UNIVERSIDADE FEDERAL DE LAVRAS

RAFAELLA TEIXEIRA MACIEL OLIVEIRA

EFFECTS OF THE CONVERSION OF NEOTROPICAL SAVANNAS INTO PASTURES ON DUNG BEETLES BIODIVERSITY AND THEIR ECOLOGICAL FUNCTIONS

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

Prof. Dr. Julio Neil Cassa Louzada
Orientador
Prof. Dr. Rodrigo Fagundes Braga
Coorientador

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RESUMO GERAL

A substituição de sistemas naturais causada pela expansão da agricultura e pecuária tem sido o principal determinador da biodiversidade nas regiões tropicais. Associada às mudanças de uso do solo, as mudanças climáticas têm causado fortes impactos nos sistemas biológicos e podem alterar a distribuição e as interações das espécies. Estima-se que um quinto da população humana mundial viva em regiões de savanas tropicais e dependem diretamente desses sistemas, fazendo com que este seja um dos sistemas que sofrem mais distúrbios atualmente. O Cerrado brasileiro é a savana tropical mais biodiversa e com maiores taxas de endemismo, no entanto, tem sido amplamente devastado para a implementação de áreas destinadas à agricultura e pecuária. Os besouros rola-bostas são sensíveis às mudanças climáticas, já que o clima influencia diretamente seu ciclo de vida. Além disso, esses besouros têm sido amplamente usados como bioindicadores por apresentarem especificidade de habitat e por responderem às mudanças nas condições ambientais. Devido a isso, tanto as mudanças climáticas quanto distúrbios nos sistemas naturais podem afetar a comunidade de besouros rola-bostas, mudando as associações de habitat e reduzindo as taxas de remoção de fezes e demais funções associadas. Neste trabalho, investigamos os efeitos da conversão de savana tropical em pastagens na biodiversidade e funções ecossistêmicas, usando os rola-bostas como modelo de estudo. Nós também utilizamos variável climática e variáveis ambientais para testar seus efeitos diretos e indiretos na comunidade de rola-bosta e suas funções ecológicas de remoção de fezes, revolvimento do solo, e a interação entre besouros e moscas detritívoras. Para isso, selecionamos áreas experimentais de Cerrado e pastagens exóticas introduzidas em diferentes localidades no estado de Minas Gerais, Brasil. Nós encontramos que a conversão de savana em pastagens tem efeito negativo tanto na diversidade taxonômica quanto na diversidade funcional, causando declínio na riqueza de espécies, riqueza funcional e equitabilidade funcional dos besouros. Também encontramos que a conversão do Cerrado em pastagens pode causar um efeito em cascata, já que a perda de cobertura vegetal leva à perda na riqueza de espécies, o que por sua vez causa declínio da biomassa total e diversidade funcional, afetando as funções ecológicas e a interação entre besouros e moscas detritívoras. No entanto, o efeito da mudança de uso do solo em savana tropical é dependente da zona bioclimática. Nossos resultados mostram a importância do Cerrado para a biodiversidade e manutenção do funcionamento dos ecossistemas, e sugerimos que políticas públicas sejam tomadas de forma a avaliar as regiões submetidas a diferentes condições bioclimáticas de maneira independente, já que a resposta das comunidades de besouros rola-bosta se mostrou dependente do contexto regional.

Palavras-chave: Diversidade taxonômica. Diversidade funcional. Funcionamento do ecossistema. Zona bioclimática. Mudança de uso do solo. Cerrado.

GENERAL ABSTRACT

The replacement of natural systems caused by the expansion of agriculture and livestock has been the main driver of biodiversity in tropical regions. Associated to the land use changes, the climate change are having a strong impact on biological system and may altered the biodiversity distribution and interactions. It is estimated that one-fifth of the world's population live in tropical savannas regions and depends directly on these systems, making than one of the most impacted ones. The Brazilian Cerrado is the largest, richest tropical savannah, with a high rate of endemism, however it has been extensively cleared for agriculture and livestock. The group of organisms of dung beetles are sensitive to climate changes, since climate has direct influence on their life cycle. Besides, these beetles has been widely used as bioindicator since they show habitat specificity and respond to changes in environmental conditions. Due so, both climate changes and disturbances in natural systems may affect dung beetle communities, changing the habitat associations and reducing the rates of dung removal and the associated functions. Here, we aim to understand how conversion of savannah into pasture affects biodiversity and ecosystem functioning using dung beetles as a study group. We also assessed climatic and environmental variables to test their direct and indirect effects on dung beetle communities and associated ecological functions dung removal, soil bioturbation, and dung beetles interaction with dung-feeding fly. To do these, we selected experimental study areas of Cerrado and exotic cattle pastures in different municipalities in the state of Minas Gerais, Brazil. We found that conversion of savanna into pasture has a negative effect on both taxonomic and functional diversity metrics, causing loss of species richness, functional richness and equitability. We also found that Cerrado conversion into pasture can have a cascade effect, as the loss of vegetation cover leads to loss of dung beetle species richness, which causes loss of biomass and functional indices, affecting dung beetle functions and interaction with dung flies. However, the effect of land use changes in tropical savannas is dependent of the bioclimatic zones. Our results showed the importance of Cerrado habitat for biodiversity and the maintenance of ecosystem functioning, and we suggest that pubic politics should be thought to evaluate separately each region, submitted to the effects of different bioclimatic conditions, since the responses of dung beetles communities are context dependent.

Keywords: Taxonomic diversity. Functional diversity. Ecosystem functioning. Bioclimatic zone. Land use change. Cerrado.

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PRIMEIRA PARTE

INTRODUÇÃO GERAL

A crescente demanda para produção de alimento tem sido o principal responsável pela substituição de sistemas naturais em áreas destinadas à agricultura e pecuária (Aide et al., 2013; Houghton, 2012; Sy et al., 2015). Essa mudança de uso do solo causa declínio da biodiversidade, afetando o funcionamento dos ecossistemas e a provisão de serviços ambientais essenciais para o bem estar humano (Braga et al., 2013; Cardinale et al., 2012; Foley, 2005; Suarez-castro et al., 2015). Juntamente com a degradação ambiental, o clima vem tornando-se uma importante causa de extinção, com as mudanças climáticas em andamento nos dias de hoje (Lemes et al., 2019; Pacifici et al., 2015; Thomas et al., 2004). Já é conhecido que as mudanças climáticas têm forte impacto em sistemas biológicos, alterando as populações, comunidades e processos ecossistêmicos, com possíveis consequências no funcionamento dos ecossistemas (Milotić et al., 2017; Parmesan, 2006; Thomas et al., 2004).

Estudos recentes têm mostrado que as espécies já estão respondendo a mudanças microclimáticas, através de mudanças na distribuição geográfica e altitudinal (Birkett et al., 2018; Parmesan, 2006; Pecl et al., 2017). Além disso, a interação entre as espécies e suas respostas a variações do clima são dependentes do contexto do habitat (González-Megías and Menéndez, 2012; Slade et al., 2016). Sendo assim, as variações climáticas associadas às mudanças de uso do solo podem não só afetar a distribuição das espécies, mas também a interação entre elas, produzindo cenários imprevisíveis (González-Megías and Menéndez, 2012). Diante disso, torna-se essencial entender a relação entre as variações climáticas e mudanças de uso do solo e seus efeitos nas comunidades e suas funções, para prever os efeitos negativos e tomar medidas de conservação necessárias.

A conversão de sistemas naturais em pastagens para criação de gado tem tido fortes impactos em sistemas florestais, devido à abrupta perda na cobertura vegetal (Ratnam et al., 2011). No entanto, tem sido sugerido que em sistemas de fitofisionomias naturalmente mais abertas, tais como as savanas tropicais, essa mudança de uso do solo pode causar apenas mudanças sutis, e a degradação, perda de biodiversidade e funcionamento do ecossistema podem ser mais discretas e menos visíveis comparado a sistemas florestais (Almeida et al., 2011; Parr et al., 2014; Zaloumis and Bond, 2011). Nas últimas décadas, estudos usando métricas de diversidade funcional para complementar a abordagem taxonômica, para quantificar a resposta da biodiversidade e suas funções à degradação ambiental tem aumentado (Barragán et al., 2011; Elmqvist et al., 2003; Gagic et al., 2015). Com isso, a inclusão da abordagem funcional tem permitido o melhor entendimento dos mecanismos que determinam essa resposta da biodiversidade às mudanças no ecossistema (Beiroz et al., 2018; Mouillot et al., 2013; Petchey and Gaston, 2006). Além disso, alguns estudos têm sugerido que métricas funcionais melhor predizem o funcionamento dos ecossistemas do que os tradicionais índices baseados em espécies (Gagic et al., 2015). No entanto, as métricas funcionais mais utilizadas são baseadas em características categóricas comportamentais, e não consideram as características morfológicos dos indivíduos, o que pode causar perda de informações (Griffiths et al., 2015; Petchey and Gaston, 2006).

Um dos sistemas que tem sido mais degradado atualmente, são as savanas tropicais. Savanas tropicais cobrem mais de 20% da superfície da terra (Scholes and Archer, 1997), e estima-se que um quinto da população mundial dependa diretamente desse sistema, em grande parte para criação de gado (Lehmann et al., 2009; Olsson and Ouattara, 2013). O Cerrado brasileiro é uma das maiores e mais rica savana tropical, com altas taxas de endemismo, sendo considerado um importante *hotspot* para a biodiversidade (Myers et al., 2000). No entanto é também um dos sistemas mais ameaçados. Nas últimas décadas, o Cerrado tem sido extensivamente degradado para implementação de agricultura e pecuária, e estima-se que metade de suas áreas naturais tenham sido perdidas nos últimos 50 anos (Beuchle et al., 2015; Overbeck et al., 2015).

O Cerrado constitui a segunda maior formação vegetal do Brasil e está localizado, em sua maioria, na região central do país (Alho, 2005). Este sistema é formado por um complexo mosaico de fitofisionomias nativas que variam desde o campo limpo (predominância de gramíneas, usadas tradicionalmente como pastagem), passando pelo campo sujo e Cerrado *sensu strictu* até florestas semidecíduas (Cerradão e florestas ciliares) (Ribeiro and Walter, 1998). A substituição de áreas nativas por pastagens de gramíneas exóticas, em sua maioria *Urochloa* spp., vem sendo implementada em muitas regiões com o objetivo de aumentar a capacidade suporte de gado (Martha and Vilela, 2002; Cavalcanti and Joly, 2002). O efeito da conversão de savanas tropicais em sistemas antrópicos na biodiversidade tem sido bem documentada (Arcoverde et al., 2017; de Queiroz et al., 2017; Lemes et al., 2019), mas pouco se sabe sobre esses efeitos na diversidade funcional e nas funções ecossistêmicas.

Dentre todos os organismos, os insetos, como os besouros rola-bosta (Coleoptera: Scarabaeidae: Scarabaeidae), são aqueles mais afetados pelas mudanças climáticas, já que o clima tem influência direta no seu desenvolvimento, reprodução e sobrevivência (Bale et al., 2002; Menendez, 2007). Além disso, esses besouros apresentam especificidade de habitat e a estrutura de sua comunidade é fortemente afetada pelo tipo de vegetação, respondendo a mudanças nas condições ambientais, e por isso têm sido amplamente utilizados como bioindicadores (Bicknell et al., 2014; Costa et al., 2017; Filgueiras et al., 2015; Halffter and Arellano, 2002). Bioindicadores são aqueles organismos ou comunidades nos quais as funções vitais estão intimamente relacionadas com fatores ambientais e podem ser utilizados para observar os efeitos de agentes estressantes, como poluentes e degradação da vegetação em ambientes naturais (Goodsell et al., 2009; Mcgeoch, 1998).

Os besouros rola-bosta têm hábito alimentar detritívoro, utilizando material orgânico como principal fonte de alimento. Esses besouros podem ser divididos em três grupos funcionais de acordo com a forma que alocam o recurso alimentar: telecoprídeos (roladores), paracoprídeos (escavadores) e endocoprídeos (residentes) (Halffter and Edmonds, 1982). Devido a esse hábito alimentar e comportamental, os rola-bostas realizam importantes funções ecológicas, como remoção da matéria orgânica em decomposição, incorporação de nutrientes, bioturbação, aeração do solo e dispersão secundária de sementes (Griffiths et al., 2015; Nichols et al., 2008; Sitters et al., 2014). Além disso, a utilização de depósitos de fezes e carcaças como fonte alimentar e de nidificação é um dos aspectos econômicos mais importantes entre suas funções ecológicas, pois colabora com a redução populacional de organismos que causam problemas ao homem, como moscas hematófagas e detritívoras, e que também utilizam bolos fecais e carcaças como locais de reprodução (Braga et al., 2012; Slade et al., 2007; Wu and Sun, 2010).

Mudanças na paisagem podem afetar diretamente esses besouros, agindo como um regulador das condições microclimáticas ou, indiretamente, alterando a fauna de vertebrados e, consequentemente, a disponibilidade de recurso alimentar (Estrada and Coates-Estrada, 2002; Raine et al., 2018; Vieira et al., 2008). Por estarem diretamente relacionados a vertebrados, devido à utilização de suas fezes como recurso alimentar, os rola-bostas têm sido utilizados também para estudar o efeito cascata em mudanças de hábitat (Gillett et al., 2016; Raine et al., 2018; Raine and Slade, 2019). Além disso, mudanças climáticas e distúrbios nos sistemas naturais podem afetar as comunidades de besouros rola-bosta, através de alterações nas distribuições das espécies, reduzindo as taxas de remoção de fezes e as funções ecológicas associadas (Beynon et al., 2012; Menéndez et al., 2016). Sendo assim, nesse trabalho utilizamos os besouros rola-bosta como ferramenta de estudo, para avaliar os efeitos da conversão de Cerrado em pastagens em diferentes regiões bioclimáticas.

A presente tese está dividida em dois capítulos. No primeiro capítulo nós avaliamos como a conversão de Cerrado em pastagens afeta a diversidade taxonômica e funcional de besouros rola-bosta. Nós utilizamos a riqueza de espécies, abundância, biomassa total e composição de espécies de besouros como parâmetros da diversidade taxonômica. Para a diversidade funcional, usamos características morfológicas e comportamental para gerar índices de riqueza, equitabilidade e divergência funcional. Nesse capítulo, buscamos responder as seguintes perguntas: 1) A conversão de Cerrado em pastagens resulta em perda na riqueza de espécies, abundância, e biomassa total de besouros, e altera a composição de espécies? 2) A conversão de Cerrado em pastagens causa perda de diversidade funcional levando à simplificação do ecossistema?

No segundo capítulo, nós selecionamos três zonas bioclimáticas para testar os efeitos da conversão de Cerrado em pastagens em regiões submetidas a diferentes condições climáticas. Nós então utilizamos a variável climáticas e variáveis ambientais para: 1) testar se o efeito da conversão de Cerrado em pastagens é dependente da zona bioclimática; 2) verificar os efeitos diretos e indiretos da zona bioclimática e da mudança de uso do solo na comunidade de besouros; e 3) identificar os principais fatores que explicam as funções ecológicas. Para isso, obtivemos a heterogeneidade e densidade da vegetação como variáveis ambientais; a riqueza, biomassa e índices de diversidade funcional dos besouros rola-bosta; e remoção de fezes, revolvimento do solo, abundância de moscas detritívoras adultas e larvas como variáveis funcionais.

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SEGUNDA PARTE - ARTIGOS

ARTIGO 1

Normas do periódico Ecological Indicators (versão preliminar)

Cerrado conversion to pasture affects dung beetle community structure and functioning

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ABSTRACT

The replacement of natural systems with agriculture and livestock is the most important driver of land cover change in tropical regions, driven by population growth and increased demand for food. Tropical savannas cover more than 20% of the global land surface, and it is estimated that one-fifth of the world's population depends directly on these systems, making than one of the most impacted regions. The Brazilian Cerrado is the largest and richest tropical savanna, with a high rate of endemism, however it has been extensively cleared for agriculture and livestock. Here, we aim to understand how the conversion of savanna into pasture affects biodiversity and ecosystem functioning, using dung beetles as a study group. Dung beetles show habitat specificity and respond to changes in environmental conditions, and so are widely used as bioindicators. We collected dung beetles in six municipalities in the state of Minas Gerais, Brazil. In each municipality, three paired sites of Cerrado and pasture were selected. We used species diversity, richness, abundance, total biomass, and species composition as taxonomic parameters. To look at functional diversity changes, body mass, body mass-adjusted front leg area, body mass-adjusted pronotum volume, back:front leg lengths, and nesting strategy traits were used to calculate functional richness, equitability, dispersion indices, and functional composition. We found that conversion of savanna has a negative effect on both taxonomic and functional diversity metrics, causing a loss of species and functional richness and equitability, which will have knock-on effects for ecosystem functioning. Our results showed the importance of Cerrado habitat for biodiversity and the maintenance of ecosystem functioning.

Key words: Taxonomic diversity. Functional diversity. Morphological traits. Biodiversity conservation. Ecosystem functioning.

1. Introduction

The increasing demand for food by human society has been the driving factor in the replacement of vast areas of natural systems with pasture and agricultural land across tropical regions (Aide et al., 2013; Houghton, 2012; Sy et al., 2015). This replacement leads to the erosion of biodiversity, affecting ecosystem functioning and the provision of ecological services crucial to human well-being (Braga et al., 2013; Cardinale et al., 2012; Foley, 2005; Suarez-castro et al., 2015). The conversion of natural lands into cattle pastures has been shown to have large impacts in forested systems due to the abrupt shift of vegetation-covered areas to open-sunny systems with little or no arboreal cover (Ratnam et al., 2011). However, it has been suggested that for many naturally open systems, such as tropical savannas, this land use conversion will only result in subtle changes, and the degradation of the system and concurrent loss of biodiversity and functioning will be less visible than in forested systems (Zaloumis and Bond, 2011; also see Parr et al., 2014).

It is estimated that one-fifth of the global human population depends directly on tropical savanna systems for their livelihoods, including the use of uncleared lands for grazing, fuel wood, food, and medicinal plants (Lehmann et al., 2009; Olsson and Ouattara, 2013). Despite this, the value of the biodiversity of tropical savannas is poorly known (Murphy et al., 2016). In particular, savannas and grasslands in the Neotropical region have the highest concentrations of ranged-restricted vertebrates making them particularly important for biodiversity conservation (Murphy et al., 2016). The Brazilian Cerrado is the largest and most biodiversity rich savanna, with high rates of endemism. It is also one of the most threatened tropical savannas, and is considered an important hotspot for biodiversity (Myers et al., 2000). This biome covers around 2 million km², forming a mosaic of many vegetation physiognomies such as grasslands, woodlands and riparian forests, comprising a complex and heterogeneous landscape (Ribeiro and Walter, 1998). Nevertheless, the Cerrado has been extensively cleared for agriculture and livestock, with more than half of the land area lost in the past 50 years (Beuchle et al., 2015; Overbeck et al., 2015).

The negative effects caused by anthropogenic impacts on the Cerrado´s biodiversity is well documented (Almeida et al., 2011; Arcoverde et al., 2017; de Queiroz et al., 2017; Lemes et al., 2019). However, there are few studies that link the loss of biodiversity to the functioning of the Cerrado ecosystem (Correa et al., 2019b; Lehmann and Parr, 2016). In the last decade, studies using functional metrics to complement the taxonomic approach to quantifying the biodiversity response to anthropogenic change has increased (Barragán et al., 2011; Beiroz et al., 2018; Elmqvist et al., 2003; Gagic et al., 2015). The inclusion of functional approaches in ecological studies has allowed a greater understanding of the mechanisms that drive the responses of biodiversity to ecosystem changes (Beiroz et al., 2018; Mouillot et al., 2013; Petchey and Gaston, 2006). Moreover, some studies have suggested that using functional metrics better predicts functioning of the ecosystem than traditional species-based indices (Gagic et al., 2015). However, these functional diversity approaches are often derived from categorical trait information (Beiroz et al., 2019; Braga et al., 2013; Slade et al., 2007), without accounting for morphological traits, which risks a loss of information (Griffiths et al., 2015; Petchey and Gaston, 2006; but see Raine et al., 2018a).

Here we used dung beetle taxonomic indices (species richness, abundance of individuals, total biomass, and species composition), and functional indices parameters based on morphological and behavioural traits (functional richness, evenness and dispersion, and functional composition) to evaluate the effects of conversion of the Cerrado into introduced cattle pastures. Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are widely used as bioindicator species as they show habitat specificity, and are responsive to changes in environmental conditions (Audino et al., 2014; Bicknell et al., 2014; Costa et al., 2017; Halffter and Arellano, 2002). They are also tightly linked to vertebrate communities through their reliance on dung for feeding and breeding, and so can be used to study the cascading effects of habitat change (Gillett et al., 2016; Griffiths et al., 2015; Raine et al., 2018b; Raine and Slade, 2019; Vieira et al., 2008). Conversion of tropical savannas to cattle pastures has been shown to increase the populations of some dung beetle species, resulting in overall lower species richness but a higher total biomass, due to an increase in food resources, and abundances of some species (Tonelli et al., 2018). However, there are only few studies evaluating the impacts of this conversion on dung beetle functional diversity.

Here, we aim to answer the following questions:

1) Does conversion of Cerrado to cattle pasture result in a loss of species richness, abundance, and total biomass of dung beetles and changes in community composition? Due to the high availability of food resources, we hypothesize that cattle pastures can maintain the abundance and biomass of dung beetles, but that richness will decline, and community composition change, due to vegetation oversimplification resulting in the loss of some more specialised species.

2) Does conversion of Cerrado to cattle pasture cause a loss of functional diversity, leading to ecosystem simplification? Despite the maintenance of a high abundance and biomass of beetles, we hypothesize that the distribution of functional traits will be negatively affected, and functional diversity will decline as species are lost, resulting in changes in the functional composition of the community.

2. Materials and methods

2.1 Study site

The study was conduct in a tropical savanna (Cerrado *sensu stricto*) in Minas Gerais State – Brazil (Fig. 1). Six municipalities were selected (minimum of 100 km apart): Januária, São Romão, Arinos, Unaí, Paracatu and Formiga (15º27’13.45” – 20º33’52.19”S, 44º43”59.77” – 46º53’41.65”W). The altitude ranges from 471 to 882 m. The climate of the Cerrado biome is classified as rainy tropical (Aw – Köppen classification) but varies considerably. The average annual temperature ranges from 18° to 28°C, and rainfall, from 800 to 2.000 mm, with a very strong dry season from April to September, the southern winter (Oliveira-Filho and Ratter, 2002; Ribeiro and Walter, 1998).

The Cerrado in Minas Gerais State is an important livestock region and the bovine herd has been increasing since 1980’s. This has had direct consequences on the land use in this region and in the last 30 years, as exotic grasses (*Urochloa* spp.) have been introduced to increase the carrying capacity of cattle (Cavalcanti and Joly, 2002; Martha and Vilela, 2002).

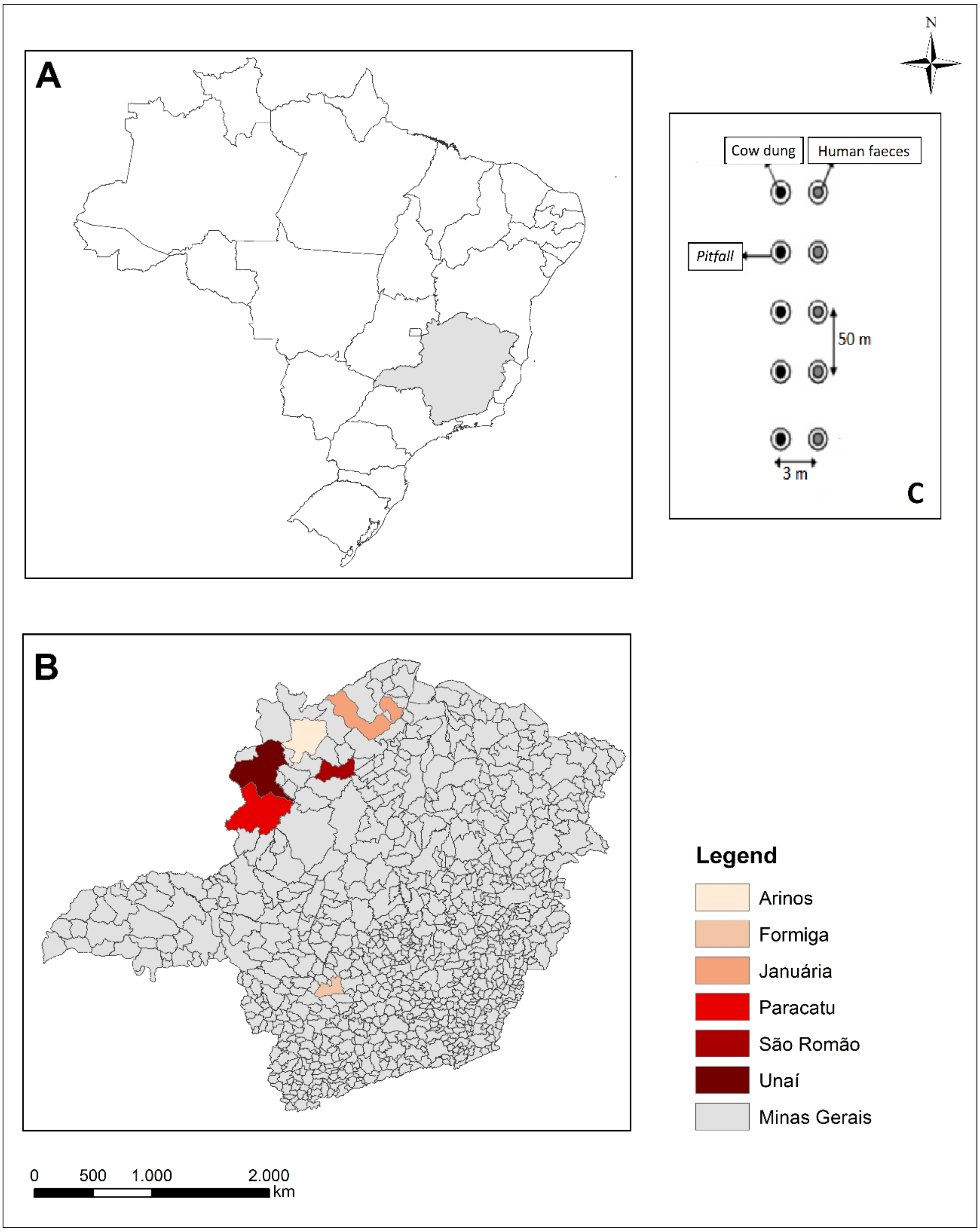

Fig. 1 Study area map showing A) the study region - Minas Gerais State, Brazil; B) the municipalities in Minas Gerais State, Arinos, Formiga and Januária; and C) the transect with pitfall traps baited with 30 g of human faeces, and 500 g of cow dung.

2.2 Dung beetle data

We sampled the dung beetle community in 2016 during the wet season, the period of greatest activity of these beetles in tropical ecosystems (Halffter, 1991). In each of the six municipalities we selected three sites at least 3 km apart, in each of two land use types: Cerrado *sensu stricto* and exotic cattle pasture (*Urochloa* spp.), totalling 36 samples sites. At each site, we placed a transect with five sample points with two pitfall traps, separated by 3 m, one baited with 30 g of human faeces, and the other with 500 g of fresh cow dung (Fig. 1C), in order to sample as much of the local dung beetle community as possible. The pitfalls were arranged in a 200 m linear array, with sampling points aligned 50 m apart, totalling 10 pitfalls in each transect. Pitfall traps consisted of plastic containers (19 cm diameter and 11 cm deep), which were partially filled with a saline solution and detergent. Each trap was protected from rain with a plastic lid suspended 20 cm above the surface. Contents of the trap were collected after 48 hours.

Dung beetle specimens were transported in 80% alcohol from the field to the laboratory – Laboratório de Ecologia e Conservação de Invertebrados at Universidade Federal de Lavras (LECIN - UFLA), then sorted, dried in drying oven (40ºC) for 72h or until they are completely dried, and stored in paper envelopes. We identified the dung beetles using a key to the genera and subgenera of subfamily Scarabaeinae of the New World (Vaz-de-Mello et al., 2011), the reference collection at Coleção de Referência de Escarabeíneos Neotropicais (CREN – UFLA), and confimed identifications with Dr. Fernando Z. Vaz-de-Melo at Universidade Federal do Mato Grosso (UFMT). Voucher specimens were deposited at CREN - UFLA in Minas Gerais State, Brazil.

2.3 Dung beetle traits

To determine dung beetle morphological traits, we follow the methodology proposed by Griffiths et al. (2015). We measured pronotum area, front tibia and femur area, and front and back leg length using ImageJ software with photographs obtained using a stereomicroscope Leica M205 A (Leica, Wetzlar, Germany). These traits were chosen since they were directly related to the functions performed by dung beetles (Table 1). We measured pronotum height with digital callipers (0.01 mm resolution); and dry body mass using a Shimadzu AY220 balance (Shimadzu Corporation, Kyoto, Japan) with a precision of 0.0001 g. All traits were measured from 20 randomly selected individuals (or the maximum number available), to obtain a mean value for each species. Front tibia and femur area were summed to provide a total front leg area, and pronotum height and area were multiplied to estimate pronotum volume. As these traits were significantly collinear with body mass, we divided front leg area and pronotum volume by the dry body mass of the same individual (body mass-adjusted traits). Then, we transformed the body mass-adjusted front leg and pronotum volume to the residual of the linear relationship between these traits and body mass so these variables were uncorrelated. Back leg length was divided by front leg length to obtain a ratio (back:front leg length). The morphological traits body mass, body mass -adjusted front leg area, body mass -adjusted pronotum volume, and back:front leg lengths were then used in the calculation of the multi-trait diversity metrics described below. We also included the categorical trait - nesting strategy obtained from the literature: (i) rollers, which roll portions of dung away from the dung pile in small balls; (ii) tunnelers, which take a small portion of the dung and bury it directly below or around the dung pile; and (iii) dwellers, which nest inside the dung (Halffter and Matthews, 1966).

Table 1 Functional traits with an explanation of functional meaning and measurement taken, and their relationship with ecological functions.

Functional trait	**Functional meaning**	**Measurement**	**Relationship with ecological function ***
Body-mass (BM)	Size	Dry body-mass	Dung removal and burial amount
BM-adjusted front leg area	Front leg robustness	Front tibia and femur area/BM of that species	Digging ability and dung burial
BM-adjusted pronotum volume	Pronotum robustness	Pronotum area x pronotum height/BM of that species	Muscle tissue accommodation related to digging ability
back:front leg lengths	back:front leg size	Back leg length/front leg length	Capability of dung ball construction and rolling
Nesting strategy	Resource allocation strategy	Rollers, tunnelers or dwellers	How resource is removed and soil is excavated

* (Halffter and Edmonds, 1982)

2.4 Diversity metrics calculations

Species richness was calculated as the number of different species at each site, the abundance as the sum of the number of individuals of each species in each site, and total biomass was calculated by multiplying the mean mass of each species by its abundance and summed at each sites. As total biomass was significantly collinear with abundance, we transformed the biomass to the residual of the linear relationship between biomass and abundance making both variables uncorrelated, and we refer to this as biomassR.

We calculate three functional diversity indices using five traits (body mass, body mass-adjusted front leg area, body mass-adjusted pronotum volume, back:front leg length, and nesting strategy) in the FD package (Laliberté et al., 2012) in R 3.5.2 (R Development Core Team 2018). The traits were given equal weighting and species were weighted by their relative abundance. The chosen indices were: (1) functional richness (FRic) - the range of traits in a community quantified by the volume of functional trait space occupied; (2) functional evenness (FEve) - the regularity in spacing and abundances of species in trait space; and (3) functional dispersion (FDis) - the distribution of abundances in trait space relative to an abundance-weighted centroid, and the volume of space occupied (Laliberté and Legendre, 2010).

To calculate functional composition, we created functional groups to categorise species with similar morphological traits. We obtained the mean value of each morphological trait for each species and then categorized it as very small (VS), small (S), medium (M), large (L) and very large (VL) by calculating the 95% and 99% confidence intervals (CI) (see Table S1). Species with trait sizes below the 99% CI were classified as VS, within the 99-95% CI as S, at the 95% CI as M, between 95-99% as L, and those above the 99% CI as VL. We determined the functional composition at each site using the abundance of distinct functional groups present in each site.

2.5 Statistical analyses

2.5.1 Taxonomic diversity

In order to compare the species diversity patterns in the two different land uses, and to verify the sample effort efficacy, we calculated species accumulation curves based on the number of individuals collected, extrapolating the number of individuals to the mean abundance value of the systems. The extrapolation curves were generated using iNEXT (Interpolation and extrapolation for species diversity) package (Chao and Jost, 2012; Hsieh et al., 2013). A hundred bootstrap replications were used to estimate 95% confidence intervals.

To evaluate the effects of land use on the taxonomic diversity of dung beetles, we ran generalised linear mixed-effect models (GLMM) using a Poisson distribution for species richness, a negative binomial distribution for individual abundance, and a Gaussian distribution for biomassR. We considered municipalities as random effects, land use type as the explanatory variable and species richness, abundance and biomassR as response variables.

2.5.2 Functional diversity

To evaluate the effects of land use system on the functional diversity of dung beetles, we ran linear mixed-effect models with a Gaussian distribution. We considered municipalities as random effects, land use type as the explanatory variable and FRic, FEve and FDis as response variables. All these analyses were performed in R software version 3.5.2 (R Development Core Team 2018) using the ‘‘lme4’’ package (Bates et al., 2015).

2.5.3 Taxonomic and functional composition

To assess taxonomic and functional composition in the different land uses, spatial differences in dung beetle communities and functional groups in the two different land use systems were verified using Non-metric Multidimensional Scaling (nMDS), based on a Jaccard similarity matrix, with data standardized by square root transformation. We used permutation variance multivariate analysis (PERMANOVA) to measure the statistical differences in taxonomic and functional composition among the two land uses, using the software Primer v.6 with PERMANOVA + (Clarke and Gorley, 2006).

3. Results

3.1 Taxonomic diversity

We collected 33,681 individuals of 114 dung beetle species (see Table S1 for species list, mean traits values, and abundances). In the Cerrado we recorded 9,704 individuals of 103 species, and in cattle pasture 23,977 individuals of 59 species. In the Cerrado, 55 species only occurred in this system (53.4%) and 27 (26.21%) were rare species (singletons or doubletons). In cattle pastures, 11 species were exclusive to that land use (18.64%) and 28 were rare species (47.45%). The Cerrado sites presented the highest species richness, and species accumulation curves reached their asymptote, indicating that our sampling provided a good representation of the overall dung beetle community (Fig. 2). Mean species richness was higher in the Cerrado (n = 36, d.f. = 3, $\chi^2 = 74.01$, p <0.01) than in cattle pasture (Fig. 3A), and there was no difference in abundance (n = 36, d.f. = 4, $\chi^2 = 0.18$, p = 0.66) and biomassR between land uses (n = 36, d.f. = 4, $\chi^2 = 0.94$, p = 0.33) (Figs. 3B and C).

3.2 Functional diversity

Cerrado presented the highest functional richness (n = 35, d.f. = 4, $\chi^2 = 41.79$, p <0.001) and functional evenness (n = 35, d.f. = 4, $\chi^2 = 4.85$, p = 0.02) (Figs. 3D and E). There was no difference in functional dispersion between Cerrado and cattle pasture (n = 36, d.f. = 4, $\chi^2 = 0.006$, p = 0.93) (Fig. 3F).

3.3 Taxonomic and functional composition

The two land uses differed in terms of taxonomic (Fig. 4A) and functional composition (Fig. 4B), (PERMANOVA, d.f. = 5, Pseudo-F = 1.78; p = 0.002; d.f. = 5, Pseudo-F = 3.32 and p = 0.004 respectively).

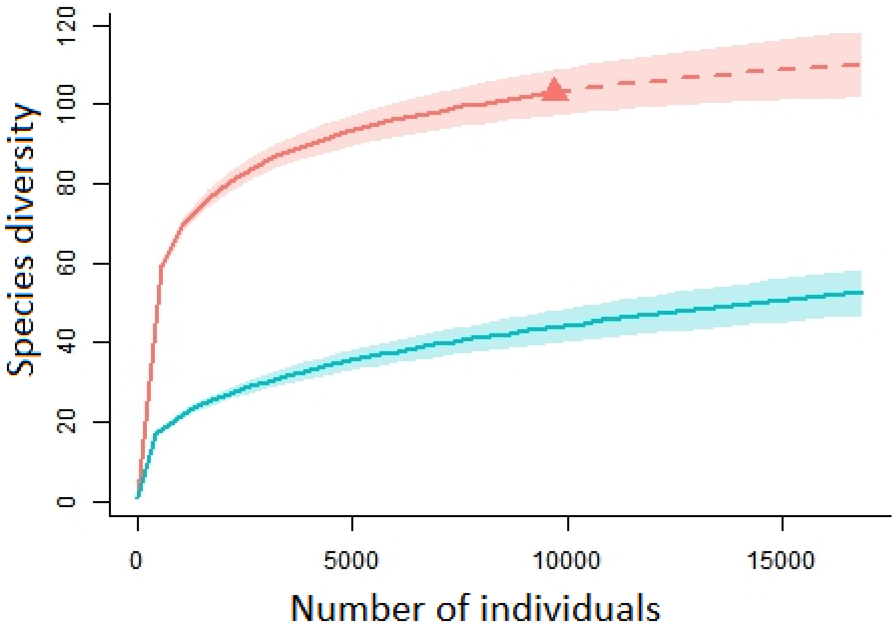

Fig. 2 Extrapolation curves based on the number of dung beetle individuals collected in Cerrado (red line) and cattle pasture (blue line) from 36 collection sites in Minas Gerais State, Brazil. The dotted line indicates the extrapolation value and the shading indicates the 95% confidence intervals.

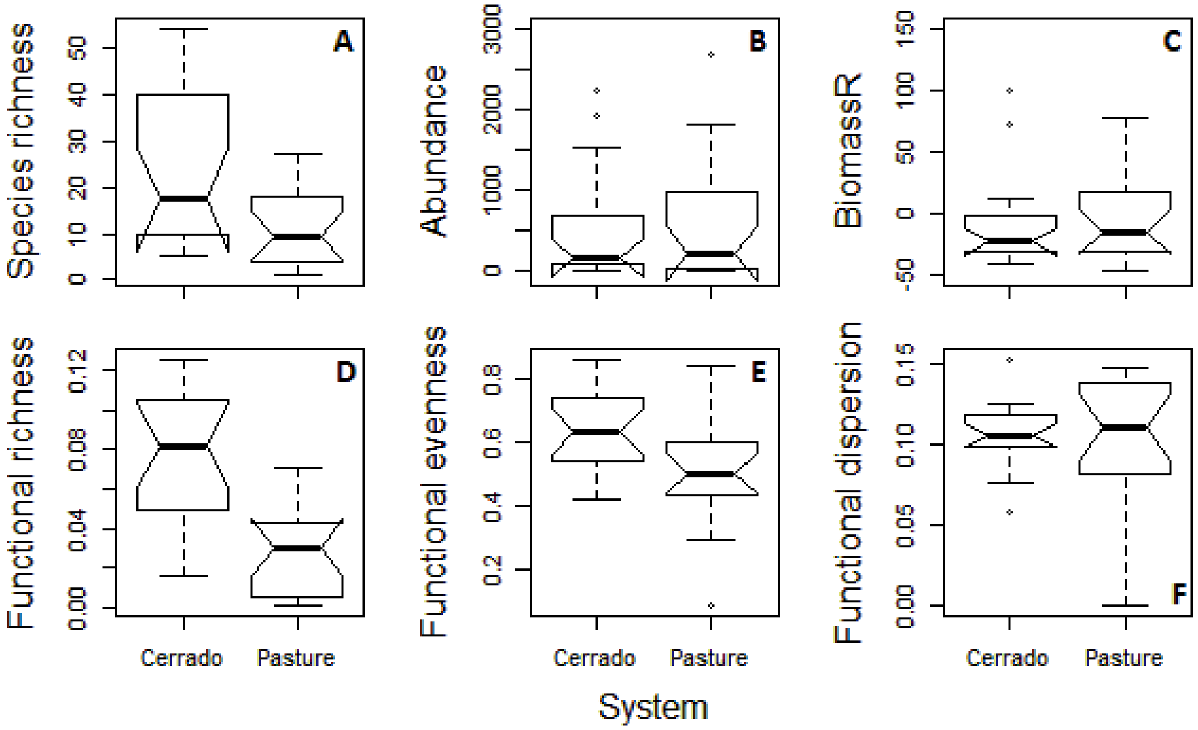

Fig. 3 Differences in A) species richness; B) abundance; C) biomassR (abundance-adjusted total biomass); D) functional richness; E) functional evenness; and F) functional dispersion of dung beetles between Cerrado and cattle pasture land uses.

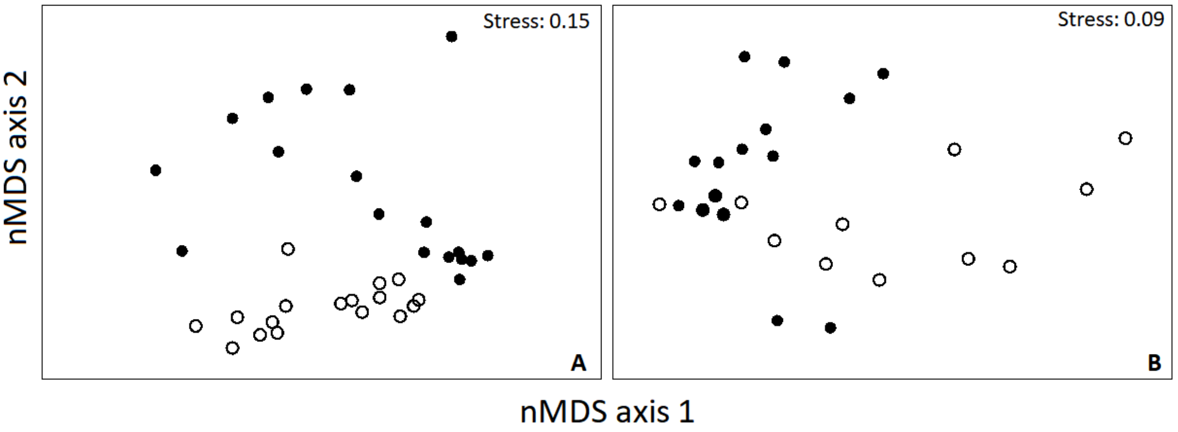

Fig. 4 Nonmetric Multidimensional Scaling (nMDS) based on the Jaccard distance matrix of A) abundance of dung beetles species; and B) abundance of dung beetles functional groups in each land use. Black circles = Cerrado and open circles = cattle pasture

4. Discussion

We show that despite maintaining dung beetle abundance and biomass, the conversion of neotropical savannas (Cerrado) into cattle pastures causes a reduction in species and functional richness. We find that both species and functional composition changed as a result of land use change, in part because of a loss of functional traits in cattle pasture habitats. This could lead to community simplification and consequently a loss of ecosystem functionality. Our findings contribute to the understanding of the effects of Cerrado conversion to introduced cattle pastures on dung beetle communities and their associated functions. As cattle pastures expand across the tropics, and increasing encroach on the remaining savannah ecosystems, it is important to document the potential changes that will occur, both for biodiversity and the ecosystem functions associated with it.

4.1 Taxonomic diversity

We observed a loss of species richness in cattle pastures when compared to savannas. Otherwise, there was no significant change in abundance and total biomass. Dung beetle assemblage organization in tropical regions is influenced by vegetation cover and vegetation type (Audino et al., 2014; Halffter and Arellano, 2002; Hanski and Cambefort, 1991), in particular land use heterogeneity (Costa et al., 2017; Lobo and Martín-Piera, 2002). In addition, dung beetles are dependent on the vertebrate fauna, especially large mammals, for feeding and breeding (Barlow et al., 2010; Estrada et al., 1999; Nichols et al., 2013). Studies on the effects of habitat change on dung beetles in tropical forests have shown that species richness, abundance of individuals, and biomass can be reduced with fragmentation, disturbance, and environmental simplification (Braga et al., 2013; Correa et al., 2016; Korasaki et al., 2013). In contrast, cattle pastures are simpler and hostile environments compared to native systems, because they have more compacted soils, due to the presence of livestock (Tonelli et al., 2018; Vries et al., 2007). Despite that, pastures are abundant in food resources due to the constant presence of cattle, which may favour the persistence of large populations of certain disturbance tolerant species, and thus a high overall biomass of dung beetles (Lobo, 2006; Tonelli et al., 2018; Halffter et al., 1992; Navarrete and Halffter, 2008).

Despite having low species richness, some species present in cattle pasture had a high abundance of individuals, such as *Genieridium cryptops* (Arrow, 1913) (10,719 individuals), *Dichotomius geminatus* (Arrow, 1913) (5,622), *Trichillum heydeni* Harold, 1868 (1,776), *Ontherus appendiculatus* (Mannerheim, 1829) (1,646), *Ateuchus frontalis* (Boucomont, 1928) (1,038) and *Digitonthophagus gazella* (Fabricius, 1787) (1,033). All these species also occurred on Cerrado, and three of them also had the highest abundance in this system as well (*G. cryptops*, *O. appendiculatus*, *A. frontalis* with 2,196; 537 and 517 respectively) (see table

S1). *D. gazella* is a South African dung beetle with a high invasion potential which has been introduced in several countries due to its potential to bury faeces and control fly populations (see Filho et al., 2018). This species was introduced to Brazil in the 1990's by EMBRAPA (Brazilian Agricultural Research Corporation) to control the horn fly (*Haematobia irritans irritans* Linnaeus, 1758) and gastrointestinal nematodes of cattle. Currently, *D. gazella* is present in all states of Brazil (Tissiani et al., 2017) and has been recorded in almost all countries in Central and South America, from Mexico to Uruguay (Filho et al., 2018; Matavelli and Louzada, 2008; Noriega et al., 2017, 2010; Rivera and Wolff, 2007; Vidaurre and Noriega, 2008).

4.2 Functional diversity

Besides having lower species richness, cattle pastures also lost functional characteristics compared to native savanna systems. Functional diversity indices have been studied in tropical forest systems with conflicting results. The loss of functional richness when habitats change has been demonstrated for dung beetle communities in tropical forests (Audino et al., 2014; Barragán et al., 2011; Griffiths et al., 2015), although other studies have found no changes in functional diversity metrics (e.g. Beiroz et al., 2018). However, in Cerrado systems there is little knowledge about the effects of habitats change on functional diversity indices, only been found no changes in functional diversity metrics until now (Correa et al., 2019b). Here, we found that when Cerrado is converted to cattle pasture there is a loss of functional richness (FRic) and evenness (FEve), indicating that abundances in pasture are less evenly distributed among species or functional distances among species are less regular (Villéger et al., 2010). We also found that species and functional richness decreased when savanna was converted to cattle pasture. This causes a shift in functional space by removing species with traits that are poorly adapted to the new environment and allowing colonization by better-adapted species (Mouillot et al., 2013).

The loss of functional diversity observed in our study was probably due to the loss of morphological traits in the pasture systems (see Fig. S2). This in turn suggests that functions performed by the beetles (such as dung removal and soil bioturbation) could be affected. However, further work is need to see if this is the case or if these functions are be maintained through density-compensation (Correa et al., 2019a). Current concerns about the decline of dung beetles are particularly focused on large-bodied species, which have been suggested to be both the most extinction-prone (Larsen et al., 2008) and the most functionally efficient

(Lähteenmäki et al., 2015; Larsen and Forsyth, 2005). We found a dominance of small-bodied species in pasture areas and a loss of the larger species (Fig. S2 A and B), as has been observed in previous studies (Filho et al., 2018; Nichols et al., 2007; Scheffler, 2005). This suggests that it is the larger bodied species that are most affected when Cerrado is converted to cattle pasture.

4.3 Taxonomic and functional composition

We found that both the taxonomic and functional composition of dung beetle communities were altered when Cerrado was replaced with cattle pastures. Pastures can cause changes in vegetation structural heterogeneity, and habitat diversity, leading to more homogeneous and simplified environments (Vries et al., 2007). In addition, cattle pastures have altered environmental conditions, such as soil compaction, temperature increases and humidity decreases, which can affect the species composition of the dung beetle community (Correa et al., 2019b; Costa et al., 2017; Halffter and Arellano, 2002).

4.4 Final considerations

Many studies have estimated the conservation value of ecosystems using taxonomic or functional diversity, although it is only recently that they have been assessed together (e.g. Baiser and Lockwood, 2011; Beiroz et al., 2018; Moretti et al., 2009; Villéger et al., 2010). Here, we investigated the effects of the conversion of Cerrado, an important tropical savanna, into cattle pasture on dung beetles taxonomic and functional diversity. We used species morphological traits to calculate functional diversity parameters for the first time in Cerrado systems. We conclude that the change of land use causes a negative effect on both taxonomic and functional metrics, causing loss of dung beetle richness and morphological traits, leading to a loss of functional diversity, which could affect associated ecosystem functioning. In addition, we emphasize the importance of using both taxonomic and functional metrics as they give complementary responses.

In agricultural systems, dung beetles play an important role by contributing to many ecological processes, including nutrient cycling, soil aeration, reducing greenhouse gases emissions, secondary seed burial, increasing primary productivity, and suppressing parasites of livestock (Manning and Cutler, 2018; Nichols et al., 2008; Slade et al., 2016). Thus, maintaining fully functional dung beetle communities is central to maintaining ecosystem functioning. Our findings emphasize the importance of conservation the Cerrado ecosystem, both for the maintenance of biodiversity and for ecosystem functioning.

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Supplementary material

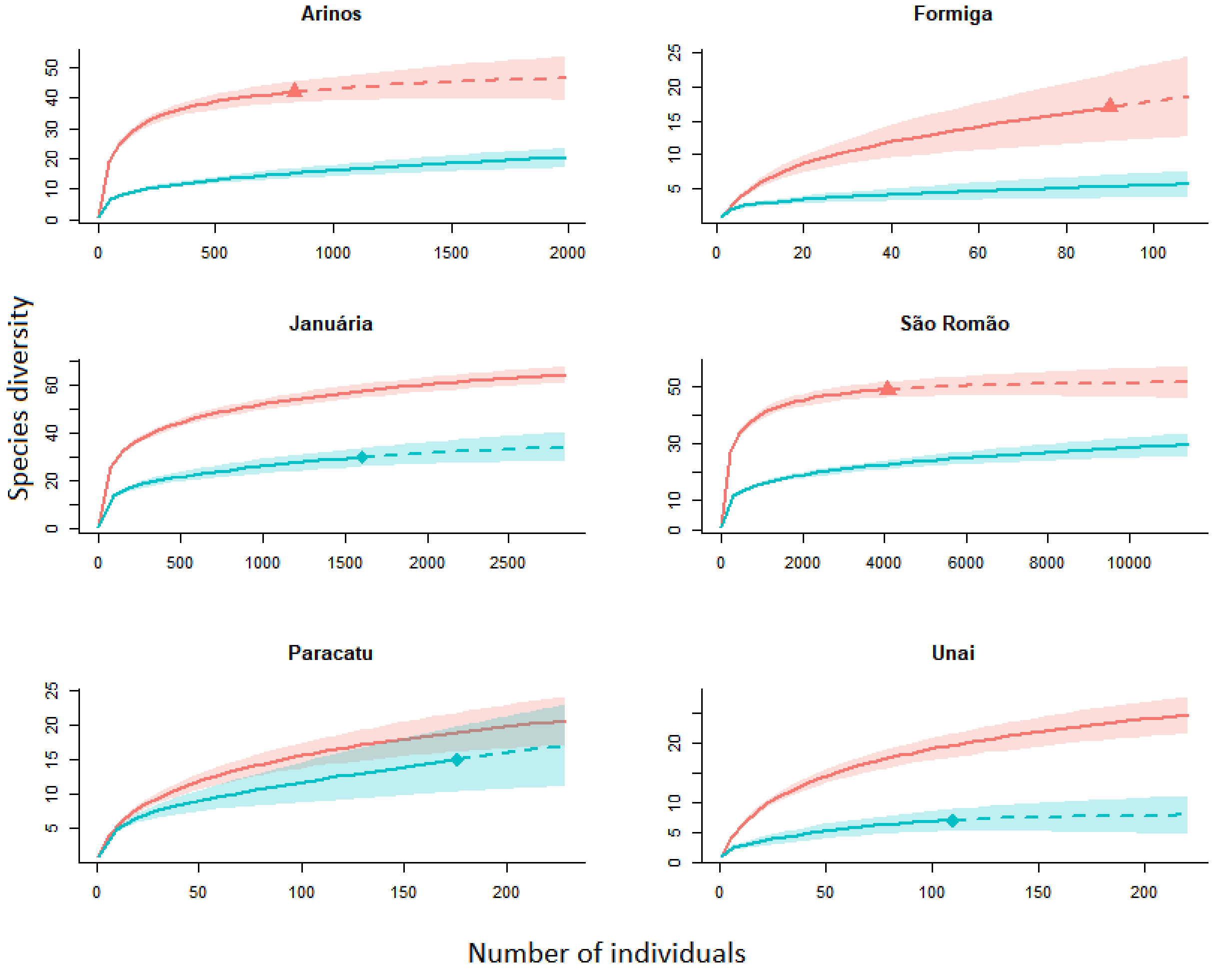

Fig. S1 Extrapolation curves based on the number of dung beetle individuals collected in Cerrado (red line) and cattle pasture (blue line) from six municipalities in Minas Gerais State, Brazil. The dotted line indicates the extrapolation value and the shading indicates the 95% confidence intervals.

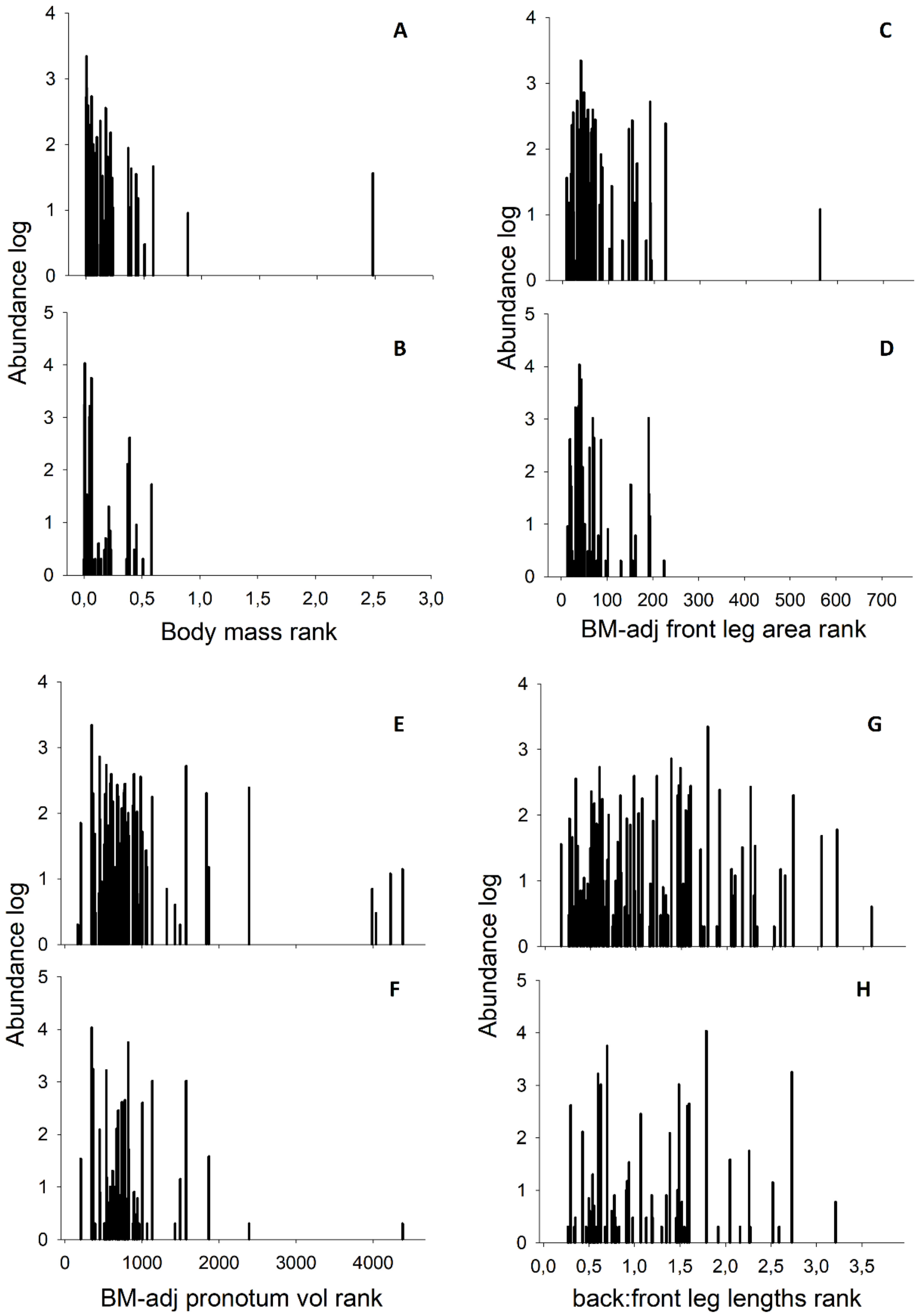

Fig. S2 Rank abundance distribution of Body mass (BM) (A & B); BM-adjusted leg area (C & D); BM-adjusted pronotum volume (E & F); and back:front leg lengths (G & H) in Cerrado (A, C, E, G) and cattle pasture (B, D, F, H).

Table S1 Species list, abundances, mean trait values, and nesting strategy of dung beetles collected in six municipalities in Minas Gerais State, Brazil. Letters in parentheses relate to morphological trait sizes: VS= very small, S= small, M= medium, L= large, and VL= very large (see methods for how traits were measured).

Species list	**Cerrado**	**Cattle pasture**	**Body mass (BM)**	**BM-adj front leg area**	**BM-adj pronotum vol**	**back:front leg lengths**	**Nesting strategy**
Agamopus unguicularis (Harold, 1883)	0	1	0,0029 (VS)	76,55 (VL)	713,9 (S)	2,16 (VL)	-
Agamopus viridis Boucomont, 1928	267	55	0,0015 (VS)	151,62 (VL)	675,05 (VS)	2,26 (VL)	-
Ateuchus aff. *ovalis* Boucomont, 1928	1	0	0,0052 (VS)	56,15 (M)	558,35 (VS)	1,54 (VL)	Tunneler
Ateuchus frontalis (Boucomont, 1928)	517	1038	0,0015 (VS)	190,68 (VL)	1572,25 (VL)	1,49 (VL)	Tunneler
Ateuchus pauperatus (Germar, 1824)	70	33	0,0230 (VS)	41,15 (VS)	203,38 (VS)	0,94 (VS)	Tunneler
Ateuchus puncticolllis (Harold, 1867)	0	14	0,0177 (VS)	38,19 (VS)	541,52 (VS)	0,92 (VS)	Tunneler
Ateuchus semicribratum (Harold, 1868)	177	282	0,008 (VS)	61,91 (M)	690,11 (VS)	1,07 (S)	Tunneler
Ateuchus sp.1	3	1	0,0072 (VS)	130,04 (VL)	1425,33 (VL)	1,3 (L)	Tunneler
Ateuchus sp.2	2	0	0,0143 (VS)	35,04 (VS)	395,36 (VS)	1,27 (M)	Tunneler
Ateuchus sp.3	1	0	0,011 (VS)	49,91 (S)	746,09 (M)	0,79 (VS)	Tunneler
Ateuchus striatulus (Borre, 1886)	2	9	0,0107 (VS)	44,54 (VS)	651,68(VS)	0,91 (VS)	Tunneler
Ateuchus vividus (Germar, 1823)	80	7	0,0154 (VS)	35,16 (VS)	450,91 (VS)	1,19 (M)	Tunneler
Ateuchus volxemi Borre, 1886	721	122	0,006 (VS)	46,07 (S)	449,47 (VS)	1,39 (VL)	Tunneler
Besourenga sp.1	6	0	0,0006 (VS)	83,89 (VL)	3983,62 (VL)	0,41 (VS)	Dweller
Besourenga sp.2	2	0	0,0006 (VS)	70 (L)	4035,18 (VL)	0,26 (VS)	Dweller
Besourenga sp.3	13	1	0,0006 (VS)	80 (VL)	4381,76 (VL)	0,34 (VS)	Dweller

Canthidium barbacenicum Borre, 1886	282	9	0,0093 (VS)	50,7 (M)	587,41 (VS)	1,47 (VL)	Tunneler
Canthidium multipunctatum Balthasar, 1939	2	7	0,0021 (VS)	101,67 (VL)	895,28 (M)	1,35 (VL)	Tunneler
Canthidium refulgens Boucomont, 1928	391	0	0,008 (VS)	65,51 (M)	894,21 (M)	1,23 (M)	Tunneler
Canthidium sp.1	1	27	0,0157 (VS)	47,25 (S)	766,85 (M)	1,07 (S)	Tunneler
Canthidium sp.2	0	2	0,0193 (VS)	38,75 (VS)	685,47 (VS)	0,79 (VS)	Tunneler
Canthidium sp.3	0	2	0,01 (VS)	57,76 (M)	680,63 (VS)	1,2 (M)	Tunneler
Canthidium sp.4	2	0	0,0099 (VS)	42,65 (VS)	580,78 (VS)	1,03 (S)	Tunneler
Canthidium sp.5	3	0	0,0091 (VS)	41,43(VS)	578,89 (VS)	0,65 (VS)	Tunneler
Canthidium sp.6	1	0	0,0089 (VS)	15,39 (VS)	165,22 (VS)	1,89 (VL)	Tunneler
Canthidium sp.7	29	0	0,0036 (VS)	59,01 (M)	546,97 (VS)	1,71 (VL)	Tunneler
Canthidium sp.8	9	1	0,0094 (VS)	49,44 (S)	812,36 (M)	0,68 (VS)	Tunneler
Canthidium sp.9	8	0	0,0039 (VS)	65,35 (M)	662,34 (VS)	1,52 (VL)	Tunneler
Canthidium sp.10	9	7	0,0205 (VS)	43,69 (VS)	739,69 (M)	0,78 (VS)	Tunneler
Canthidium sp.11	1	0	0,0121 (VS)	25,21 (VS)	345,6 (VS)	1,15 (M)	Tunneler
Canthidium sp.12	1	0	0,018 (VS)	20,55 (VS)	163,17 (VS)	2,07 (VL)	Tunneler
Canthidium sp.13	5	0	0,0082 (VS)	63,11 (M)	737,65 (M)	1,33 (L)	Tunneler
Canthon aff. *conformis*	6	0	0,0156 (VS)	43,93 (VS)	743,99 (M)	0,99 (VS)	Roller
Canthon aff. *macadoi*	1	0	0,0069 (VS)	52,75 (M)	451,63 (VS)	1,73 (VL)	Roller
Canthon aff. *virens*	2	0	0,0148 (VS)	44,34 (VS)	767,21 (M)	1,05 (S)	Roller
Canthon chlorophanus	241	1	0,0041 (VS)	224,46 (VL)	2388,68 (VL)	1,92 (VL)	Roller
Canthon cinctellus (Germar, 1824)	5	5	0,0062 (VS)	80,81 (VL)	938,83 (M)	1,52 (VL)	Roller
Canthon enkerlini (Martinez, Halffter & Halffter, 1964)	81	0	0,0117 (VS)	83,46 (VL)	920,26 (M)	1,59 (VL)	Roller
Canthon s. histrio (Serville, 1828)	88	0	0,0406 (VS)	46,49 (S)	759,11 (M)	0,9 (VS)	Roller
Canthon ibarragrossoi	7	0	0,0097 (VS)	42,9 (VS)	615,25 (VS)	1,3 (L)	Roller
Canthon lituratus (Germar, 1813)	14	37	0,0029 (VS)	191,25 (VL)	1865,25 (VL)	2,05 (VL)	Roller

Canthon melancholicus Harold, 1968	128	1	0,0943 (M)	39,95 (VS)	876,65 (M)	0,63 (VS)	Roller
Canthon sp.1	26	0	0,0044 (VS)	107,28 (VL)	1051,68 (VL)	1,79 (VL)	Roller
Canthon sp.2	8	0	0,0133 (VS)	66,95 (M)	879,97 (M)	1,16 (M)	Roller
Canthon sp.3	1	0	0,0044 (VS)	57,27 (M)	586,58 (VS)	1,75 (VL)	Roller
Canthon sp.4	0	1	0,0047 (VS)	97,02 (VL)	904,64 (M)	2,27 (VL)	Roller
Canthon sp.5	0	1	0,0089 (VS)	42,81 (VS)	511,85 (VS)	1,49 (VL)	Roller
Canthon sp.6	117	1	0,0075 (VS)	64,56 (M)	737,38 (S)	1,55 (VL)	Roller
Canthon sp.7	11	0	0,0040 (VS)	68,96 (M)	614,77 (VS)	2,09 (VL)	Roller
Canthon sp.8	3	0	0,0015 (VS)	182,23 (VL)	965,82 (L)	3,59 (VL)	Roller
Canthon sp.9	199	0	0,0036 (VS)	144,32 (VL)	1835,48 (VL)	1,58 (VL)	Roller
Canthon tristis (Harold, 1862)	105	0	0,0267 (VS)	66,42 (M)	933,14 (M)	1,03 (S)	Roller
Chalcocopris inexpectatus Rossini & Vaz-de-Mello, 2015	1	0	0,0331 (VS)	40,03 (VS)	469,11 (VS)	1,51 (VL)	Tunneler
Coprophanaeus cyanescens (d'Olsoufieff, 1924)	2	1	0,5077 (VL)	14,03 (VS)	677,91 (VS)	0,28 (VS)	Tunneler
Coprophanaeus ensifer (Germar, 1824)	35	0	2,48 (VL)	8,63 (VS)	800,76 (M)	0,18 (VS)	Tunneler
Coprophanaeus spitzi (Pessôa, 1934)	14	8	0,4518 (VL)	13,96 (VS)	652,38 (VS)	0,3 (VS)	Tunneler
Coprophanaeus thalassinus (Perty, 1830)	33	0	0,1707 (VL)	22,52 (VS)	813,89 (M)	0,36 (VS)	Tunneler
Deltochilum aff. *komareki* Balthasar, 1939	1	0	0,089 (M)	16,32 (VS)	370,44 (VS)	0,74 (VS)	Roller
Deltochilum enceladus Kolbe, 1893	8	0	0,8804 (VL)	14,27 (VS)	477,21 (VS)	0,47 (VS)	Roller
Deltochilum pseudoicarus Balthasar, 1939	34	2	0,4331 (VL)	22,51 (VS)	697,82 (S)	0,52 (VS)	Roller
Deltochilum sp.1	3	0	0,1494 (L)	12,19 (VS)	384,93 (VS)	0,7 (VS)	Roller
Deltochilum sp.2	38	1	0,0511 (S)	36,04 (VS)	765,07 (M)	0,8 (VS)	Roller

Deltochilum sp.3	9	0	0,0903 (M)	22,87 (VS)	695,13 (S)	0,64 (VS)	Roller
Diabroctis mirabilis (Harold, 1877)	87	1	0,3661 (VL)	22,73 (VS)	901,07 (M)	0,27 (VS)	Tunneler
Dichotomius aff. *carbonarius*	15	0	0,1825 (VL)	19,41 (VS)	508,67 (VS)	0,5 (VS)	Tunneler
Dichotomius aff. *cuprinus*	32	1	0,1446 (M)	19,47 (VS)	506,31 (VS)	0,59 (VS)	Tunneler
Dichotomius aff. *triangulariceps*	0	1	0,1465 (L)	29,7 (VS)	898,65 (M)	0,47 (VS)	Tunneler
Dichotomius aff. *zikani*	3	0	0,4509 (VL)	17 (VS)	731,19 (S)	0,32 (VS)	Tunneler
Dichotomius ascanius (Harold, 1869)	1	0	0,0513 (S)	35,07 (VS)	596,67 (VS)	0,83 (VS)	Tunneler
Dichotomius bicuspis (Germar, 1824)	0	2	0,1771 (VL)	23,87 (VS)	572,89 (VS)	0,55 (VS)	Tunneler
Dichotomius bos (Blanchard, 1843)	42	410	0,3915 (VL)	18,49 (VS)	736,59 (S)	0,3 (VS)	Tunneler
Dichotomius carbonarius (Mannerheim, 1929)	4	0	0,1519 (L)	20,54 (VS)	581,49 (VS)	0,46 (VS)	Tunneler
Dichotomius geminatus (Arrow, 1913)	99	5622	0,0619 (M)	43,95 (VS)	820,24 (M)	0,7 (VS)	Tunneler
Dichotomius glaucus (Harold, 1869)	149	19	0,2130 (VL)	20,96 (VS)	616,76 (VS)	0,54 (VS)	Tunneler
Dichotomius lycas (Felsche, 1901)	64	4	0,1866 (VL)	21 (VS)	559,75 (VS)	0,56 (VS)	Tunneler
Dichotomius mormon (Ljungh, 1799)	1	0	0,5034 (VL)	12,63 (VS)	595,4 (VS)	0,36 (VS)	Tunneler
Dichotomius nisus (Olivier, 1789)	10	128	0,376 (VL)	19,69 (VS)	669,56 (VS)	0,43 (VS)	Tunneler
Dichotomius puncticollis (Luederwaldt, 1935)	20	0	0,0493 (S)	35,38 (VS)	702,32 (S)	0,69 (VS)	Tunneler
Dichotomius smaragdinus (Perty, 1830)	0	1	0,0381 (VS)	50,73 (M)	960,96 (L)	0,59 (VS)	Tunneler
Dichotomius sp.	30	6	0,2246 (VL)	21,1 (VS)	700,33 (S)	0,5 (VS)	Tunneler
Dichotomius transiens Luederwaldt, 1929	6	0	0,1664 (VL)	39,65 (VS)	1320,3 (VL)	0,39 (VS)	Tunneler
Digitonthophagus gazella (Fabricius, 1787)	175	1033	0,0459 (S)	68,98 (M)	1131,7 (VL)	0,63 (VS)	Tunneler

Eurysternus caribaeus (Herbst, 1789)	73	1	0,0705 (M)	36,76 (VS)	785,9 (M)	0,57 (VS)	Dweller
Eurysternus navajasi Martínez, 1988	1	0	0,0036 (VS)	80,28 (VL)	641,75 (VS)	2,33 (VL)	Dweller
Eurysternus nigrovirens Génier, 2009	55	0	0,0092 (VS)	44,08 (VS)	593,42 (VS)	1,92 (VL)	Dweller
Eurysternus paralellus Castelnau, 1840	3	0	0,0357 (VS)	49,25 (S)	958,03 (M)	0,88 (VS)	Dweller
Genieridium cryptops (Arrow, 1913)	2196	10719	0,0052 (VS)	39,41 (VS)	346,99 (VS)	1,79 (VL)	Dweller
Isocopris foveolatus (Luederwaldt, 1931)	6	0	0,1754 (VL)	34,3 (VS)	778,96 (M)	0,49 (VS)	Tunneler
Isocopris hypocrita (Lucas, 1857)	45	52	0,5814 (VL)	21,01 (VS)	822,5 (M)	0,3 (VS)	Tunneler
Leotrichillum sp.	59	5	0,0011 (VS)	162,32 (VL)	788,44 (M)	3,21 (VL)	-
Malagoniella aff. *astyanax*	2	3	0,1231 (M)	33,01 (VS)	571,88 (VS)	0,75 (VS)	Roller
Malagoniella puncticollis (Blanchard, 1843)	12	0	0,1313 (M)	32,93 (VS)	549,03 (VS)	0,84 (VS)	Roller
Ontherus appendiculatus (Mannerheim, 1829)	537	1646	0,0474 (S)	31,33 (VS)	534,96 (VS)	0,6 (VS)	Tunneler
Ontherus digitatus Harold, 1868	48	2	0,0215 (VS)	43,29 (VS)	575,09 (VS)	0,98 (VS)	Tunneler
Ontherus erosioides Luederwaldt, 1930	392	0	0,0161 (VS)	55,03 (M)	598,4 (VS)	0,98 (VS)	Tunneler
Ontherus sp.	198	1	0,0295 (VS)	39,29 (VS)	523,9 (VS)	0,83 (VS)	Tunneler
Ontherus ulcopygus Génier, 1996	41	0	0,0613 (M)	36,31 (VS)	545,3 (VS)	0,59 (VS)	Tunneler
Onthophagus bucullus Mannerheim, 1829	51	399	0,0050 (VS)	86,48 (VL)	1003,89 (L)	1,58 (VL)	Tunneler
Onthophagus hircus Billberg, 1915	201	2	0,0050 (VS)	63,52 (M)	763,75 (M)	1,46 (VL)	Tunneler
Onthophagus ptox Erichson, 1847	278	444	0,0044 (VS)	70,96 (L)	777,34 (M)	1,6 (VL)	Tunneler

Oxysternon palaemo Castelnau, 1840	358	0	0,1704 (VL)	22,65 (VS)	979,77 (L)	0,34 (VS)	Tunneler
Phanaeus kirbyi Vigors, 1825	10	2	0,2316 (VL)	23,17 (VS)	931,01 (M)	0,35 (VS)	Tunneler
Phanaeus palaeno Blanchard, 1843	227	3	0,1244 (M)	19,82 (VS)	769,71 (M)	0,51 (VS)	Tunneler
Pseudocanthon sp.	1	13	0,0012 (VS)	193,59 (VL)	1493,12 (VL)	2,52 (VL)	-
Trichillum adjunctum Martínez, 1967	0	2	0,0021 (VS)	60,95 (M)	809,51 (M)	1,13 (M)	Dweller
Trichillum externepunctatum Borre, 1886	0	1	0,002 (VS)	30 (VS)	388,85 (VS)	2,27 (VL)	Dweller
Trichillum heydeni Harold, 1868	199	1776	0,0024 (VS)	38,15 (VS)	361,24 (VS)	2,73 (VL)	Dweller
Trichillum sp.	47	0	0,00132(VS)	54,45 (M)	387,62 (VS)	3,04 (VL)	Dweller
Uroxys sp.1	14	1	0,0009 (VS)	156,47 (VL)	1064,61 (VL)	2,59 (VL)	-
Uroxys sp.2	33	0	0,0037 (VS)	50,59 (M)	379,01 (VS)	2,31 (VL)	-
Uroxys sp.3	11	0	0,0004 (VS)	561,92 (VL)	4223,05 (VL)	2,64 (VL)	-
Uroxys sp.4	5	0	0,0023 (VS)	57,18 (M)	373,63 (VS)	2,3 (VL)	-
Uroxys sp.5	31	0	0,0024 (VS)	47,58 (S)	349,52 (VS)	2,17 (VL)	-
Uroxys sp.6	5	0	0,0033 (VS)	54,62 (M)	439,13 (VS)	2,08 (VL)	-
Total	**9704**	**23977**					

ARTIGO 2

Normas do periódico Science of the Total Environment (versão preliminar)

The pathways of climatic and environmental control on dung beetle communities and functions in tropical savannas

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ABSTRACT

The expansion of agriculture and livestock has been the main drivers of biodiversity in the tropics. Additionally, climate change is having a strong impact on biological system, and associated with land use changes may alter biodiversity distribution and interactions. Dung beetles are sensitive to climate change, since climate has direct influence on their life cycle. Besides, dung beetles show habitat specificity, and are responsive to changes in environmental conditions. Hence, both climate changes and disturbances in natural systems may affect dung beetle communities, changing the habitat associations and reducing the rates of dung removal and the associated functions. Here, to test the effect of tropical savannas conversion into pastures in regions submitted to different climatic conditions, we selected three bioclimatic zones (BZ) distributed along Brazilian savanna (Cerrado) using structural equations modelling (SEM). To do so, we select three municipalities in the state of Minas Gerais, Brazil to set up an ecological function experiment and to collected dung beetles and dung feeding-fly. In each municipality, three paired sites of Cerrado and cattle pasture were selected. We found that the effect of land use changes in tropical savannas is dependent of the bioclimatic zones. Land use system and BZ directly and indirectly affect dung beetle communities, functions, and dung flies abundance. Besides, dung beetle richness was the most important variable among all models evaluated, positively affecting directly and/or indirectly all other variables of dung beetles and ecological functions. We conclude that Cerrado conversion into pasture can have a cascade effect, as the loss of vegetation cover leads to loss of dung beetle species richness, which causes loss of biomass and functional indices, affecting dung beetle functions and interaction with dung flies. However, the community of dung beetles and the ecological functions are affected in different ways, depending on the context. Due so, we suggest that public politics should be thought to evaluate separately each region, submitted to the effects of different climatic conditions.

Key words: bioclimatic zone, land use change, structural equations modelling, Cerrado, dung flies.

1. Introduction

The land use changes caused by the expansion of agriculture and livestock has been the main drivers of biodiversity loss, but some lines of research suggest that climate could mediate the intrinsic relationship between biodiversity and environment, becoming an important cause of extinction with climate changes in progress nowadays (Lemes et al., 2019; Pacifici et al., 2015; Thomas et al., 2004). The climate changes are having a strong impact on biological systems through changes in species populations, communities and ecosystem processes, with potential consequences for ecosystem functioning and future provision of ecological services (Milotić et al., 2017; Parmesan, 2006; Thomas et al., 2004). It is know that the outcome of species interactions and their responses to climate changes are species-dependent, but also habitat and context-dependent (González-Megías and Menéndez, 2012; Slade et al., 2016). Due so, the habitat modification associated with climate variations may revert positive and negative interactions producing unpredictable scenarios associated to land use (González-Megías and Menéndez, 2012).

There is increasing evidence that species are already responding to microclimate changes by adjusting their geographic and altitudinal distributions (Birkett et al., 2018; Nunes et al., 2016; Parmesan, 2006; Pecl et al., 2017). Insects are the organisms most likely to be affected by climate change, and dung beetles are particularly sensitive, since climate has a direct influence on their development, reproduction and survival (Bale et al., 2002; Menendez, 2007). Dung beetles use dung to feeding and nesting, and dung removal drives all the other ecological functions performed by them (Andresen, 2002; Braga et al., 2012; Slade et al., 2007), such as nutrient cycling and bioturbation (Brown et al., 2010; Sitters et al., 2014). These organisms is also known for their potential to reduce detritus-feeding fly abundances on pastures systems, due to the competition for resource (Braga et al., 2012; Hanski and Cambefort, 1991).

However, both climate changes and disturbances in natural systems may affect dung beetle communities, changing the habitat associations and reducing the rates of dung removal and the associated functions (Beynon et al., 2015, 2012; Menéndez et al., 2016). The reduced ecological functions can cause accumulation of dung on the pastures, reducing the available grazing area and facilitating the spread of pests (Beynon et al., 2012). Due so, understand the links of climate and human disturbance on biotic communities and their functioning can be important in anticipating and planning conservation needs.

Tropical savannas cover more than 20% of the global land surface, and it is estimated that one-fifth of the global human population depends directly on this regions for their livelihoods, making it one of the most impacted systems in the present (Lehmann et al., 2009; Olsson and Ouattara, 2013). The conversion of tropical savannas to cattle pastures, even considered as a subtle change, negatively affects the dung beetle community and its ecological functions (Almeida et al., 2011; Correa et al., 2019). However, little is known about the effects of climate change on biodiversity and ecological functions in these systems. Due so, to test the effect of tropical savannas conversion into pastures in regions submitted to different climatic conditions, we selected three bioclimatic zones (BZ) distributed along Brazilian savanna (Cerrado).

The Cerrado is considered an important hotspot for biodiversity, because of its high species richness and rate of endemism (Myers et al., 2000). However, this system has been extensively cleared for agriculture and livestock (Beuchle et al., 2015; Overbeck et al., 2015). Here, we assessed climatic and environmental variables to test their direct and indirect effects on dung beetle communities and associated ecological functions (dung removal, soil bioturbation, and dung beetles interaction with dung-feeding fly), using structural equations modeling (SEM). Specifically, we aimed to 1) test if the effect of Cerrado's conversion into pasture is dependent of bioclimatic zone; 2) verify the direct and indirect effect of bioclimatic zone and system changes on dung beetle communities and ecological functions; and 3) identify the key factors explaining the ecological functions.

2. Materials and methods

2.1 Study site

The study areas are located in Minas Gerais State– Brazil (Fig. 1). We selected three municipalities in geographical core of tropical savanna (Cerrado *sensu stricto*) region, immersed in different bioclimatic zone (BZ) (Roriz, 2012): Januária (BZ 12), Arinos (BZ 20) and Formiga (BZ 16) (15°27'13.45"S 44°48'43.83"W, 15°54'26.36"S 45°59'48.49"W and 20°28'15.54"S 45°28'48.23"W respectively). Januária and Arinos have a tropical climate, with rainfall concentrated in the summer. The climate is classified as Aw (according to Köppen and Geiger) to Januária and Arinos municipalities, with average temperature and precipitation of 24.5 ° C and 926 mm in Januária, and 23.9 ° C and 1,181 mm in Arinos. In Formiga the climate is classified as Cwa, hot and temperate, with rainfall concentrated in the summer, presenting an average temperature of 20.6 ° C and annual average rainfall of 1,437 mm (Source: Climate-data). The altitude of the region ranged from 471 to 882 m. The average temperature during the experiment varied from 26° to 28°C, and precipitation from 50 to 460 mm.

In each BZ, we selected three areas of Cerrado and three of exotic cattle pasture (*Urochloa* spp.), 3 km apart each other, and in each area we installed three independent sampling points 100 m apart each other, totalling 54 independent sampled points (see Silva and Hernández, 2015).

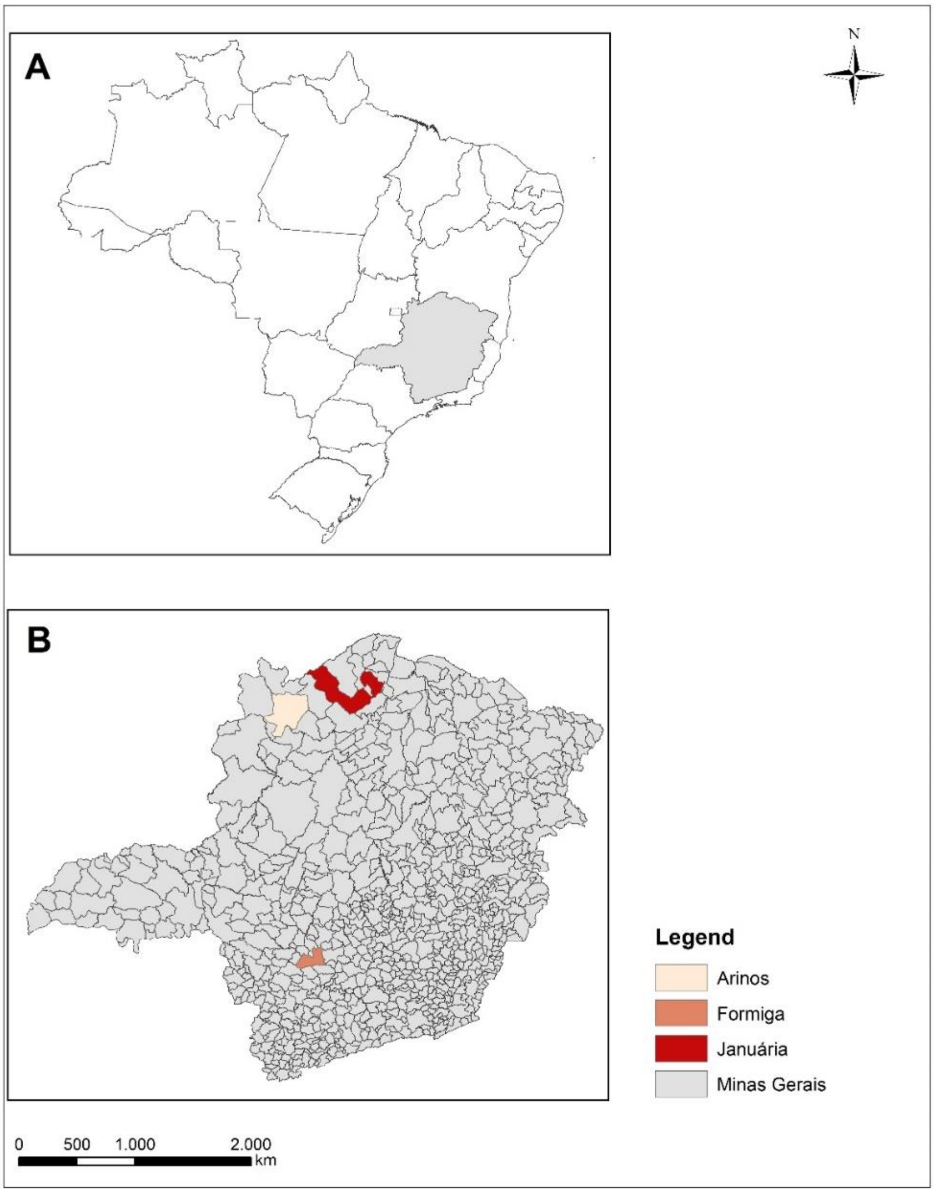

Fig. 1 Study area map showing (A) localization of the studied region Minas Gerais State—Brazil, and (B) the three studied municipalities in Minas Gerais State, Arinos, Formiga and Januária.

2.2 Dung beetle sampling

We sampled dung beetles between January to March 2016 (the wet season), period of greatest activity of dung beetles in tropical ecosystems (Halffter, 1991). In each sampling point we set up two pitfall traps 3 m apart baited one with 30 g of human faeces and the other with 500 g of cow dung, in order to sample the largest possible local dung beetle community.

Baits was placed at the center of trap using a wire as bait holder. Pitfall traps consisted of plastic containers with 19 cm diameter and 11 cm deep, partially filled with 250 ml water, salt and detergent. The traps was protect from rain with a plastic lid suspended 20 cm above the surface and collections took place over a period of 48 h at each sampling site.

Dung beetle specimens were transported in 80% alcohol from the field to the laboratory – Laboratório de Ecologia e Conservação de Invertebrados at Universidade Federal de Lavras (LECIN - UFLA), then sorted, dried in drying oven 40ºC for 72h or until they are completely dried, and stored in paper envelopes. We identified the dung beetles using a key to the genera and subgenera of subfamily Scarabaeinae of the New World (Vaz-de-Mello et al., 2011), the reference collection at Coleção de Referência de Escarabeíneos Neotropicais (CREN – UFLA) and the identification was confirm by the specialist Dr. Fernando Z. Vaz-de-Melo at Universidade Federal do Mato Grosso (UFMT). Voucher specimens were deposited at CREN - UFLA in Minas Gerais State, Brazil.

We considered the species richness as the number of different species at each sampling point. We measured the dry body mass from 20 randomly selected individuals (or the maximum number available), to obtain mean value for each specie, and obtained total biomass by multiplying each species mean weight by its abundance and summing across sites.

2.3 Dung beetle functions

We set up an ecological function experiment in each sampling point at the day before the dung beetles sampling. Ecological functions consisted in a circular plot “arena”, 1 m in diameter, the border of which delimited by a fence (approximately 15 cm high) built using a nylon net with a mesh size of 0.08 mm, held by bamboo sticks (Fig. S1). The nylon fence limited the horizontal movement of dung by the beetles to the contained area, allowing a more accurate quantification of the examined functions. We cleared the soil surface of each arena of litter and vegetation to further facilitate the measurement of ecological functions (for details see Braga et al., 2013). In the center of each arena we placed an experimental dung pile consisting of 200 g of a mixture of 4:1 proportion of fresh swine and human dung, protected for the rain by a plastic lid. In each sampling site we used a humidity loss control consisting of 30 g of fresh human faeces wrapped in a nylon fabric and suspended over the soil by a bamboo stick, to account for water loss or gain in the calculation of dung removal rates.

We measured dung removal and soil bioturbation 24 h after the placement of the experimental dung piles. To determine dung removal rates, the amount of remaining dung was collected, weighed and then dung removal was calculated by subtracting from the original dung weight added to the arena. To determine the amount of soil excavated by dung beetles, loose soil around and beneath the experimental dung pile was collected, taken to laboratory and dried at 80°C until a constant weight.

2.4 Larvae and adult flies sampling

We installed a trap to catch dung flies 3 m away from each arena. The trap consists of a pet bottle, with openings at the bottom, baited with 30 g human faeces. Flies entering through the openings of the trap are able to oviposit in the dung pad, but are trapped in the top when they attempt to exit. After 24 h of exposure the traps were removed from the field. The adults were transported in 80% alcohol from the field to the laboratory (LECIN - UFLA), sorted and counted. The dung sample was then incubated for 48 h to produce as fly larvae as possible to agree with visual counting. Both adult and larval flies were used as a proxy for the dung fly communities (see Braga et al., 2012).

2.5 Vegetation structural characterization

We recorded the vegetation density and vegetation fractal dimension using SIDELOOK software (Nobis, 2005). Fractal dimension (number that characterizes the geometry of a fractal) was used as a proxy of vegetation heterogeneity, and from hereinafter we will refer just as vegetation heterogeneity. To do so, we took photographs of the understory according to a methodology adapted from Nobis (2005), and analyzed them in the software. In each sampling point we took four photographs of a black panel (1 × 1 m) placed behind vegetation 3 m away. We used a camera positioned 1 m above the soil with parallel and perpendicular orientation to the pair of *pitffall* traps. The vegetation density was calculated using the following formula: $VD = A \times (BP / WP) / W$. Where, VD = vegetation density; A = area of the panel (height multiplied by the width); BP = black pixels; WP = white pixels and W = panel width.

2.6 Data analysis

2.6.1 Variables

We calculated two functional diversity indices using morphological (body mass - bm, bm-adjusted front leg area, bm-adjusted pronotum volume, and back:front leg lengths) and nesting strategy (rollers, tunnelers and dwellers) dung beetles traits in FD package (Laliberté et al., 2012) in R 3.5.2 (R Development Core Team 2018). The chosen indices were functional richness (FRic) and functional evenness (FEve) (Laliberté and Legendre, 2010), since we found different responses between Cerrado and pasture in previously study (Maciel et al. data not published).

We selected climatic, environmental, dung beetles and functional variables. The climatic variable selected was bioclimatic zone (BZ). The environmental variables was system, vegetation heterogeneity and vegetation density. The dung beetle variables was species richness, total biomass, functional richness and functional evenness, and the functionality variables was dung removing, soil bioturbation, adult dung flies and larvae abundances. All variables were submitted to Spearman’s correlation to test the collinearity between them.

To avoid the use of variables that display redundant information and to extract the most predictive information, we used principal component analysis (PCA) to verify the congruence between variables related to functional indices (FRic and FEve), dung beetles functions (dung removal and soil bioturbation) and dung flies (adult dung flies and larvae abundance) in factoextra package. The PCA is an analysis capable of verifying the correlation between variables and joining them in axes created based on eigenvectors. We used the first axis (PC1) for analyses of functional indices, dung beetles functions and dung flies in the subsequent SEM analyses, and we test the effect of the axis to verify the direction of the relationship with each variable separately. As a result, PC1 explained 77% of variation of functional indices, 88% of functions and 51% of flies’ abundance in full model, 77%, 90% e 79% in Cerrado model and 71%, 88% and 56% in Pasture model. Only dung flies PCA for full model and Pasture model was negatively related to larvae abundance.

2.6.2 Structural Equations Modeling

We used Structural Equations Modeling (SEM), also known as path analysis, through the lavaan package, to create models expressing the interactions among variables. SEM allows testing a hypothesis of causal order among a set of variables. It allows us to calculate all relations between the independent (exogenous) variables and their ability to explain a given phenomenon (dependent or endogenous variable) (Grace, 2006; Eisenhauer et al., 2015; Veen et al., 2010). The variable matrix was submitted to mardia test using MVN package and since they are not normal, we submitted the models to bootstrap of 1000 randomizations.

We create hypothetical models with possible interactions between variables (Fig. 2), using only interactions with biological sense or theory based (Valdés and García, 2011). The hypothetical models was based in all sample data (full model) and by land use systems separately (Cerrado and pasture models). The exogenous variables was: system and BZ, and the endogenous variables was: vegetation heterogeneity, vegetation density, dung beetles species richness, dung beetles total biomass, functional indices, dung beetles functions and flies abundance. After performing the analyses, the non-significant interactions were excluded to better fit the model. We measured the direct and indirect effect of BZ and system in dung beetle and functions variables. Direct effects was values obtained by standardized partial regression coefficients between the exogenous and endogenous variables. The indirect effects was calculated as the sum of the products of all standardized partial regression coefficients over all paths between the exogenous and endogenous variables.

To confirm whether the observed data support the tested hypothetical model (model a priori) we used goodness of fit tests. We used three indices to test the fit of the model: 1) RMSEA (root mean square error of approximation) - tells how well the model, with unknown but optimally chosen parameter estimates would fit the hypothetical model. Well-fitting models obtaining values less than 0.05. 2) SRMR (standardised root mean square residual) - are the square root of the difference between the residuals of the hypothetical model and the null model. Range from 0 to 1 with well fitting models obtaining values less than 0.05 (Hooper et al., 2008). 3) CFI (comparative fit index) - compares the hypothetical model with the null model (perfect fit model). Ranges from zero to one with well-fitting models obtaining values > 0.90. All analyses was performed in R software version 3.4.4 (R Development Core Team 2018).

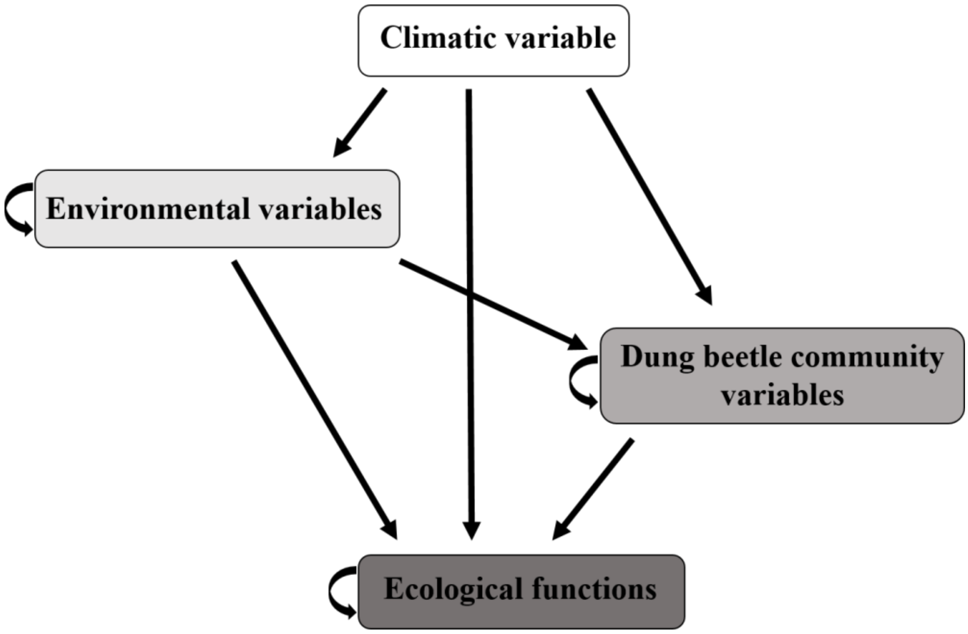

Fig. 2 Theoretical model of the connections between climatic, environmental, dung beetle community and ecological functions variables. Arrows indicate the direction of interactions.

3. Results

The final models presented good adjustment according to RMSEA, but Cerrado model did fit in the SRMR, but not in CFI full model (Tab. 1). In the full model, system directly affect vegetation structure (vegetation heterogeneity and density) and indirectly affect dung beetle richness. In addition, system affect directly and indirectly dung beetle functions and flies abundance. BZ directly affect dung beetle richness and functions and indirectly affect biomass, functional indices and dung flies abundance (Table 2).

Cerrado conversion into pastures negatively affect the vegetation structure, which in turn positively affect dung beetles richness and functions. Besides, Cerrado conversion into pasture affect positively dung beetle function and adult dung flies abundance, and negatively affect larvae abundance. BZ negatively affect dung beetle richness and functions, what means that in BZ 12 (Januária) there is more dung beetle richness and functions, and in the 16 and 20 (Formiga and Arinos respectively), richness and functions decrease. Functional indices positively affect dung beetle function, and biomass affect negatively adult dung flies and positively larvae abundance. Lastly, dung beetle functions affect positively adult dung flies and negatively larvae abundance (Fig. 3).

In the best Cerrado model selected, we found that BZ have direct effect in dung beetle richness and indirect effect in biomass, functional indices and functions (Table 2). Dung beetle richness is negatively affected by vegetation heterogeneity and BZ and positively by vegetation density. In turn, dung beetle richness positively affect functional indices, dung beetle biomass and functions, showing that the higher the dung beetle communities parameters, the more functions are performed. Besides, dung beetle biomass positively affect dung flies abundances (Fig. 4A). In the best pasture model selected, BZ directly positively affect dung beetle biomass and negatively affect functions (Table2). Vegetation density positively affect dung beetle richness, that positively affect dung beetle biomass, functional indices, functions and adult dung flies abundance in turn. Dung beetle richness also affect negatively larvae abundance (Fig. 4B).

Table 1 Values of fit indices of the full, Cerrado and pasture structural equations models.

Model	Model fit indices		
	RMSEA	SRMR	CFI
Values of a model with fitting	<0.07	<0.08	>0.90
Full	0.003	0.120	0.893
Cerrado	0.038	0.079	0.902
Pasture	0.008	0.110	0.911

Nomenclature: RMSEA= root mean square error of approximation, SRMR= standardised root mean square residual and CFI= comparative fit index.

Table 2 Direct, indirect and total effects of system and bioclimatic zone (BZ) in functions, flies abundance, richness, biomass and functional indices for full, Cerrado and Pasture models.

		Full model			Cerrado model			Pasture model		
Endogenous	**Exogenous**	**Direct**	**Indirect**	**Total**	**Direct**	**Indirect**	**Total**	**Direct**	**Indirect**	**Total**
Functions	System	0.31	-0.08	0.23	---	---	---	---	---	---
	BZ	-0.48	-	-0.48	-	-0.45	-0.45	-0.51	-	-0.51
Flies abundance	System	0.32	0.09	0.41	---	---	---	---	---	---
	BZ	-	-0.14	-0.14	-	-	-	-	-	-
Richness	System	-	-0.31	-0.31	---	---	---	---	---	---
	BZ	-0.31	-	-0.31	-0.53	-	-0.53	-	-	-
Biomass	System	-	-	-	---	---	---	---	---	---
	BZ	-	-0.23	-0.23	-	-0.43	-0.43	0.45	-	0.45
Functional indices	System	-	-	-	---	---	---	---	---	---
	BZ	-	-0.24	-0.24	-	-0.38	-0.38	-	-	-

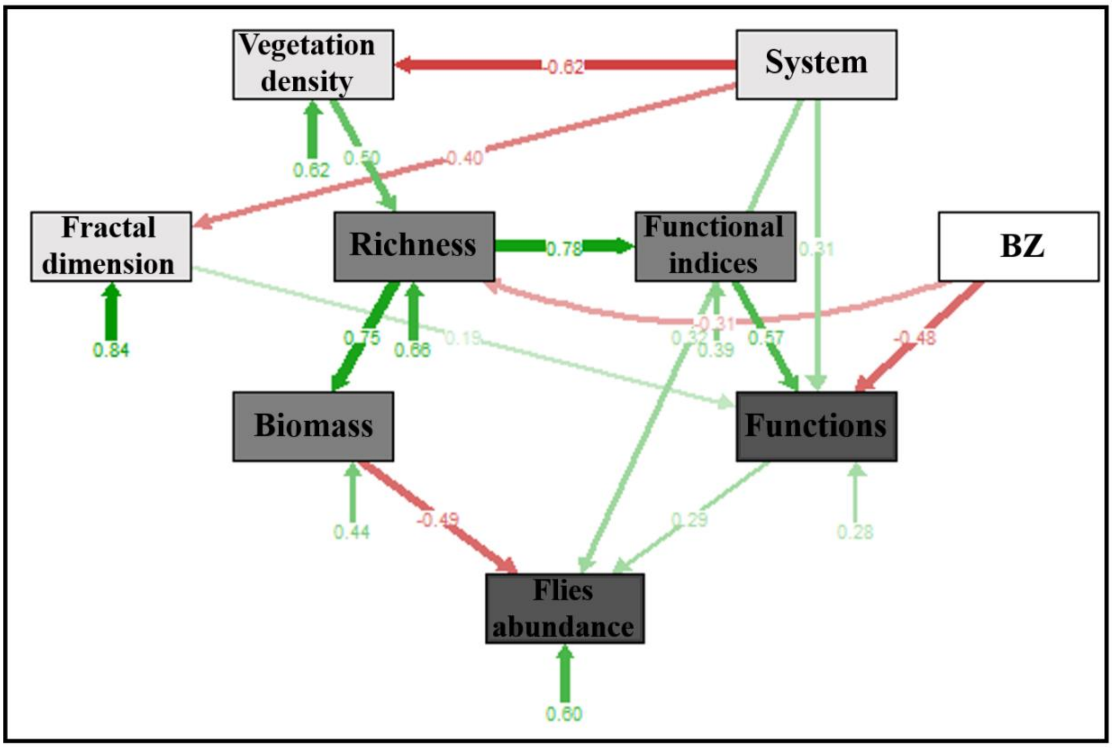

Fig. 3 Structural equation model result for full model. Green lines represent the positive effects and red lines the negative effects. Values between the arrows represent the path coefficients with standardized values. Residual variances are displayed in small arrows under each variable. BZ= bioclimatic zone.

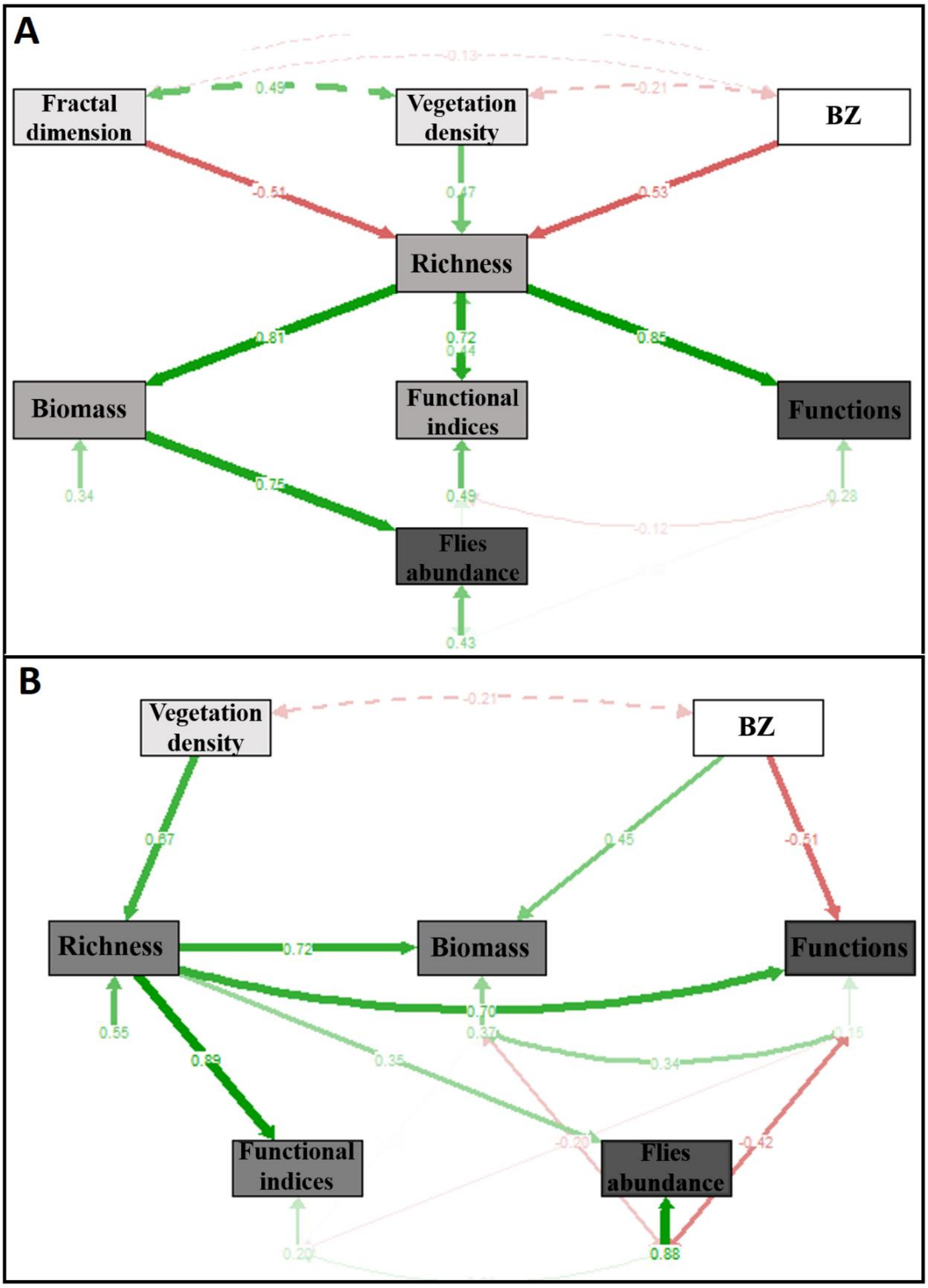

Fig. 4 Structural equation model result for A) Cerrado and B) Pasture. Green lines represent the positive and red lines the negative effects. Values between arrows represent the path coefficients with standardized values. Residual variances are displayed in small arrows under each variable. Dotted lines represent covariations between exogenous variables. Bidirectional arrows represent covariations without cause/effect relation. BZ= bioclimatic zone.

4. Discussion

In this study, we evaluated environmental and climate drivers acting over dung beetle communities and their ecological functions. We found that the effect of land use changes in tropical savannas is dependent of the bioclimatic zones. We also found that land use system and BZ directly and indirectly affected dung beetle communities, functions, and dung flies abundance. Our result suggested a cascade effect, since the loss of vegetation cover leads to losses in dung beetle communities' parameters and consequently ecological functions. Dung beetle richness was the most important variable among all models evaluated, positively affecting directly and/or indirectly all other variables of dung beetles and ecological functions. Due so, the loss of species richness cause decreases in dung beetle biomass, functional indices and ecological functions, affecting the ecosystem functioning.

The system and BZ had important effects on dung beetle communities' structure and the ecological functions. Cerrado conversion into pasture leads to vegetation structure changes and loss of vegetation coverage. Here, we showed that the vegetation density and vegetation heterogeneity were positively related to dung beetle species richness and functions in full model. In system models, the vegetation structure also is determinant for dung beetles species richness. Due so, the substitution of the vegetation by pasture leads to loss of dung beetle richness and functions. This result was expected, since for dung beetles of tropical regions, the vegetation cover is one of the most important factors (Audino et al., 2014; Costa et al., 2017; Halffter and Arellano, 2002).

On the other hand, our results suggested that Cerrado conversion into pasture positively affect dung removal and soil bioturbation. In both, Cerrado and pasture models, species richness positively affected directly dung beetle biomass, functional indices and ecological functions. This could be explained by the high availability of food resource, due to the cattle presence in pastures, which may favour the persistence of large populations and total biomass of dung beetles (Lobo, 2006; Tonelli et al., 2018) and consequently their functions. However, it is important to emphasize that the conversion of natural systems in anthropogenic systems leads to species richness loss in several tropical biomes (Beiroz et al., 2018; Correa et al., 2019; Solar et al., 2015; Tavares et al., 2019). Due so, since we found that species richness is a important variable, the loss of species richness could lead to a cascade effect.

The conversion of Cerrado into pasture also leads to an increase in the abundance of adult dung flies, but the number of larvae decreases. On the other hand, the increase of dung beetle total biomass leads to a decrease in adult dung flies abundance. In Cerrado, the increase of biomass leads to increases in functions and in dung flies abundance. In pasture, the increase in species richness leads to an increase in biomass, functional structure and functions, and leads to a decrease in the larvae abundance, although the adult flies increases. Dung beetle is knowing for their potential to reduce detritus-feeding fly abundances, due to the competition for resource, since both organism use dung and carrion for feeding and nesting (Hanski and Cambefort, 1991; Nichols et al., 2008; Wu and Sun, 2010). However, the land-use intensification and simplification could interfere in the dung beetles and flies interaction mediated by dung beetles functions (Braga et al., 2012; Sladecek et al., 2017). Other factors also could influence flies abundance, like climatic changes, since we found that BZ has negative effect on dung flies abundance, although it is a weak effect.

In full and Cerrado models, the BZ negatively affected directly and/or indirectly all dung beetle and functional variables. In pasture model the BZ affected directly biomass and functions. Januária (BZ12) was the BZ whith more species richness, biomass, functional indices and functions, compared to Arinos and Formiga (BZ 16 and 20 respectively) (also see Fig. S2). Diversity-ecosystem functioning relationships may be dependent not only on the functions, but also to the environmental context (Slade and Roslin, 2016 and references cited), as we found here. Besides, the expansion of agriculture, overexploitation and introduction of invasive alien species have been the main drivers of biodiversity loss, but several lines of research suggest that climate change could become an important cause of extinction (Lemes et al., 2019; Pacifici et al., 2015; Thomas et al., 2004).

Indeed, theory predicts that species will change their distribution ranges, their habitat associations (Menéndez et al., 2014), and cause the extinction of many species (Lemes et al., 2019; Thomas et al., 2004). Climate change will not only affect the strength of species interactions, but may also turn positive interactions into negative ones or vice versa (González-Megías and Menéndez, 2012), with consequences for ecosystem functioning (Barton et al., 2009; Durant et al., 2007; Slade et al., 2016). Dung beetles can change habitat associations in response to different and changing bioclimatic conditions, suggesting that global warming will affect their habitat selection (Menéndez et al., 2016; Menéndez and Gutiérrez, 2004). Due so, our results could help to understand and predict the effects of climate changes associated to land use changes, since we found different responses of dung beetle communities and interactions with flies, and thus help to create strategies to remedy negative effects.

In this work, we highlight the importance of climatic variation associated with land use changes, to determine the parameters related to dung beetle communities and the ecosystem functions. We conclude that Cerrado conversion into pasture can have a cascade effect, as the loss of vegetation cover leads to loss of dung beetle species richness, which causes loss of biomass and functional indices, affecting dung beetle functions and interaction with dung flies. However, the community of dung beetles and the ecological functions are affected in different ways, depending of the BZ. Therefore, we suggest that public politics should be thought to evaluate separately each region, submitted to the effects of different climatic conditions, since the responses of dung beetles communities are context dependent.

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Supplementary material

Fig. S1 Experimental arena used for measuring the dung beetles ecological functions: dung removal and soil bioturbation (see main text for description).

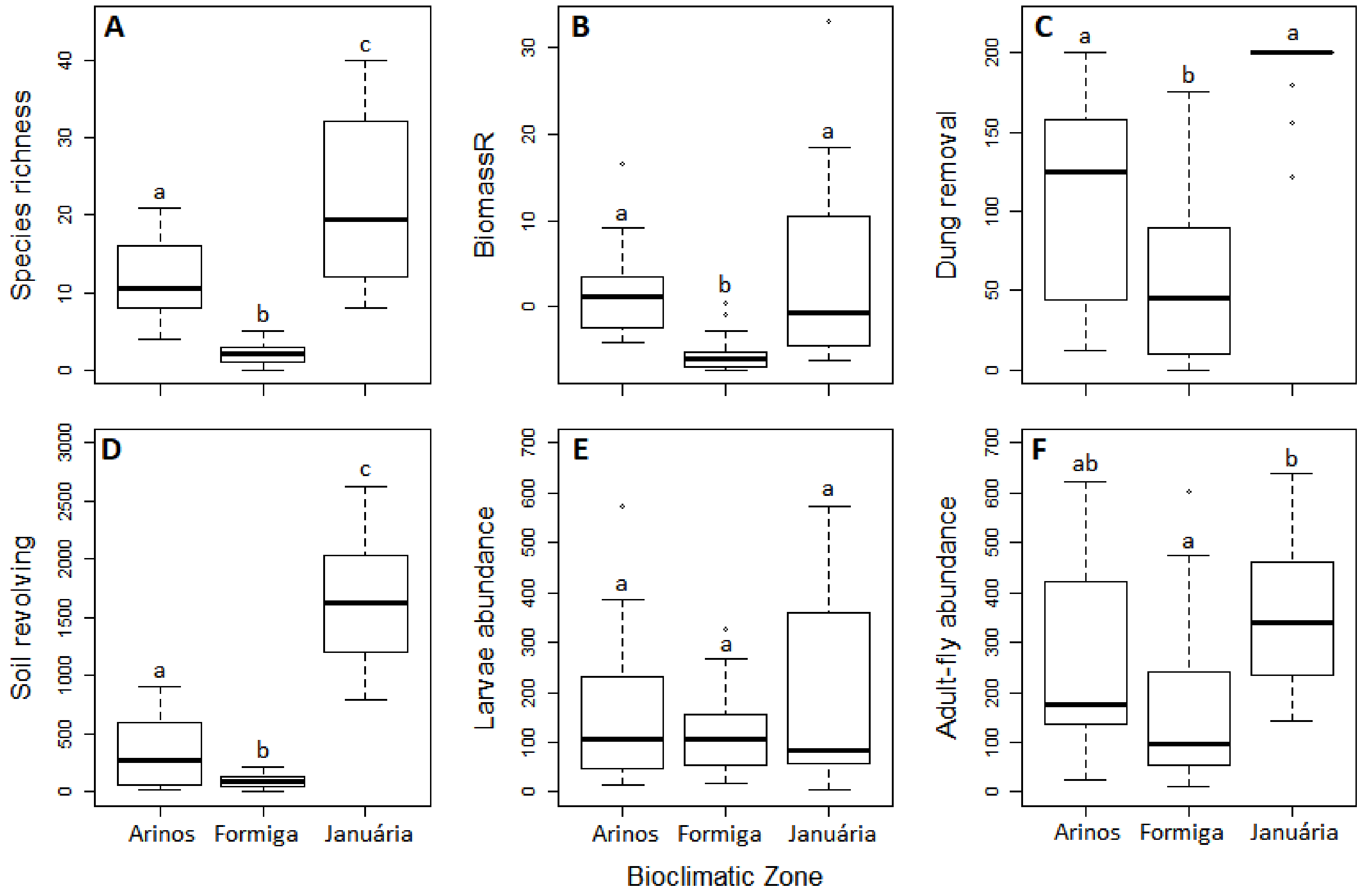

Fig. S2 Differences in A) dung beetle species richness; B) dung beetle total biomass; C) dung removal; D) soil bioturbation; E) larvae abundance; and F) adult-fly abundance among bioclimatic zones: Arinos, Formiga and Januária. Identical letters above the bars indicate that there were no significant differences among the bioclimatic zone ($p > 0.05$).

CONCLUSÃO GERAL

Neste trabalho avaliamos como a conversão de savana tropical (Cerrado) em pastagens afeta a biodiversidade e as funções ecossistêmicas associadas, utilizando os besouros rola-bosta como ferramenta de estudo. Utilizamos características morfológicas e comportamental para calcular os parâmetros de diversidade funcional, e testamos como a diversidade taxonômica (riqueza, abundância, biomassa e composição) e a diversidade funcional (riqueza, equitabilidade e divergência funcionais, e composição funcional) são afetadas pelas mudanças no uso do solo. Além disso, selecionamos três diferentes zonas bioclimáticas e avaliamos como variáveis ambientais e climática afetam a comunidade de besouros rola-bosta e suas funções de remoção de fezes, revolvimento do solo, e interação entre besouros e moscas detritívoras.

Encontramos que a conversão do Cerrado em pastagens afeta tanto a diversidade taxonômica quanto a diversidade funcional. Houve declínio na riqueza de espécies, e na riqueza e equitabilidade funcional, possivelmente causada pela perda de características funcionais nas pastagens. A mudança de uso do solo altera também a composição de espécies e a composição funcional. Encontramos também que os efeitos da mudança de uso do solo são dependentes da zona bioclimática e ambos têm efeitos diretos e indiretos na comunidade de rola-bosta e suas funções. A riqueza de espécies foi a variável mais importante, tendo efeito em todas as outras variáveis da comunidade de besouros, nas variáveis funcionais e de moscas detritívoras. Com isso, nossos resultados sugerem um efeito cascata, mostrando que a perda na riqueza de espécies causada pela conversão de Cerrado em pastagens leva à perda da funcionalidade do ecossistema. No entanto, mostramos que a comunidade de besouros e suas funções são afetadas de maneira diferente, dependendo da região bioclimática em que se encontram, sendo fortemente dependentes do contexto regional.

Como o aumento da substituição de áreas nativas para implementação de pastagens para criação de gado e áreas agrícolas, impulsionado pelo aumento populacional e crescente demanda para produção de alimento (Aide et al., 2013; Sy et al., 2015), torna-se importante entender as potenciais consequências dessa alteração na biodiversidade e nas funções ecossistêmicas. Associada às mudanças de uso do solo, as mudanças climáticas também têm tido importante impacto nos sistemas biológicos, podendo afetar a distribuição das espécies e as interações entre elas (González-Megías and Menéndez, 2012; Milotić et al., 2017; Parmesan, 2006), sendo juntas as principais responsáveis pela perda da biodiversidade em regiões tropicais (Lemes et al., 2019; Pacifici et al., 2015). Em sistemas agrícolas os besouros rola-bosta desempenham importantes funções, tais como remoção de fezes, revolvimento de solo, dispersão secundária de sementes e controle de moscas hematófagas, e com isso contribuem para diversos processos ecológicos (Braga et al., 2012; Halffter and Favila, 1993; Manning and Cutler, 2018; Nichols et al., 2008). Sendo assim, manter comunidades funcionais desses organismos é crucial para a manutenção do funcionamento dos ecossistemas.

Nossos resultados ajudam a compreender os efeitos da conversão de savanas tropicais em pastagens na biodiversidade e suas funções, assim como os efeitos das variações climáticas associadas a essas mudanças de uso do solo. Com esse trabalho, enfatizamos a importância de manter a conservação do Cerrado para manutenção da biodiversidade e da funcionalidade dos ecossistemas, e sugerimos que políticas públicas sejam tomadas de forma a considerar o contexto climático, já que as comunidades de besouros e suas funções se mostraram dependentes das características regionais.

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