-plant cover in plots subject to different fire regimes (H = high intensity; M = moderate intensity; U = unburnt). Different letters indicate statistical differences between the means. B. Relationship between dung-beetle abundance and woody-plant cover ($R^2 = 0.60$).

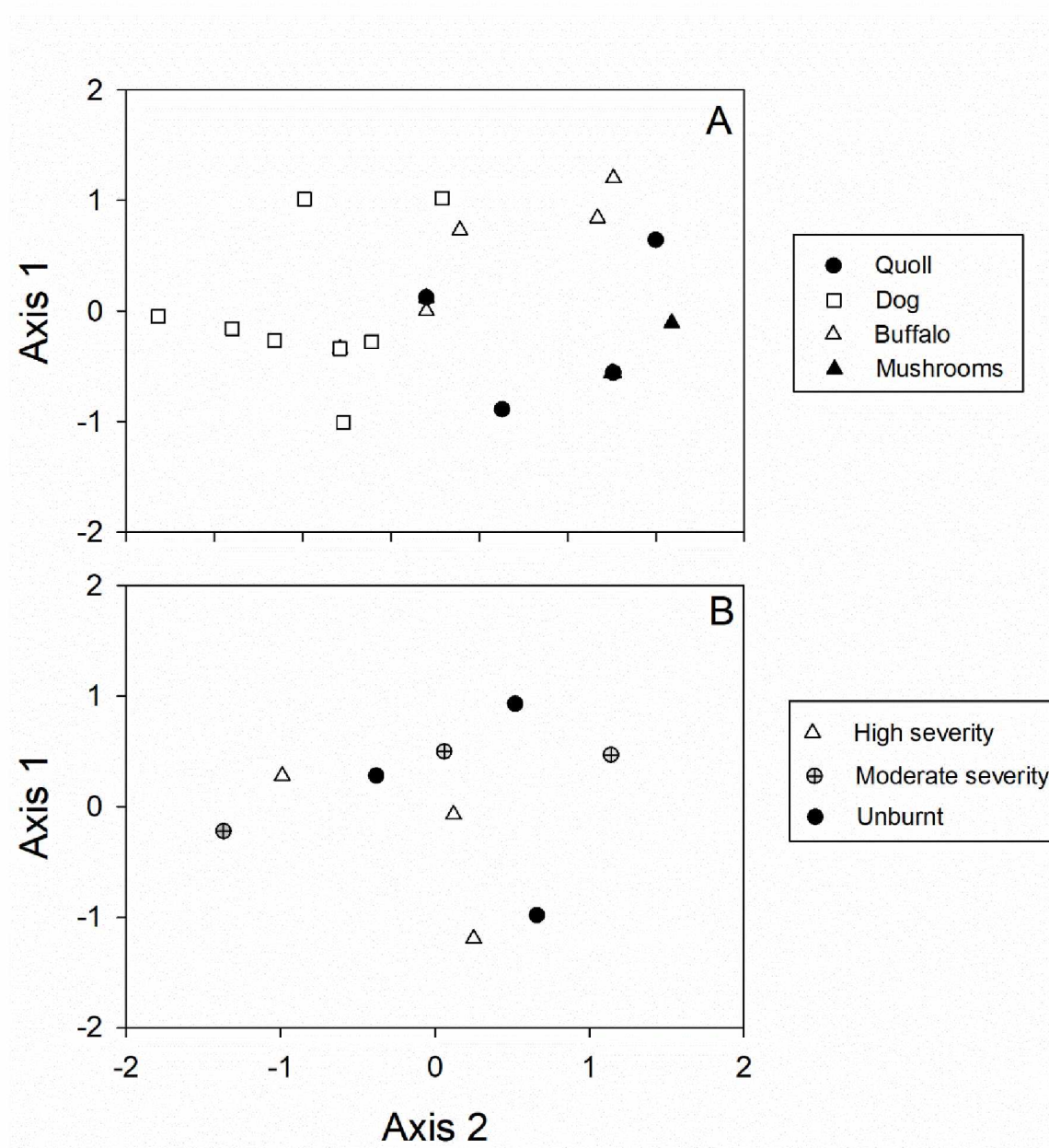


Fig. 5 – NMDS represents the points on the ordinations of dung-beetle species composition in relation A. different types of baits (baits with no beetles are not shown) (Stress: 0.11) or B. different fire regimes. (Stress: 0.12)

Discussion

Australia has a dung-beetle fauna that is well-known taxonomically, but the environmental associations and food preferences of its species are poorly known. Ours is the first ecological study of a dung-beetle assemblage in the Australian monsoonal tropics, and it is the first study of the effects of variation in fire regimes on an Australian dung-beetle assemblage. Our sampled dung beetle assemblage was comprised entirely of native species of *Onthophagus*. Frequent fire can promote dung-beetle abundance, but fire did not affect species composition.

Our first aim was to document assemblage composition, and remarkably our samples were comprised entirely of species of *Onthophagus*. This is one of the richest of all animal genera, with more than 1,500 species worldwide (Scholtz *et al.* 2009), including at least 230 in Australia (Matthews 1972; T. Weir unpublished data). Eight of our nine species are described, all of which are widely distributed in northern Australia, occurring also in Western Australia and/or Queensland (Matthews 1972). *Onthophagus* nr *quadripustulatus* is an undescribed species known only from Berry Springs and Kakadu National Park (approximately 200 km east of Berry Springs). Our species represent a fraction of the regional *Onthophagus* fauna, with at least 27 additional species known from the Greater Darwin region. Many other dung-beetle genera also occur in the broader region, including *Amphistomus*, *Coptodactyla*, *Lepanus*, *Tesserodon* and *Temnoplectron* (Matthews 1972, 1974, 1976). Dung-beetle species often have locally patchy distributions, especially in relation to soil (Davis 1996; Hanski & Cambefort 1991). However, it is unclear if the absence from our samples of so many taxa from the regional species pool is due to a lack of occurrence at our study site, or the bait type used.

In Australia, *Onthophagus* occurs primarily in open habitats (Matthews 1972; Ebert *et al.* 2019), which reflects its African origin and adaptation to aridity (Tarasov & Genier 2015;

Tarasov & Dimitrov 2016). *Onthophagus* species dominate the dung-beetle fauna of open forests in Australia's wet tropics (Ebert *et al.* 2019), and our results suggest that such dominance is even more extreme in the Australian monsoonal tropics, as proposed by Matthews (1972, 1974). As is typical of the genus in Australia, all the species of *Onthophagus* in our study are relatively small (≤ 10 mm body length) and are 'tunnelers' (Kenyon *et al.* 2016), storing dung and other food resources in tunnels dug immediately below the food source (Hanski & Cambefort 1991). Small species tend to have higher thermal tolerances (Verdú *et al.* 2006; Barragán *et al.* 2011), and tunneler species are often favored in open habits because they are not very sensitive to hot and dry conditions (Escobar *et al.* 2004; Correa *et al.* 2016).

Our second aim was to document food preferences, as indicated by attraction to different bait types. Dog dung was by far the most attractive of our six bait types, attracting all nine species and nearly 80% of all individuals. More individuals were similarly attracted to the dung of carnivores than herbivores at Lamb Range in the Australian Wet Tropics (Vernes *et al.* 2005). However, in another study in the Australian Wet Tropics herbivore dung attracted more individuals, and a similar number of species, compared to carnivore dung (Ebert *et al.* 2019). The food preferences of dung-beetle faunas therefore vary markedly in tropical Australia.

Five of our nine species (*O. glabratus*, *O. ocelliger*, *O. rubescens*, *O. nr. quadripustulatus* and *O. erichsoni*) were recorded only at dog and quoll dung. We had only very few records of *Onthophagus ocelliger* and *O. rubescens*, but Matthews (1972) noted that both species are only rarely if ever attracted to herbivore dung. All five species probably can be considered carnivore specialists. Only three species (*O. minisculus*, *O. discolor* and *O. fabricii*) were recorded at both carnivore and herbivore (buffalo) dung, and therefore can be considered dietary generalists. *Onthophagus parrumbal* was the only species occurring primarily at mushroom baits; it has

previously been recorded from decayed fungus (Matthews, 1972, T. Weir unpublished data) and appears to be a mushroom specialist.

Surprisingly, we recorded no beetles at traps baited with wallaby dung, despite wallaby dung being known to attract a range of dung-beetle species (Gollan *et al.* 2011; Ebert *et al.* 2019). Compared with buffalo, wallabies produce relatively dry and fibrous dung, and it is possible that the high temperatures and lack of rain during our sampling made our baits drier and harder, and therefore less attractive to dung beetles (Gardner *et al.* 2008). If so, wallaby dung would frequently be unattractive to dung-beetles at our study site even over the wet season. Magpie goose dung also failed to attract any dung beetles. It is unclear if this is because the magpie goose is a wetland bird not occurring in savanna habitats and therefore unfamiliar to our sampled species, or if it reflects a lack of attraction to bird dung more generally. However, only a very few species of Australian native dung beetles have been associated with bird dung, mostly species of *Lepanus* (T. Weir unpublished data). Four species of *Lepanus* are known to occur in the Greater Darwin Region (Gunter & Weir 2019, T. Weir unpublished data) but none of these were recorded in our study.

Our final aim was to assess the responses of dung beetles to experimental fire regimes, comparing plots burned with high fire severity, moderate fire severity and long unburned. Our study design is limited by relatively small (1 ha.) plot size, which potentially allowed movement between plots. The distances that Australian dung beetle species can detect food resources is unknown (Gollan *et al.* 2011), but a minimum distance of 100 m between traps has been suggested for avoiding lack of independence of catches (Silva & Hernández, 2015). Any movement between plots would act to reduce apparent fire effects, but we found significant differences in dung-beetle abundance among fire treatments. Overall dung-beetle abundance was

highest under high fire severity and lowest in the long-term absence of fire, and it was negatively correlated with the cover of woody vegetation. Such a relationship between dung-beetle abundance and woody cover also occurs in Amazonian savannas (Louzada *et al.* 2010). Vegetation cover can affect dung beetles by regulating microclimate (Menendez & Gutierrez, 2004), as well as by affecting the vertebrate fauna and therefore resources for dung beetles (Nichols *et al.* 2009). However, vegetation cover can also affect sampling efficiency, through both the distance that bait odor can spread and the accessibility of baits (Riffell *et al.* 2008). The relative importance of habitat preference and sampling efficiency as drivers of our higher catches at sites with lower vegetation cover is unclear. The highest overall abundance under high fire severity (and lowest woody cover) was driven by the two most common species (*O. nr. quadripustulatus* and *O. minisculus*), whereas most of the less common species occurred primarily under moderate fire severity (moderate woody cover) or in the absence of fire (highest woody cover). Such patterns of occurrence cannot be explained by sampling efficiency, and therefore reflect habitat preferences. Notably, no species occurred exclusively in long-unburnt plots.

Although fire had a marked impact on the overall abundance of dung beetles at baits, it had no effect on species richness or presence/absence composition. However, as mentioned previously this might be at least partly an artefact of our relatively small plot size, which potentially allowed movement of species between plots.

The functional composition of dung beetle assemblages can provide valuable insights into intercontinental comparisons of biomes where contemporary climate, vegetation structure and key processes such as fire are shared, but evolutionary histories vary markedly. Dung beetles are closely associated with mammals, and it is not surprising that highest species richness occurs

in African savannas (Camberfort *et al.* 1991), where the diversity and abundance of large mammals is also highest. A high availability of large dung resources favors large dung beetles and the roller functional trait (Doubé 1991; Hanski & Camberfort 1991; Kunz & Krell 2011). Our results are consistent with the expectation that, compared with Africa, dung-beetle assemblages in Australian savannas have smaller body sizes and are dominated by tunnelers rather than rollers.

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Conclusão geral

Os resultados dessa tese fornecem um melhor entendimento de como as comunidades de besouros Scarabaeinae e formigas são estruturadas e como eles respondem aos impactos antrópicos em regiões tropicais de savanas. A maioria dos estudos anteriores foi realizada em florestas tropicais (e.g., Vasconcelos et al. 2000; Braga et al. 2013), mas os resultados desses estudos não podem ser extrapolados para as savanas, já que as respostas da comunidade de besouros e formigas são contexto-dependentes, e estão diretamente relacionadas a fatores ambientais (Griffiths et al., 2015; Oliveira et al., 2017; Nunes et al., 2018).

No primeiro capítulo eu demonstrei que a conversão de savanas e florestas em habitats manejados pelo homem alterou a estrutura funcional da comunidade de besouros, sendo que quase todas as métricas funcionais foram afetadas. Entretanto essas diferenças foram muito mais acentuadas nas comparações envolvendo pastagens e plantações de soja do que aquelas envolvendo as plantações de eucalipto. As comunidades de besouros de savanas e de florestas apresentaram respostas semelhantes à conversão em áreas de pastagens e de agricultura. Essa conversão resultou na perda de besouros de corpo grande e de escavadores, e em um aumento de besouros pequenos e residentes. Tais mudanças podem afetar o funcionamento do ecossistema, já que não existe uma compensação para todas as funções ecológicas (Nichols et al. 2007; Slade et al. 2007). Por outro lado, a conversão de áreas florestais em plantações de eucaliptos teve efeito maior sobre a comunidade de besouros de floresta do que de savana. Uma meta-análise realizada por Nichols et al. (2007) demonstrou que o contexto da paisagem é importante para entender a resposta dos besouros a modificação dos habitats. Como as áreas de savana tem distribuição predominante na paisagem estudada, possivelmente isto esteja influenciando o pool de espécies de besouros encontrados nas plantações de eucalipto. Para uma melhor compreensão de como a

estrutura funcional das comunidades de besouros é afetada é necessário levar em consideração as características dos ambientes nativos e dos sistemas manejados, assim como ter conhecimento dos elementos que compõem a paisagem estudada. Dessa forma é possível prever as consequências sobre o funcionamento do ecossistema. Entretanto destaco a necessidade de mensurar as funções ecológicas (ex: remoção de fezes, solo revolvido e dispersão de sementes) realizadas pelos besouros Scarabaeinae, já que existem poucas informações se as métricas de diversidade funcional atuam como bons preditores das funções ecológicas realizadas pelos besouros em ambientes nativos e agrícolas (mas ver Griffiths et al. 2015).

No segundo capítulo, eu demonstrei que besouros e formigas, táxons que são comumente usados como bioindicadores, apresentaram respostas contrastantes ao manejo da terra na savana brasileira. Dessa forma eles forneceram diferentes indicações do impacto do manejo das pastagens sobre a biodiversidade. A estrutura da vegetação foi o principal direcionador da variação da comunidade de formigas, enquanto a comunidade de besouros respondeu principalmente a frequência no uso de parasiticidas. As formigas indicaram a importância da estrutura da vegetação, particularmente da presença de árvores em fornecer lugares para a nidificação, e recursos alimentares para a fauna (Frizo and Vasconcelos 2013; Neilly et al. 2018). Alguns grupos funcionais de formigas e os besouros roedores pequenos indicaram o efeito de ambientes abertos sobre o microclima e a atividade locomotora de outros artrópodes. Já os besouros e as formigas cultivadoras de fungos superiores indicaram o impacto negativo do uso de parasiticidas sobre os invertebrados que alimentam e/ou nidificam nas fezes. Por isso é necessária uma fiscalização rígida de órgãos do governo, e também políticas públicas que conscientize os proprietários dos riscos ambientais e na saúde, associados com a utilização exagerada desses produtos veterinários. Além disso, são necessárias ações que incentivem os

produtores a substituírem os produtos à base de Ivermectina, por produtos que causem menos impactos. Uma alternativa seria a utilização de produtos à base de *Azadirachta indica* (Nim), que é uma planta, que contém substâncias com potencial inseticida (Chagas & Vieira 2007). O Nim tem pouco impacto na fauna de insetos não alvo (Souza et al. 2016) e não causa consequências sobre a saúde humana (Schmutter 1990). Além das políticas públicas, eu sugiro que uma maior comunicação entre pesquisadores e produtores, possa ajudar os produtores a ter conhecimento da importância da biodiversidade nas pastagens. Destaco também a necessidade de trabalhos que valorem os serviços ecossistêmicos fornecidos pelos besouros nas pastagens brasileiras. Estudos realizados nos Estados Unidos e Reino Unido valoraram os serviços em US\$380 e £367 milhões, respectivamente (Losey and Vaughan 2006, Beynon et al. 2015). Porém como esses estudos foram realizados em países desenvolvidos, esses resultados não podem ser transferidos para os países tropicais, já que as práticas de manejo, as características abióticas e a fauna são diferentes.

No terceiro capítulo, realizado na savana australiana, eu demonstrei que a fauna de besouros no local de estudo é composta apenas de besouros pequenos e escavadores do gênero *Onthophagus*. As fezes de cachorro foi a mais atrativa, capturando todas as espécies amostradas e também 80% dos indivíduos. Meus resultados também mostraram que o fogo frequente promoveu uma alta abundância de besouros Scarabaeinae por meio da manutenção de uma estrutura de habitat aberto. Já a ausência de fogo, resultou em uma menor abundância de besouros. Esse trabalho contribuiu para um melhor entendimento entre a associação de mamíferos e besouros, já que esse conhecimento ainda é limitado, especialmente na Austrália (Raine and Slade 2019). A baixa abundância e riqueza de espécies de besouros coletados podem estar associadas com os recursos que foram utilizados como isca atrativa. Alguns estudos têm demonstrado que a utilização de fezes de mamíferos comuns na região, atrai menos do que fezes

humanas ou de porco (ver Raine et al. 2018). Entretanto o tipo de recurso escolhido como isca atrativa irá depender do objetivo de cada trabalho.

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