UNIVERSIDADE FEDERAL DE LAVRAS

CÉSAR MURILO DE ALBUQUERQUE CORREA

CATTLE GRAZING IMPACTS ON DUNG BEETLE COMMUNITIES AND THEIR ECOLOGICAL FUNCTIONS IN THE BRAZILIAN PANTANAL

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

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IMPACTOS DO PASTEJO DO GADO NAS COMUNIDADES DE BESOUROS ROLA-BOSTAS E SUAS FUNÇÕES ECOLÓGICAS NO PANTANAL BRASILEIRO

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

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“Have I not commanded you? Be strong and courageous. Do not be afraid; do not be discouraged, for the LORD your God will be with you wherever you go.”

Joshua 1.9

RESUMO GERAL

Os ecossistemas campestres dominam os trópicos sustentando uma biodiversidade única e fornecendo serviços ecológicos valiosos para a humanidade. No entanto, estes ecossistemas têm sido extensivamente desmatados para agricultura, florestas plantadas e principalmente usado como pastagem para o bovino. Diante disso, objetivou-se com essa tese avaliar o impacto causado pelo pastejo de bovinos na comunidade de besouros rola-bostas (Coleoptera: Scarabaeinae) e nas funções ecológicas desempenhadas por estes insetos num ecossistema campestre tropical, inserido no Pantanal Brasilieiro. Realizou-se a coleta dos insetos em 24 áreas de campos nativos com diferentes tempos de abandono de pastejo de bovinos no Pantanal de Aquidauana, Mato Grosso do Sul, Brasil. No primeiro capítulo, avaliou-se o efeito do pastejo bovino nas métricas da comunidade (abundância, biomassa, riqueza, composição de espécies e grupos funcionais) e nas funções ecológicas (remoção de fezes e bioturbação do solo) desempenhadas por besouros rola-bostas, em 10 áreas regularmente pastejadas pelo gado e seis áreas não utilizadas como pasto (> 20 anos de abandono). Verificou-se que a presença do gado, embora cause uma modificação na composição de espécies, não afeta a abundância, riqueza, biomassa e as funções ecológicas dos besouros rola-bostas. No segundo capítulo, foi estudada a trajetória sucessional da comunidade de besouros rola-bostas ao longo de uma cronoseqüência de pastagens naturais com diferentes idades de exclusão de pastoreio do gado (0,4 a 22 anos). Foi encontrada uma redução na abundância e riqueza de espécies de besouros rola-bostas nos primeiros dez anos de abandono do gado. No entanto, após dez anos, houve um aumento nesses parâmetros. Após três anos de abandono a composição taxonômica foi diferente do controle, com a formação de uma comunidade de espécies distinta. A diversidade funcional não foi afetada pelo abandono do pastejo, demonstrando ser menos sensível à ausência de gado do que à diversidade taxonômica. Dessa maneira, conclui-se que a criação de gado em pastagens naturais do Pantanal não causam impactos relevantes na comunidade de besouros rola-bostas (principalmente da diversidade funcional) e suas funções ecológicas. Isso demonstra que o manejo pecuário utilizado (com pouco uso de produtos veterinários e baixa densidade de bovinos por hectare) pode integrar a produção pecuária com a conservação da biodiversidade, além de fornecer oportunidades para manter os campos nativos, sem que esses sejam convertidos em outros usos da terra. Finalmente, a exclusão do pastoreio do gado, em um espaço relativamente curto de tempo (20 anos) pode ser uma estratégia ineficiente para a recuperação dos ecossistemas campestres tropicais.

Palavras-chave: Conservação da biodiversidade, Cronosequência, Diversidade funcional, Manejo pecuário, Pastagens nativas, Scarabaeinae, Serviços ecossistêmicos, Zonas úmidas.

GENERAL ABSTRACT

Grassy ecosystems dominate the tropics sustaining unique biodiversity and providing valuable ecological services to humankind. However, these ecosystems have been extensively cleared for agriculture and planted forests or used as pasture for livestock. Thus, the aim of this thesis was to assess the impact of cattle grazing on dung beetle community and its ecological functions in a tropical grassy ecosystem, inserted in Brazilian Pantanal. The insects were collected in 24 areas of native grasslands with different times of cattle grazing abandonment, in the Pantanal of Aquidauana, Mato Grosso do Sul, Brazil. In the first chapter, I evaluated the effects of cattle grazing on community metrics (abundance, biomass, richness, species composition and functional groups) and ecological functions (dung removal and soil bioturbation) performed by dung beetles, in 10 regularly grazed by cattle and six control ungrazed areas, used as pastures (> 20 years of abandonment). I found that the cattle grazing, despite causing changes in species composition, does not affect the abundance, richness, biomass and ecological functions performed by dung beetles. In the second chapter, I studied the successional trajectory of dung beetle communities after cattle grazing abandonment along a chronosequence of natural grasslands with different cattle grazing exclusion ages (0.4 – 22 years). I found a strong decrease of dung beetle abundance and species richness in the first ten years of cattle grazing abandonment. However, after ten years there is an increase in these parameters. After three years of abandonment the taxonomic composition was different from the control, with the formation of a species community distinct. Functional diversity was not affected by cattle grazing abandonment, demonstrating that it is less sensitive to cattle absence than taxonomic diversity. Thus, these results provide evidence that livestock farming in natural grasslands of Brazilian Pantanal do not cause significant impacts on the dung beetle community (mainly functional diversity) and their ecological functions. This demonstrates that livestock management (with reduced use of veterinary drugs) can integrate livestock production with biodiversity conservation, as well as provide opportunities to maintain native fields, without them being converted to other land uses. Finally, cattle grazing exclusion, in a relatively short time (20 years), may be an inefficient management tool for restoration and conservation of tropical grassy ecosystems.

Key words: Biodiversity conservation, Chronosequence, Ecosystem services, Functional diversity, Livestock management, Native pastures, Scarabaeinae, Wetlands.

FIGURE CAPTIONS

Article 1

Article 2

TABLE LIST

Article 1

Article 2

SUMMARY

FIRST PART

1. GENERAL INTRODUCTION

Tropical grassy ecosystems (e.g. savannas and grasslands) dominate the tropics and account for 20% of the global surface area (SCHOLES; ARCHER, 1997), sustaining unique biodiversity and providing valuable ecological services to humankind (PARR et al., 2014). Most grasslands ecosystems are located in tropical countries; where currently about one-fifth of the world's human population depends directly on them for their livelihood, including for land uses such as pastures for animals, firewood and medicinal plants (PARR et al., 2014; VELDMANN et al., 2015). Despite their importance, the grasslands have been neglected in terms of public policies for natural resources conservation (OVERBECK et al., 2015). Overall, grassland ecosystems has been extensively cleared for crops and forest plantation or used as pasture for livestock (BOND; PARR, 2010).

Currently, livestock farming, the largest land-demanding sector on Earth, occupies more than 30% of the planet's continental surface (FAO, 2012). Population growth in the last half of the 20th century has led to an increase in the demand for food and biofuels, stimulating the expansion of agricultural frontiers (TILMAN et al., 2012). Thus, technological advances have sustained agricultural expansion (crop plantations and livestock farming) in the tropics, resulting in productive areas previously unexplored (LAURENCE et al., 2014). In Brazil, the process of agricultural expansion started in the South region and expanded to areas of the Cerrado (Brazilian savannas) (KLINK; MOREIRA, 2002), and is currently expanding to areas of Brazilian Pantanal (HARRIS et al., 2005) and Amazon (SOARES-FILHO et al., 2006). Pasture expansion and agriculture intensification are currently among the main decline causes of global biodiversity and ecosystem services (CHAPLIN-KRAMER et al., 2015; LAURENCE et al., 2014). The negative effects of livestock on biodiversity are related to the conversion of native to exotic vegetation, increase in grazing intensity, the replacement of wild grazers by domestic animals and land management (e.g., use of fertilizers and veterinary drugs) (ALKEMADE et al., 2013; LEHMANN; PARR, 2016).

Cattle grazing is a traditional agricultural activity, and one of the main economic activities carried out in tropical grassy ecosystems (PARR et al., 2014). Grazing by large mammalian herbivores has historically and prehistorically been a major structuring force in tropical grassy ecosystems (VELDMANN et al. 2015; BAKKER et al., 2015). These ecosystems evolved with and depended on herbivory, heavy hoof action, nitrogen deposits, and decomposing carcasses of large herbivores (BOND; PARR, 2010), directly influencing their biodiversity and ecosystem services (DETTENMAYER et al. 2017; van KLINK et al. 2015).

Although the role of livestock farming as a global agent for the degradation of grassy ecosystems is recognized (PARR et al., 2014; OVERBECK et al., 2015; VELDMANN et al., 2015), cattle grazing in suitable density and frequency may be beneficial for the biodiversity of grassland ecosystems (OVERBECK et al., 2007). For this reason, there is an increasing debate in scientific literature about the effects of cattle grazing on the biodiversity of tropical grassy ecosystems (LEHMANN; PARR, 2016; OVERBECK et al., 2015; PARR et al., 2014; VELDMANN et al., 2015). The central point is the debate about the trade-offs between livestock grazing and/or exclusion and the potential for grassland ecosystem regeneration (LISTOPAD et al., 2018; TÖROK et al., 2016).

Functional diversity is a measure of biodiversity that quantifies the diversity of characters; capturing differences in species morphology and physiology, life history traits, and ecological niches that affect community responses to the disturbance, and consequently, changes in ecological functions (CADOTTE et al., 2011; GERISCH et al., 2012; AUDINO et al., 2017; CORREA et al., 2019). Monitoring species and functional diversity can be an important strategy to understand the impacts of cattle grazing activity in tropical grassy ecosystems. In this sense, dung beetles (Coleoptera: Scarabaeidae) has been considered efficient indicators of environmental changes across the globe (NICHOLS et al., 2007), being often used as focal organisms to access both anthropic and natural impacts (e.g., GARDNER et al., 2008; BARRAGÁN et al., 2011; GERLACK et al., 2013; FRANÇA et al., 2016). These insects exhibit a sort of life history strategies that are evidenced in easily measureable functional traits (HALFFTER; EDMONDS, 1982; HANSKI; CAMBEFORT, 1991; GRIFFITHS et al., 2015). Thus, they are good models to studies aiming to use the functional diversity to understand the effects of anthropic actions on ecosystem processes (BARRÁGAN et al., 2011; AUDINO et al., 2014, 2017; CORREA et al., 2019).

In addition, dung beetles are essential for maintaining the pasture functionality (LOUZADA; CARVALHO e SILVA, 2009). They bury the manure produced by herds for nesting and feeding their offspring (HANSKI; CAMBEFORT, 1991), resulting in important ecological functions, such as: nutrient cycling (SLADE et al., 2007; YAMADA et al., 2007), improved soil fertility and physical characteristics (BANG et al., 2005; BROWN et al., 2010), reduced fly and gastrointestinal parasites (BRAGA et al., 2012; NICHOLS; GÓMEZ, 2014), facilitated vegetation development (JOHNSON et al., 2016) and greenhouse gas emission control (PENTILLÄ et al., 2013; SLADE et al., 2016). Many of these ecological functions can be translated in ecosystem services (*sensu* de GROOT et al., 2002).

The establishment of sustainable management in tropical grassy ecosystem has been one of the greatest challenges for the current livestock model adopted across Brazil (EATON et al., 2017; OVERBECK et al., 2007). Reconciling economic activity with biodiversity conservation is vital for current economic sustainability models (BAUMGÄSTNER; QUAAS, 2010). However, the effects of livestock farming on biodiversity are little known in the tropical grassy ecosystems. In this context, this thesis is composed by two chapters (presented as manuscripts) that have as shared objective to evaluate the cattle grazing impacts on dung beetle communities and their ecological functions in a tropical grassy ecosystem. For this, we sampled dung beetles in 24 natural grasslands in the Brazilian Pantanal. The Pantanal, a World Heritage Site and Biosphere Reserve, is a tropical grassy ecosystem considered the largest Neotropical seasonal freshwater wetland on Earth (160.000 km^2). The vast expanse of the grassland plains, allied with a favorable climate, promotes the cattle extensive ranching in the Pantanal (SEIDL et al., 2001). Over the last two centuries livestock production has been the dominant economic land use activity of the Pantanal (HARRIS et al., 2005).

In the first chapter, I evaluated the effects of cattle grazing on dung beetle community attributes (species richness, abundance, biomass, functional groups and species composition) as well their ecological functions (bioturbation and dung removal) in the Pantanal. In the second chapter, I studied the successional trajectory of dung beetle communities in a tropical grassy ecosystem after cattle grazing removal. For this, we evaluated, for the first time, patterns of dung beetle taxonomic and functional diversity along a chronosequence of natural grasslands with different cattle grazing removal ages (0.4 – 22 years). Finally, in conclusion section, I highlight the implications of my thesis to livestock farming and biodiversity conservation in tropical grassy ecosystems, and Brazilian Pantanal in particular.

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SECOND PART

PAPER 1 - Dung beetle diversity and functions suggest no major impacts of cattle grazing in Brazilian Pantanal wetlands

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Dung beetle diversity and functions suggest no major impacts of cattle grazing in the Brazilian Pantanal wetlands

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Abstract

1. Dung beetles perform relevant ecological functions in pastures, such as dung removal and parasite control. Livestock farming is the main economic activity in the Brazilian Pantanal. However, the impact of cattle grazing on the Pantanal´s native dung beetle community, and functions performed by them, is still unknown.

2. We evaluated the effects of cattle activity on dung beetle community attributes (richness, abundance, biomass, composition and functional group) as well as their ecological functions (dung removal and soil bioturbation) in the Pantanal. In January/February 2016, we sampled dung beetles and measured their ecological functions in 16 sites of native grasslands in Aquidauana, MS, Brazil, 10 areas regularly grazed by cattle and six control ungrazed areas (> 20 years abandonment).

3. We collected 1169 individuals from 30 species of dung beetles. Although, abundance, species richness and biomass did not differ between grasslands with and without cattle activity, species composition and functional groups differed among systems. Large roller beetles were absent from non-cattle grasslands, while the abundance, richness and biomass of medium roller beetles was higher in those systems.

4. Despite causing changes in species/functional group composition, our results show that a density compensation of functional groups in cattle grazed natural grasslands seems to have conserved the ecological functions (dung removal and soil bioturbation), with no significant differences between systems.

5. Therefore, our results provide evidence that cattle breeding in natural grasslands of the Brazilian Pantanal can integrate livestock production with the conservation of the dung beetle community and its ecological functions.

Key words: Biodiversity conservation, Ecosystems services, Grassland management, Land use intensity, Scarabaeinae.

Introduction

Technological advances have sustained agricultural expansion in the tropics, resulting in productive areas previously unexplored (Laurence *et al*., 2014). In Brazil, the expansion of commercial agriculture started in the South region and expanded to areas of the Cerrado in the 80's (Klink & Moreira, 2002), and is currently approaching the Brazilian Pantanal (Harris *et al*., 2005) and Amazon (Soares-Filho *et al*., 2006). The use of technologies such as fertilizers, irrigation, agricultural machinery and genetically modified plant varieties allowed the growth of agricultural activities in the Pantanal (wetlands) (Laurence *et al*., 2014). Currently, the Pantanal holds the second largest cattle herd in Brazil – 5.8 millions individuals (IBGE, 2017).

The Pantanal, a World Heritage Site and Biosphere Reserve, is the largest Neotropical seasonal freshwater wetland on Earth (160.000 km^2), with high biological diversity (e.g. 650 species of birds, 124 species of mammals) (Alho & Sabino, 2011). This ecosystem has two well-defined hydrology cycles: dry and rainy. During the dry season the surface water becomes scarce, being restricted to the perennial rivers and large ponds and during the rainy season the rainwater soaks into the soil and marshes, resulting in the overflow of ponds and rivers (Da Paz *et al*., 2014). The vast area of grassland plains, allied with a favorable climate, promotes cattle extensive ranching in the Pantanal (Seidl *et al*., 2001). Cattle (*Bos taurus* L.) was introduced into the Pantanal in the 18th century and adapted very well to the local climatic conditions (Alho *et al*., 2011). Over the last two centuries livestock production has been the main economic land use (Harris *et al*., 2005) and cultural driver (Rosseto & Brasil-Junior, 2003) of the Pantanal region.

Grazing by large herbivorous mammals is a key process for the maintenance of grassland ecosystems (Bond & Parr, 2010; Veldman *et al*., 2015). Although the role of livestock farming as a global agent for the degradation of these ecosystems is also recognized (Parr *et al*., 2014; Overbeck *et al*., 2015; Veldmann *et al*., 2015), cattle grazing at suitable stocking rates, in the majority of cases, has the potential to be positive for the biodiversity of grassland ecosystems (Overbeck *et al*., 2007; Foster *et al.*, 2014; van Klink *et al.*, 2015). Indeed, there is a prolific literature reporting a negative effect of grazing rate reduction on plants (Peco *et al*., 2012), butterflies (Pöyry *et al*., 2004), gastropods (Baur *et al*., 2006), Orthoptera (Marini *et al*., 2009) and dung beetles (Verdú *et al*., 2007; Tonelli *et al*., 2017).

Dung beetles (Coleoptera: Scarabaeinae) are key to maintain functioning pastures (Louzada & Carvalho e Silva, 2009). They bury the mammal dung pads for nesting and feeding (Hanski & Cambefort, 1991), resulting in ecological functions easily translated into ecosystems services. These include: nutrient cycling (Slade *et al*., 2007; Yamada *et al*., 2007), soil fertility and physical characteristics improvements (Bang *et al*., 2005; Brown *et al*., 2010), fly and gastrointestinal parasite reduction (Braga *et al*., 2012; Nichols & Gómez, 2014), increase in vegetation development (Johnson *et al*., 2016) and control of greenhouse gas emissions (Pentillä *et al*., 2013; Slade *et al*., 2016). In addition, they are also considered efficient indicators of environmental changes (Bicknell *et al*., 2014; França *et al*., 2016), often being used as focal organisms to assess anthropic and natural impacts (Halffter & Arellano, 2002; Braga *et al*., 2013; Costa *et al*., 2017).

Here, we evaluate the effect of cattle presence in Pantanal native grasslands on dung beetle communities and the ecological functions performed by them. Herein, we sampled dung beetles and recorded their ecological functions (dung removal and soil bioturbation) in native grasslands (*Andropogon* spp. and *Axonopus* spp.) used for cattle ranching and abandoned grasslands not currently used for cattle grazing in order to test the following hypothesis: the cattle presence alters the dung profile available for dung beetles, potentially resulting in a community reassembling/oversimplification, with cascade effects on ecological functions provided by them. We expect this because the simplification of the mammal community causes a dung beetle community reduction (Estrada *et al.*, 1999; Nichols *et al.*, 2009), since the feces profile changes the community structure (Lumaret *et al.*, 1992; Carpaneto *et al.*, 2006), which can negatively affect the functions performed by these insects.

Material and Methods

Study site

The study was carried out in the Brazilian Pantanal, in Aquidauana municipality, Mato Grosso do Sul state, Brazil (19°54'36 "S, 55°47'54" W) (Fig. 1). The climate of the region, according to the Köppen classification is Aw, i.e. tropical hot-wet, with a rainy summer and a dry winter (Alvares *et al*., 2014). The annual average temperature is 26°C (12-40°C), with higher average temperature between September and October, and the annual precipitation ranging from 1,200 to 1,300 mm. The Pantanal has a great diversity of native grasses, which make up the main food source for medium-sized wild herbivores (eg., anteaters, armadillos, deer, wolves and rodents) as well as for the domestic cattle and horses (Alho *et al*., 2011).

We sampled dung beetles in 16 areas of native grasslands (*Andropogon* spp. and *Axonopus* spp.). The areas are characterized by vast stretches of grassland plains with native vegetation in a complex mixture of aquatic and savanna formations, being composed of a ground layer with grasses, herbs, and small shrubs that are strongly influenced by annual and multi-annual flood cycles (Pott and Pott, 2009). Ten areas were regularly used for cattle grazing (here called “cattle-used”) and six were unused control sites (here called “non-cattle”). The cattle-used sites are private land and have a livestock history of at least 70 years, without intensive management (not use of fertilizers, herbicides and veterinary drugs in cattle), with stocking rates between 0.5 and 1.0 animal unit ha^{-1}, ranging in size from 50 - 500 hectares. The non-cattle sites belong to the Universidade Estadual de Mato Grosso do Sul (UEMS) and to local farmers. The UEMS acquired the property (884 hectares) in 1992, and since 1994, 100 hectares were allocated as a Legal Reserve Area. The farmers' properties also have a Legal Reserve Area classification with extensive native grasslands that have not been used for cattle grazing for at least 20 years. Therefore, in all non-cattle sites, for at least 20 years there has been no entry of cattle nor any other type of use for economic purposes (e.g., wood removal, hunting of animals and other activities). Non-cattle sites ranged from 30-120 hectares. The landscape surrounding the sampling sites is dominated by extensive exotic pasturelands (*Urochloa* spp.) and patches of savanna, with the presence of wild animals typical of the Pantanal and Cerrado biomes (eg., anteaters, armadillos, deer, wolves, tapirs, rodents and others) that also used our non-cattle study site (Correa *et al*., 2016) (Fig. S1).

Experimental design

Areas of the same system (e.g. cattle used sites) were separated by approximately 0.5 km to ensure independence of the samples (Silva & Hernández, 2015), while areas of different systems (e.g. cattle used vs. non-cattle) were separated by approximately 1 km. In each site we placed a linear transect (500 m) 50 m apart from the habitat edge and delimited three sampling points along the transect (250 m apart from each other).

Dung beetle sampling

We sampled dung beetles between January and February 2016 (middle of the rainy season) using baited pitfall traps. The rainy season is the period of greatest dung beetle activity and richness in tropical ecosystems (Correa *et al.,* 2018). At each sampling point, we set up two traps, 3 m apart, baited with about 40 g of carrion (decaying beef) or cattle dung (40 g). We used two baits in order to ensure an accurate representation of the local dung beetle functional and trophic groups (Correa *et al*., 2016a). Pitfall traps consisted of plastic containers (15 cm diameter and 9 cm deep), installed at ground level, which were partly filled with 250 mL of water, salt and detergent. Each trap was protected from rain with a plastic lid suspended 20 cm above the surface. The baits were placed in plastic containers (50 mL) at the center of each trap using a wire as bait holder. The traps were active for 48 h, after which their contents were stored in plastic bags with 70% alcohol for sorting and species identification at the lab.

Dung beetles were identified to species level by Dr. Fernando Zagury Vaz-de-Mello (UFMT). Voucher specimens were deposited in the Invertebrate Ecology and Conservation Laboratory, at the Universidade Federal de Lavras (UFLA; Lavras, Minas Gerais, Brazil). To record biomass of species all individuals collected were dried (40 ± 5°C) to constant weight and weighed on a 0.0001 (g) precision balance. For body size estimates for each species, a sample of 20 individuals (or all individuals collected for the species if less than 20) was measured (from the clypeus to the pygidium) with a digital caliper accurate to 0.01 (mm).

Dung beetle functions

Two dung beetle functions were recorded: dung removal and soil bioturbation. To do so, a circular plot “arena”, 1 m diameter and area of ~0.785 m^2, delimited by a nylon net fence (15 cm high) held by bamboo sticks, was established at each sampling point. 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 (Braga *et al*., 2013). We cleared the soil surface of each arena of litter and vegetation to further facilitate the measurement of ecological functions. In the center of each arena we placed an experimental dung pile consisting 300 g of fresh cattle dung, which was protected from the rain by a plastic lid and exposed to the beetle community for 24 h (see Braga *et al*., 2013 for more details on the methodology). To determine dung removal rates, the amount of remaining dung (when present) was collected, taken to the laboratory and weighed, then dung removal was calculated by subtracting from the original dung weight added to the arena (300 g). In all areas, to account for water loss or gain in the calculation of dung removal rates, we used a humidity loss control (n = 16) consisting of 100 g of fresh cattle dung wrapped in a voile fabric and suspended over the soil by a bamboo stick. This quantity was reduced from the dung removal value. To determine the amount of soil excavated by dung beetles, loose soil around and beneath the experimental dung pile was collected and dried at 100°C until a constant weight (Braga *et al.*, 2012, 2013; França *et al.*, 2018).

Data analysis

Dung beetle species richness, number of individuals and biomass

We generated individual-based species accumulation curves, with 95% confidence intervals to compare species richness between cattle-used and non-cattle systems. We also calculated the percentage of observed species (Sobs) of the total species richness, estimated based on the average of three abundance based nonparametric estimators: CHAO 1, JACK 1 and BOOTSTRAP, using the formula: Sampling efficiency = [Sobs X 100 / ((CHAO1+

JACK1+BOOTS) / 3)]. The richness estimates were calculated with the software EstimateS v. 9.1.0, with 999 randomizations (Colwell, 2013).

Data were first checked for normality using the Shapiro–Wilk test (Shapiro & Wilk, 1965) and for homoscedasticity using Bartellet's test. We used generalized linear models (GLMs) to test for differences in species richness, number of individuals and biomass of dung beetles among pasture systems. We used Poisson errors corrected for over-dispersion (quasi-Poisson) for dung beetle species richness, Negative binomial errors for number of individuals and Gaussian errors for biomass. All GLMs were subjected to residual analysis for fitting of the distribution of errors (Crawley 2002) and conducted with "lme4" package in R v 3.3.1 (R Development Core Team, 2016).

Species composition

We used a non-metric multidimensional scaling analysis (NMDS) based on Jaccard dissimilarity matrix presence/absence species data to graphically represent the changes in dung beetle community composition from cattle-used to non-cattle systems (Anderson & Willis, 2003). To verify differences among groups formed by the NMDS, we used permutational multivariate anova (PERMANOVA) (Anderson 2001). NMDS and PERMANOVA analyses were implemented in the Primer v.6 software with PERMANOVA+ (Clarke & Gorley, 2006). Additionally, we performed a multinomial classification analysis (CLAM) (Chazdon *et al.*, 2011) to identify dung beetle species specialist of each habitat type, using a specialization threshold (k) of 0.75 significance level of 0.05. This analysis was performed using the "Vegan" package in R (R Development Core Team, 2016).

Functional groups

To compare functional groups, we classified the sampled species into three groups related to their nesting behavior: dwellers, rollers and tunnelers (as proposed by Hanski & Cambefort, 1991). We also classified the species as small, medium or large. We used size and functional group because these traits are considered the most important for dung beetle ecological functions performance (Slade *et al*., 2007; Braga *et al*., 2013). To assign species to body size class, we obtained the mean body size of the sampled species (S = 30) and calculated the confidence interval (CI – 95%). Species with body size within the confidence interval were classified as medium, above the CI as large and below the CI as small. The species were then allocated in their respective functional groups and classified as: small, medium or large dwellers, rollers and tunnelers. We also used GLMs to test for differences between cattle-used and non-cattle systems in the number of individuals, species richness and biomass of each dung beetle functional group separately.

Ecological functions

We used GLM to test for differences in ecological functions (dung removal and soil bioturbation) between cattle-used and non-cattle systems. We used Gaussian errors for dung removal and soil bioturbation. All GLMs were subjected to residual analysis for fitting of the distribution of errors (Crawley 2002) and conducted with “lme4” package in R v 3.3.1 (R Development Core Team, 2016).

Results

Dung beetle species richness, number of individuals and biomass

We collected 1169 dung beetle individuals belonging to 30 species of 14 genera and six tribes (Table S1). In the cattle-used system we recorded 23 species (557 individuals), while in non-cattle we recorded 20 species (612 individuals) (Table S1). Of the 30 species sampled, 13 were found in both systems, whereas ten species were found exclusively in cattle-used and seven in non-cattle system (Table S1). The three species richness estimators indicated a high sampling efficiency, with 85% of the dung beetle community recorded in the cattle-used and 89% in the non-cattle system (Table S2).

The observed species richness [Sobs (Mao Tau)] did not differ among systems (Fig. 1). Species richness ($F_{1,14} = 0.75$, $p = 0.39$; Fig 2A), Number of individuals ($\chi^2_{1,14} = 1.38$, $p = 0.18$; Fig. 2B) and biomass ($F_{1,14} = 1.65$, $p = 0.22$; Fig. 2C) also did not significantly differ between cattle-used and non-cattle systems.

Community composition

NMDS analysis organized sites into two distinct groups, corresponding to the two types of grassland systems (Fig. 3), with species composition differed significantly between cattle-used and non-cattle systems (Pseudo-F = 6.01, $p < 0.01$). Of the 30 species collected, four were classified as specialist of cattle-used grasslands, three considered specialist of non-cattle grasslands, seven were habitat generalists and for the 15 species it was not possible to determine their habitat preference due the low number (Table S1).

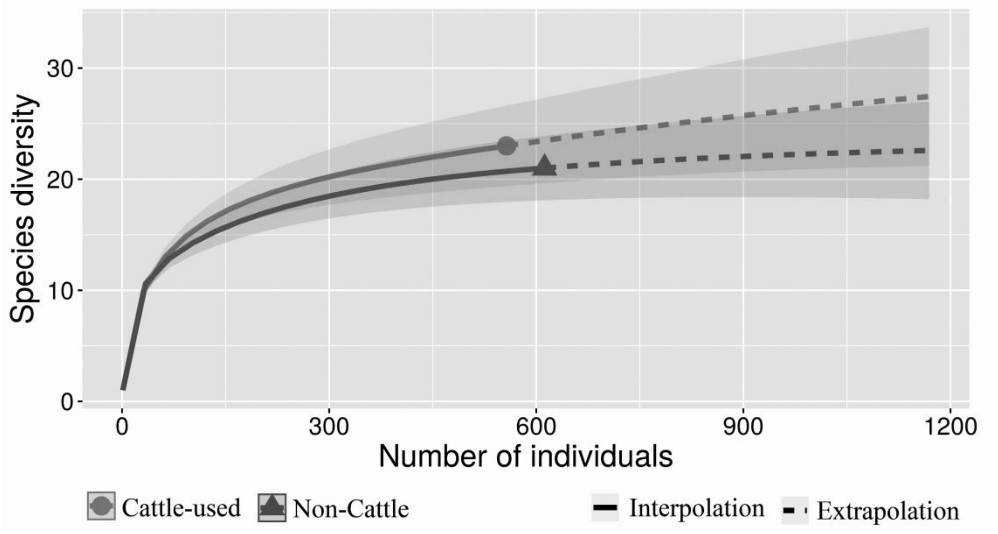

Fig. 1 Species richness accumulation curves for dung beetle communities in cattle-used and non-cattle grasslands in the Brazilian Pantanal. The *dotted lines* are 95% confidence intervals.

Functional groups

Small tunneler beetles were dominant in both systems (Fig. 4). In the cattle-used system, small dweller beetles were absent, while in the non-cattle system large roller beetles were absent. No species was classified as a large dweller beetle in our study (Fig. 4; Table S3).

The species richness of medium rollers was significantly greater in non-cattle than in cattle-used sites ($F_{1,14} = 20.52$, $p < 0.001$; Fig. 5A) but no differences were found for any of the other functional groups (Fig. 5B): small rollers ($F_{1,14} = 3.97$, $p = 0.07$); large ($F_{1,14} = 0.11$, $p = 0.73$), medium ($F_{1,14} = 0.47$, $p = 0.50$) and small tunnelers ($F_{1,14} = 0.31$, $p = 0.58$); and medium dwellers ($F_{1,14} = 1.12$, $p = 0.30$). Accumulation curves of each functional group are in the Supplementary Material (Fig. S2).

The number of individuals of medium rollers ($F_{1,14} = 38.21$, $p < 0.01$) and medium dwellers ($F_{1,14} = 5.16$, $p = 0.04$) was significantly greater in non-cattle system than cattle-used system (Fig. 5B). However, no differences in number of individuals were found between systems for any of the other functional groups (Fig. 5B): small rollers ($F_{1,14} = 0.22$, $p = 0.64$); large ($\chi^2_{1,14} = 18.41$, $p = 0.93$), medium ($F_{1,14} = 2.35$, $p = 0.10$) and small tunnelers ($F_{1,14} = 0.01$, $p = 0.89$) (Fig. 5B).

Finally, the biomass of medium rollers was higher in non-cattle than cattle-used systems (Fig. 5C; $F_{1,14} = 20.06$, $p < 0.001$) but no differences were found for any of the other functional groups (Fig. 5C): small roller ($F_{1,14} = 0.61$, $p = 0.44$); large ($F_{1,14} = 0.30$, $p = 0.58$), medium ($F_{1,14} = 3.87$, $p = 0.07$) and small tunnelers ($F_{1,14} = 0. 06$, $p = 0.81$).

Ecological functions

Both dung removal ($F_{1,14} = 0.44$, $p = 0.51$) and soil bioturbation ($F_{1,14} = 0.03$, $p = 0.86$) by dung beetles did not significantly differ between cattle-used and non-cattle systems (Fig. 6).

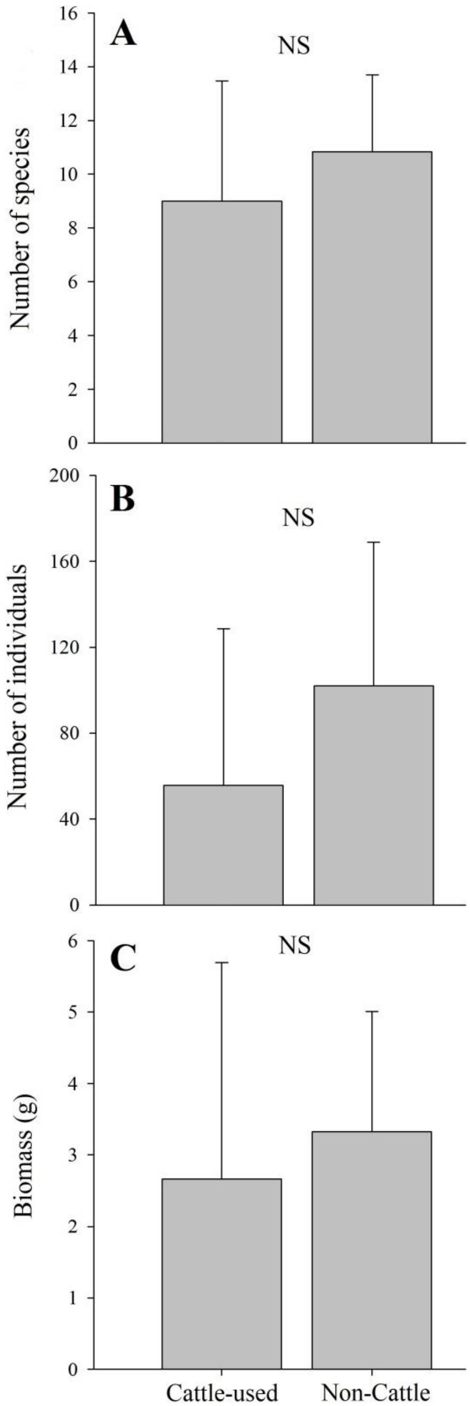

Fig. 2 Average species richness (A), average abundance (B) and biomass (C) of dung beetles sampled in cattle-used and non-cattle grasslands, in the Brazilian Pantanal. Error bars represent ± SE. NS = no significance ($p > 0.05$)

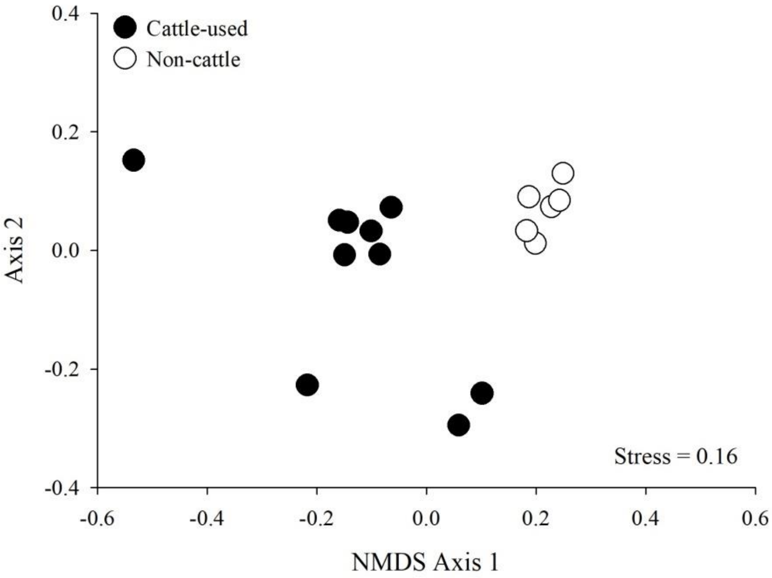

Fig. 3 Non-metric multidimensional scaling results (NMDS), constructed from Jaccard matrices, for dung beetle communities in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Stress = 0.16

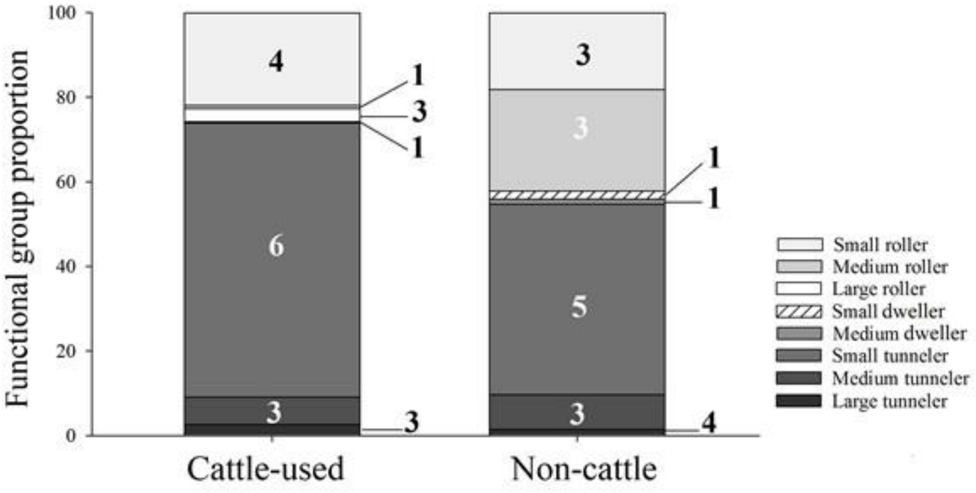

Fig. 4 Proportional change in functional dung beetle groups sampled in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Numbers inside the figure represent the species numbers in each functional group.

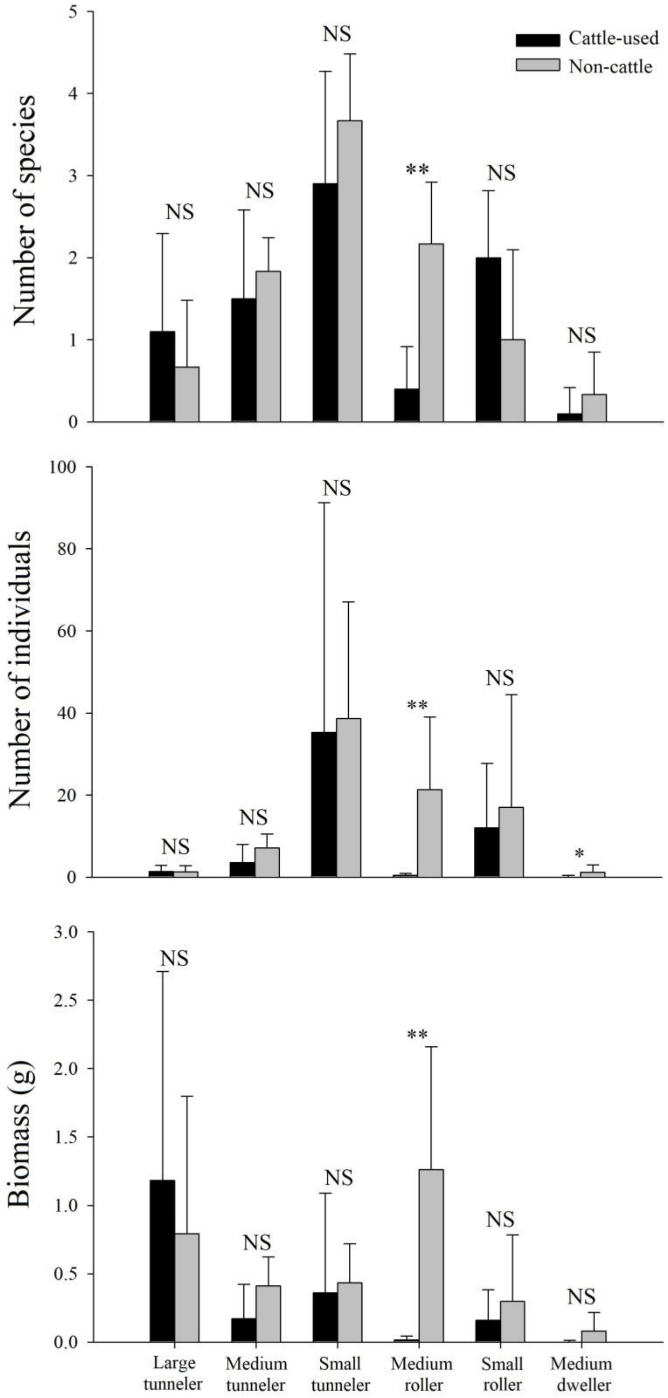

Fig. 5 Average species richness (A), abundance (B) and biomass (C) of dung beetle functional groups sampled in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Error bars represent ± SE. NS = no significance ($p > 0.05$); ** significance ($p < 0.01$); * significance ($p < 0.05$).

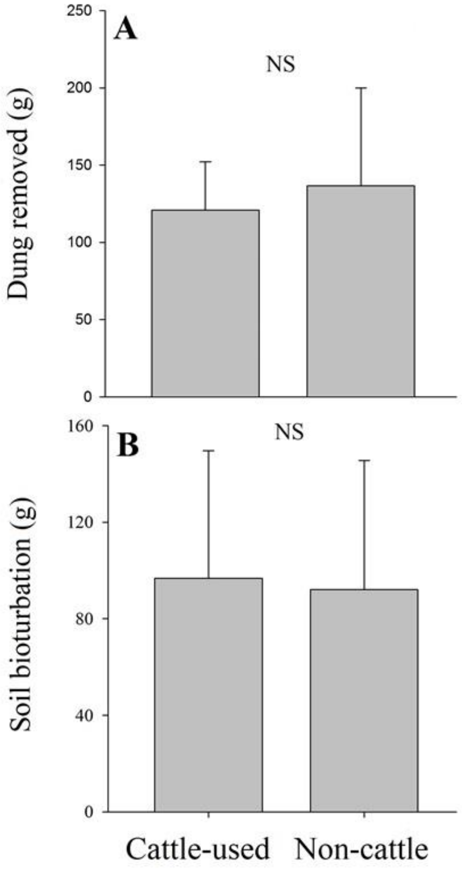

Fig. 6 Ecological functions: (A) dung removed and (B) soil excavation performed by dung beetles in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Error bars represent ± SE. NS = no significance ($p > 0.05$).

Discussion

This study evaluated, for the first time, the effect of cattle grazing on dung beetle communities and their ecological functions in the largest freshwater wetland on Earth, the Brazilian Pantanal. Our results show that, despite cattle grazing affecting the species composition, species richness and abundance of dung beetles, as well as the ecological functions performed by them are not affected. Although grazing is considered a key factor for the maintenance of dung beetle diversity in Europe (Tonelli *et al*., 2017; Numa *et al*., 2009; Jay-Robert *et al*., 2008), our results suggest that the effect of grazing on dung beetle communities could be context dependent. Dung beetles are sensitive to anthropogenic disturbances and land use changes across the globe (Nichols *et al*., 2007). Therefore, although the species composition is modified, the fact that we did not find a reduction in dung beetle species richness and their ecological functions in cattle-used pastures indicates a sustainable management of the natural grasslands in the Pantanal.

Effects of cattle grazing on patterns of abundance, species richness and biomass

Contrary to our expectations, number of individuals, biomass and species richness of dung beetles did not differ among cattle-used and non-cattle natural grasslands. The absence, and even the reduction, of grazing and/or the abandonment of previously grazed grasslands has been reported to negatively affect dung beetle communities in other regions (Tonelli *et al*., 2017; Numa *et al*., 2009; Verdú *et al*., 2007, 2000; Lobo *et al*., 2006). However, Pryke *et al*. (2016) found higher dung beetle diversity in areas grazed by wild animals when compared with areas grazed by domestic animals in Africa. Dung beetles depend on the vertebrate fauna (Estrada *et al*., 1999), especially large mammals (Barlow *et al*., 2010), for their food resource, so differences among regions as to the impact of cattle grazing on dung beetle communities may result from differences in the diversity of wild herbivores. Therefore, the high mammal richness living in the Pantanal (e.g. 124 species of mammals; Alho & Sabino, 2011), particularly in the study areas (C.M.A. Correa, 2016, personal observation), is likely aiding in the maintenance of the dung beetle communities in the region. Moreover, mammal fauna composition in low cattle impact areas in Pantanal is different and more diverse than that in high cattle impact areas (Eaton *et al*., 2017).

The total biomass of dung beetles indicates food resource availability, declining after disturbance, even if abundance increases (Barlow *et al*., 2010). In cattle grazed pastures large amounts of cattle dung are available, favoring larger dung beetle populations (Lobo *et al*., 2006). Dung availability likely varies widely in terms of pad size and spatial distribution between cattle-used and non-cattle grasslands. Our results indicate that native grasslands, not used for cattle grazing, also have high carrying capacity supporting an elevated number of dung beetle individuals, possibly reducing extinction rates and enhancing species richness (Evans *et al*., 2005).

Cattle grazing *per se* did not cause a reduction in dung beetle biodiversity. Since dung beetles are good indicators of anthropic changes (Nichols *et al*., 2007), this result indicates that extensive cattle breeding in the Pantanal is carried out in a conservationist way with low impact on biodiversity, at least for our study group. This is likely to be associated with substantial management differences in extensive versus intensive cattle systems. The low density of cattle in natural pastures (compared to introduced pastures) (Eaton *et al*., 2011), allied to the non-use of veterinary drugs for the treatment of the cattle (Sands *et al*., 2018; Verdú *et al*., 2015), help in the maintenance of highly diverse dung beetle communities.

Effects of cattle grazing on species composition

The species composition of dung beetle communities differed between cattle-used and non-cattle grasslands. Cattle grazing affect vegetation heterogeneity, affecting plant succession and controlling the growth of forage plants (Olff & Ritchie, 1998; Adler *et al.,* 2001). Additionally, the cattle presence also could result in soil compaction due to livestock trampling which might benefit the few species that are able to cope with the hardest soils (Halffter *et al.*, 1992). Indeed, we found some species are benefited by cattle grazing, such as; *Canthon cinctellus* (Germar), *Canthon curvodilatatus* Shimdt, *Deltochilum pseudoicarus* Balthasar and *Digitonthophagus gazella* (Fabricius). In contrast, *Canthon unicolor* Balthasar, *Deltochilum* aff. *komareki* and *Uroxys* aff. *corporaali* are benefited by cattle grazing absence. Among these species, only *D. gazella*, an African species exotic in Brazil, has a studied biological cycle, the cycle being completed in ~ 30 days (Blume & Aga, 1975). This species was introduced during the 1980s to help control gastrointestinal worms and parasitic flies, being strictly coprophage (Miranda et al., 2000) and widely distributed in Brazilian pastures (Tissiani *et al.,* 2017).

The change in vegetation structural heterogeneity caused by grazing implies a change in habitat diversity, bringing consequences such as a more homogeneous environment and a change in local plant diversity (Wallis-de-Vries *et al*., 2007). Thus, cattle grazing, even subtly, can alter the environmental conditions, such as temperature, humidity and soil compaction which directly affect the biology of dung beetle species, modifying the species composition of the dung beetle community in different environments (Halffter & Arellano, 2002; Costa *et al*., 2017).

Effects of cattle grazing on functional groups

Small tunneler beetles were dominant in both types of grasslands. We believe that these beetles are dominant because their size may allow for a greater number of individuals and species to share the same resource (Correa *et al*., 2016). Additionally, small species have higher thermal tolerance, lower humidity tolerance (area ratio/lower volume) and higher burial capacity in compacted soils than large species (Verdú *et al*., 2006; Barragán *et al*., 2011).

The large tunneler beetles, mainly responsible for dung removal (Slade *et al*., 2007; Nervo *et al*., 2014), were not affected by cattle grazing. Large roller beetles were absent while the abundance of medium roller beetles increased in non-cattle systems. Our results show that cattle grazing in the Brazilian Pantanal affects dung beetle functional groups differently (Slade *et al*., 2007), evidencing that large roller beetles are the most functional group benefited by the cattle presence.

Effects of cattle grazing on ecological functions

The ecological functions performed by dung beetles did not differ between cattle-used and non-cattle grasslands. The fact that cattle grazing did not reduce dung beetle diversity may be one of the reasons that explains the maintenance of the ecological functions performed by these insects in natural grasslands. Many studies have shown that a reduction in the dung beetle biodiversity significantly affects dung removal capacity (Slade *et al*., 2007; Braga *et al*., 2013; Kenyon *et al*., 2016; Frank *et al*., 2017).

Although cattle grazing cause changes in species composition, our data suggest that some species may be compensating for the function of absent species, allowing ecosystems to remain stable in the face of disturbance, causing a functional redundancy (Rosenveld, 2002). Dung beetles appear to be able to compensate for ecological functions against disturbance by increasing the abundance of some functional groups or seasonal occurrence of some species (Frank *et al*., 2017). Thus, even though large roller beetles were absent in our non-cattle grasslands, the ecological functions seem to have been maintained by the complementarity of other groups and particularly by the increase in the abundance of medium roller beetles (Slade *et al*., 2007; Frank *et al*., 2017). Although large and medium tunnelers are the most efficient group in dung removal (Slade *et al*., 2007; Nervo *et al*., 2014), and so since their species richness, abundance and biomass did not differ between systems, complementarity among different groups has been shown to be more important for ecological functions (Slade *et al*., 2007), and can also help to explain why the functions did not differ. In addition, the maintenance of biomass is also an important indicator of maintenance in dung removal capacity in these systems (Slade *et al.*, 2007; Braga *et al.*, 2013, Nervo *et al.*, 2014).

Conclusions

Until now, there has been very little information on the cattle grazing effects on dung beetle diversity and their ecological functions in Neotropical region. We show that cattle grazing in Brazilian Pantanal did not affect the diversity and abundance of dung beetles, probably due to the rich community of native mammals (Prike *et al*., 2016; Barlow *et al*., 2010) and to the low-use of veterinary drugs (Sands *et al*., 2018; Verdú *et al*., 2015) in livestock management. Despite causing changes in species composition, our results show that a density compensation of functional groups (the increase in the abundance of medium roller beetles compensated the reduction in the abundance of large roller beetles) in cattle-used grasslands seems to have preserved the ecological functions performed by this group of insects.

The use of native grasslands for livestock, besides economically helping the farmers (Latawiec *et al*., 2017), may provide opportunities to maintain or restore native fields that could be converted into introduced pastures, mechanized agriculture or other land uses, (Overbeck *et al*., 2007), that are detrimental to dung beetle biodiversity and their ecological functions (Braga *et al*., 2013; Correa *et al*., 2016). Therefore, cattle breeding in natural grasslands of the Brazilian Pantanal is efficient in the management of land resources, matching livestock production with the country's conservation objectives.

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Supplementary Material

Fig S1. Localization of the study area in South America, highlighting the Brazilian Pantanal and sampling sites.

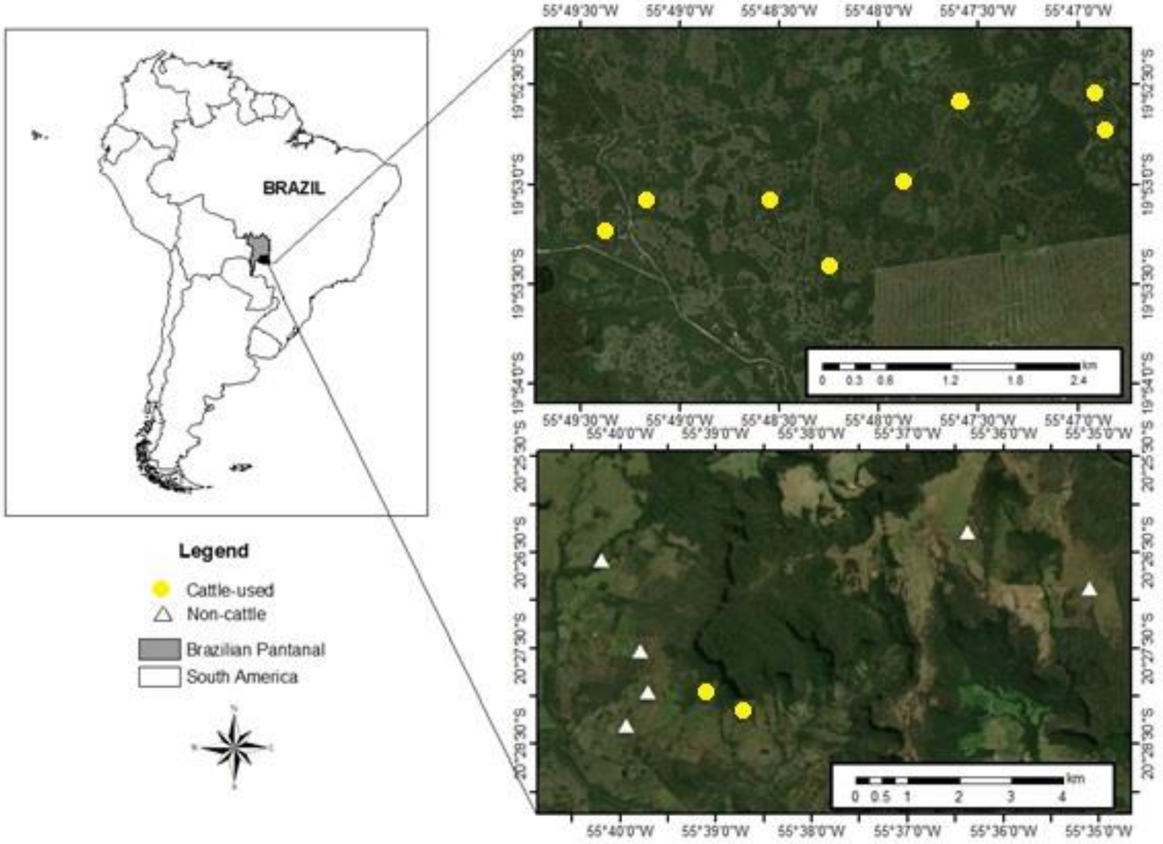

Fig S2. Species richness accumulation curves for dung beetle functional groups in cattle-used and non-cattle grasslands in the Brazilian Pantanal. The *shaded areas* are 95% confidence intervals.

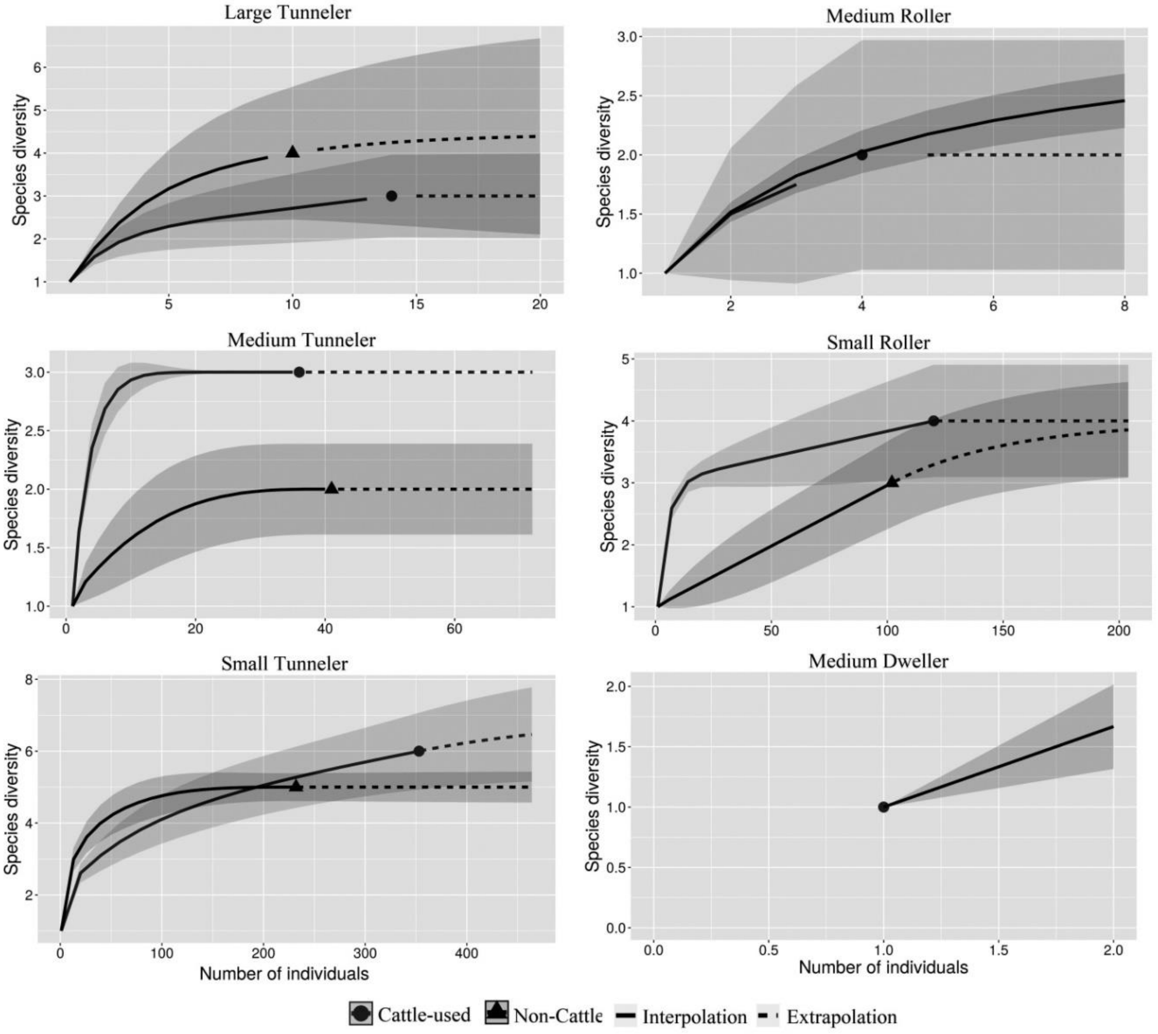

Table S1. Abundance and habitat preference (classified by CLAM analysis) of dung beetle species sampled in cattle-used (CU) and non-cattle natural (NC) grasslands in the Brazilian Pantanal (Mato Grosso do Sul, Brazil).

	Systems		**Habitat**	
Species	**Cattle-used**	**Non-cattle**	**preference**	**Total**
Ateuchini				
Ateuchus sp.	93	50	Generalist	143
Ateuchus sp. 1	1	0	Too rare	1
Ateuchus aff. *ovallis*	7	0	Too rare	7
Uroxys aff. *corporaali*	12	84	NC Specialist	96
Coprini				
Canthidium aff. *refulgens*	0	3	Too rare	3
Canthidium aff. *viride*	248	158	Generalist	406
Dichotomius bos (Blanchard)	0	4	Too rare	4
Dichotomius glaucus (Harold)	1	1	Too rare	2
Dichotomius nisus (Olivier)	5	0	Too rare	5
Dichotomius opacipennis (Luederwaldt)	9	3	Generalist	12
Ontherus appendiculatus (Manerrheim)	9	38	Generalist	47
Deltochilini				
Canthon aff. *maldonadoi*	0	1	Too rare	1
Canthon cinctellus (Germar)	21	0	CU Specialist	21
Canthon conformis Harold	75	100	Generalist	175
Canthon curvodilatatus Schimdt	23	0	CU Specialist	23
Canthon histrio (Lepelletier and Serville)	3	11	Generalist	14
Canthon unicolor Balthasar	0	81	NC Specialist	81
Deltochilum aff. *komareki*	1	35	NC Specialist	36
Deltochilum pseudoicarus Balthasar	14	0	CU Specialist	14
Dendropaemon nitidicollis Olsoufieff	1	1	Too rare	2
Malagoniella punctatostriata (Blanchard)	1	0	Too rare	1
Malagoniella puncticollis (Blanchard)	2	0	Too rare	2
Oniticellini				
Eurysternus carybaeus (Herbst)	1	7	Too rare	8
Eurysternus aenaeus Génier	0	9	Too rare	9
Onthophagini				
Digitonthophagus gazella (Fabricius)	18	0	CU Specialist	18
Onthophagus aeneus Olivier	3	16	Generalist	19
Onthophagus ptox Erichson	1	5	Generalist	6
Phanaeini				
Coprophanaeus bonariensis Gory	8	0	Too rare	8
Coprophanaeus cyanescens d'Olsoufieff	0	3	Too rare	3
Phanaeus palaeno Blanchard	0	2	Too rare	2

Table S2. Abundance, observed richness, richness estimators Bootstrap, Chao 1, Jackknife 1 and sampling efficiency (%), total biomass and mean biomass of species per site of dung beetles in cattle-used and non-cattle natural grasslands in Brazilian Pantanal (Mato Grosso do Sul, Brazil).

Ecological measures of Scarabaeinae community	Cattle-used	Non-cattle
Abundance (N)	557	612
Richness (S)	23	21
Variation of richness per area	4 to 16	7 to 15
Estimated richness		
Bootstrap	25.14	23.37
Chao 1	27.99	21.99
Jackniffe 1	27.50	25.16
Sampling efficiecy (%)	85.60	89.36
Total biomass (g)	26.67	20.47
Mean biomass per site (g)	2.67	3.41

Table S3. Body size (mm), size category and functional groups of dung beetles sampled in cattle-used and non-cattle natural grasslands in Brazilian Pantanal (Mato Grosso do Sul, Brazil).

Taxon	Body size			Functional Group
	Mean lenght ± SE	*N*	Category	
Ateuchus aff. *ovallis*	5.12 ± 0.14	7	Small	Tunneler
Ateuchus sp.	6.41 ± 0.08	20	Small	Tunneler
Ateuchus sp. 1	6.98	1	Small	Tunneler
Canthidium aff. *refulgens*	5.83 ± 0.12	3	Small	Tunneler
Canthidium aff. *viride*	7.95 ± 0.19	20	Small	Tunneler
Canthon aff. *maldonadoi*	4.88	1	Small	Roller
Canthon cinctellus	6.41 ± 0.09	20	Small	Roller
Canthon conformis	6.65 ± 0.20	20	Small	Roller
Canthon curvodilatatus	5.51 ± 0.12	20	Small	Roller
Canthon histrio	10.06 ± 0.32	14	Medium	Roller
Canthon unicolor	10.94 ± 0.22	20	Medium	Roller
Coprophanaeus bonariensis	30.82 ± 1.07	8	Large	Tunneler
Coprophanaeus cyanescens	24.60 ± 0.99	3	Large	Tunneler
Deltochilum aff. *komareki*	11.49 ± 0.12	20	Medium	Roller
Deltochilum pseudoicarus	24.76 ± 0.60	14	Large	Roller
Dendropaemon nitidicollis	7.84	1	Small	Roller
Dichotomius bos	22.42 ± 1.13	4	Large	Tunneler
Dichotomius glaucus	19.23 ± 1.32	2	Large	Tunneler
Dichotomius nisus	17.72 ± 0.69	5	Large	Tunneler
Dichotomius opacipennis	12.78 ± 0.14	12	Medium	Tunneler
Digitonthophagus gazella	10.44 ± 0.19	18	Medium	Tunneler
Eurysternus aenaeus	7.17 ± 0.19	9	Small	Dweller
Eurysternus carybaeus	14.51 ± 0.67	8	Medium	Dweller
Malagoniella punctatostriata	16.74	1	Large	Roller
Malagoniella puncticollis	17.54 ± 0.56	2	Large	Roller
Ontherus appendiculatus	10.64 ± 0.22	20	Medium	Tunneler
Onthophagus aeneus	5.47 ± 0.11	18	Small	Tunneler
Onthophagus ptox	6.05 ± 0.33	6	Small	Tunneler
Phanaeus palaeno	16.42 ± 1.97	2	Large	Tunneler
Uroxys aff. *corporaali*	3.55 ± 0.11	20	Small	Unknow

PAPER 2 - Successional trajectory of dung beetle communities in a tropical grassy ecosystem after livestock grazing removal

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Preliminary version

Successional trajectory of dung beetle communities in a tropical grassy ecosystem after livestock grazing removal

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Abstract

Grazing by large herbivore mammals is a historically structuring force in tropical grassy ecosystems (TGE), and cattle grazing is one of the main economic activities carried out in these ecosystems nowadays. Therefore, understanding the impacts of cattle grazing removal on biodiversity may be a key step for conservation of this ecosystem. Here, we studied the successional trajectory of dung beetle communities in a TGE after cattle removal. For this, we accessed the patterns of dung beetle taxonomic and functional diversity along a chronosequence of 14 natural grasslands with distinct cattle grazing removal ages (from 3 months to 22 years). Our results show a strong decrease of dung beetle abundance and species richness in the first ten years of cattle removal. However, after ten years there is an increase in these parameters. Despite the taxonomic and functional composition not being related to time of cattle removal, after three years of removal the taxonomic composition was different from the control, with the formation of a distinct species community deviating from the control. Functional diversity was not affected by cattle grazing removal, indicating that it is less sensitive to cattle absence than taxonomic diversity. Our results provide evidence that cattle grazing removal, at least in a short time (20 years), may be an inefficient management tool for restoration and conservation of TGE. However, we stress the need to investigate the reintroduction of cattle grazing after different removal times to provide complimentary information to livestock management able to integrates human use and conservation of TGE.

Key-words: Biodiversity conservation, Chronosequence, Functional diversity, Grasslands restoration, Livestock management, Scarabaeinae.

1. Introduction

Livestock farming, the largest land-use demanding sector on Earth, occupies more than 30% of the planet's continental surface (FAO, 2012). In tropical grassy ecosystems (TGE) (e.g. savannas and grasslands) cattle grazing is a traditional agricultural activity, and one of the main economic activities carried out in these ecosystems (Parr et al., 2014). Grazing by large mammalian herbivores has historically and prehistorically been a major structuring force in TGE (Bakker et al., 2015; Veldmann et al., 2015). These ecosystems evolved with and depended on herbivory, heavy hoof action, nitrogen deposits, and decomposing carcasses of large herbivores (Bond and Parr, 2010), directly influencing the biodiversity and ecosystem services (Dettenmayer et al., 2017; van Klink et al., 2015).

There is an increasing debate about the effects of cattle grazing in biodiversity of TGE (Lehmann and Parr, 2016; Overbeck et al., 2015; Parr et al., 2014; Veldmann et al., 2015). Livestock farming is considered the main driver of natural habitat loss worldwide (Alkemade et al., 2013; Herrero and Thornton, 2010). The negative effects of livestock on biodiversity are related to the conversion of native to exotic vegetation, grazing intensity, the replacement of wild grazers by domestic animals and land management (e.g., use of fertilizers and veterinary drugs) (Alkemade et al., 2013; Lehmann and Parr, 2016). In this context, some studies have reported that grazing exclusion throughout the world prevents ecosystem degradation and restores degraded areas (Al-Rowaily et al., 2015; Kröpfl et al., 2013; Listopad et al., 2018). Although the role of livestock farming as a global agent for the degradation of the ecosystems is recognized (Lehmann and Parr, 2016; Overbeck et al., 2015; Parr et al., 2014; Veldmann et al., 2015), cattle grazing in suitable density and frequency may be beneficial for the biodiversity of grasslands ecosystems (Overbeck et al., 2007). Cattle grazing affects vegetation heterogeneity, plant succession and forage-plant growth control (Adler et al., 2001; Olff and Ritchie, 1998), maintaining or restoring grasslands that would otherwise be converted into other land uses (Veldmann et al., 2015). Therefore, in some native grassy ecosystems, livestock grazing has been used as a strategy to improve biodiversity conservation (Fynn et al., 2016; Törok et al., 2016; Verdú et al., 2007). For example, in parts of Europe (Pykälä, 2003, Törok et al., 2016), African savannas (Finn et al., 2016) and Mexican grasslands (Verdú et al., 2007) low-intensity domestic livestock grazing is being used as an important factor to maintain and restore biodiversity (Veldmann et al., 2015). Indeed, both grazing and long-term cessation can differently affect various components of grassland biota (Foster et al., 2014; van Klink et al., 2015). Therefore, it is essential to understand the successional trajectory of the biotic communities along a gradient of exclusion and/or inclusion of cattle grazing, to incorporate conservation decisions into land management of TGE.

In this sense, the importance of long-term time series (more than 20 years) for analyzing the effects anthropic actions is widely recognized (Bakker et al., 1996; Peco et al., 2006; Rees et al., 2001), given that ecological processes that led to functional and biodiversity changes in grasslands ecosystems are longer term (Listopad et al., 2018; Peco et al., 2006, 2017). However, studies of the successional trajectory of biotic communities in TGE are scarce (see Cava et al., 2018), and the impacts of inclusion or exclusion of cattle grazing as a tool a ecosystem conservation are poorly known. Therefore, studies on the response of animal and/or plant groups that provide important services to the ecosystem are necessary to supply baselines for conservation policies, which may help to protect tropical grassy ecosystems around the world (Correa et al., 2019b). In this way, understanding the dynamics of these ecosystems can also be an important strategy for developing measures to restore anthropogenic landscapes (Bond and Parr 2010; Cava et al., 2018; Veldmann et al., 2015).

Here, we studied the successional trajectory of dung beetle communities in a tropical grassy ecosystem after cattle grazing exclusion. We choose dung beetles (Coleoptera: Scarabaeidae) because they are used across the globe as indicators of environmental changes (Nichols et al., 2007) and exhibit wide variation in life history strategies that are reflected in easily measurable functional traits (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). Therefore, they are good models for functional diversity studies aimed at understanding the effects of anthropic actions on ecosystem processes (Audino et al., 2014, 2017; Barrágan et al., 2011; Beiroz et al., 2018; Correa et al., 2019b). In addition, dung beetles perform important ecological functions in grassland ecosystems, such as: dung removal, nutrient cycling, improving soil fertility, secondary seed dispersion and fly and gastrointestinal parasite control (see Nichols et al., 2008).

We evaluated the patterns of dung beetle taxonomic and functional diversity along a chronosequence of natural grasslands with different cattle grazing removal ages (from 3 months to 22 years). Additionally, we compared the excluded cattle grazing sites with references sites (cattle-used sites) to answer the following questions: (1) Do species richness, number of individuals, biomass and functional diversity decrease with cattle grazing removal age? 2) Do dung beetle taxonomic and functional structure shift with increasing time of cattle grazing removal? (3) Are dung beetle communities in cattle grazing removal sites deviating from those in cattle-used system (reference sites)? We expect dung beetle richness, abundance, biomass and functional diversity to decrease with time since cattle grazing exclusion, as a result of a reduction in resource availability (Tonelli et al., 2018). We expect changes in dung beetle taxonomic and functional structure because the grazing exclusion implies changes in spatial heterogeneity of vegetation, also modifying plant diversity (Wallis-de-Vries et al., 2007).

2. Material and Methods

2.1. Study area

This study was conducted in the Aquidauana municipality, Mato Grosso do Sul state, Brazil (19°54'36 "S, 55°47'54" W), covering the southern part of Brazilian Pantanal sub region of Rio Negro (Padovani, 2010). Native vegetation in the region is a complex mixture of aquatic, savanna, and forest formations that are strongly influenced by annual and multi-annual flood cycles (Pott and Pott, 2009). The Pantanal is considered the largest Neotropical seasonal freshwater wetland on Earth, with a vast area of grassland plains often used for extensive cattle ranching (Eaton et al., 2017). Therefore, livestock production has been the main economic activity in this ecosystem, where approximately 80% of the land is used as native and introduced pastures (Eaton et al., 2011).

According to the Köppen classification (Alvares et al., 2014), the regional climate is *Aw* (tropical hot-wet), with a rainy summer and dry winter. The annual average temperature is 26°C (12-40°C), with the highest average temperature occurring between September and October, and the annual precipitation ranging from 1,200 to 1,300 mm (Cristaldo et al., 2017).

2.1. Sampling sites

We sampled dung beetles in 14 areas of natural grasslands (*Andropogon* spp. and *Axonopus* spp.) that had been used for cattle grazing in the past. These areas represent a gradient of different ages since cattle were removed: 0.4 year (3 months without cattle grazing), 1 year, 2 years, 3 years, 5 years, 6 years, 7 years, 10 years, three areas with 20 years and three areas with 22 years. Unfortunately, we did not find any area that had a cattle removal period between 10 - 20 years in the studied landscape. We also sampled dung beetles in ten areas of natural grasslands that were being used for cattle grazing (0.8 – 1.0 animals/ha) at the time of sampling, as the reference sites. All sites were separated by a distance varying from 0.5 – 80 Km, to ensure independence of the samples (da Silva and Hernández, 2015). The landscape surrounding the sampling sites is dominated by extensive exotic pasturelands (*Urochloa* spp.) and patches of natural savannas (Correa et al., 2016), with the presence of wild animals typical of Pantanal and Cerrado biomes (eg., anteaters, armadillos, deer, wolves, tapirs, rodents and others) (Eaton et al., 2017).

2.3. Dung beetle sampling and identification

Sampling was conducted during the rainy season, in January-February 2016. The rainy season is the most appropriate period to sample the greatest dung beetle richness and functional diversity in Brazilian pastures (Correa et al., 2018). We used pitfall traps baited with ~40 g of carrion (decaying beef) or cattle dung (40 g) in order to ensure an accurate representation of the local dung beetle functional and trophic groups (Correa et al., 2016). The traps consisted of a plastic container (15 cm diameter and 9 cm deep), installed at ground level, which were partly filled with 250 mL of water, salt and detergent, and a plastic lid placed above ground to protect from rain and sun. The baits were placed in plastic containers (50 mL) at the center of each trap using a wire as bait holder.

In each site, we placed three sampling points spaced 250 m apart along a linear transect (500 m) installed 50 m from the habitat edge. Each sample point contained two pitfall traps separated by 3 m, one with each bait type (feces and carrion), which were active for 48 h. Dung beetles captured were identified to the species level by Fernando Z. Vaz-de-Mello. Vouchers were deposited in the Invertebrate Ecology and Conservation Laboratory, at the Universidade Federal de Lavras (UFLA; Lavras, Minas Gerais, Brazil), and the Entomology Section of the

Zoological Collection of the Universidade Federal de Mato Grosso (UFMT, Cuiabá, Mato Grosso, Brazil).

2.4. Dung beetle traits

We analyzed seven functional traits that are directly related to the ecosystem functions performed by dung beetles (Audino et al., 2014; 2017; Barrágan et al., 2011; Braga et al., 2013, Griffiths et al., 2015; Slade et al., 2007): food relocation habitat (rollers, tunnelers and dwellers), diet (coprophagous, necrophagous or generalists), diel activity (nocturnal, diurnal or mixed), body mass, body mass-adjusted front leg area, body mass-adjusted pronotum volume, and back:front leg lengths (see Griffiths et al., 2015 for more details on the methodology) (Table S1 in Supplementary Material). We described the protocols used for trait assignments in Supplementary Material. When necessary, we also obtained additional information on dung beetle traits from the literature and specialists.

2.5. Data analysis

2.5.1. Species richness, number of individuals and biomass

We tested the effects of cattle grazing removal on total species richness, number of individuals and biomass of dung beetles using Generalized Additive Models (GAMs) with a thin plate smoother. GAMs were chosen due to their suitability to non-parametric data showing a high degree of dispersal (Wood, 2006). This analysis was implemented using the “mgcv” package in the R v 3.3.1 (R Development Core Team, 2016).

2.5.2. Taxonomic and functional structure

To evaluate if there were changes in taxonomic and functional structure of the dung beetle communities with the increase of cattle removal time, we performed Generalized Additive Models analysis. We used Bray-Curtis similarity of the natural grasslands with different ages of cattle removal to reference sites as response variable. Bray–Curtis similarity was calculate using standardized and square root transformed abundance data of each species (for taxonomic structure) or of each trait class (for functional structure) (Anderson and Willis, 2003). We performed this analysis using GAMs using the “mgcv” package in the R v.3.3.1 (R Development Core Team, 2016).

To determine whether taxonomic and functional composition of dung beetle assemblage is progressing towards or deviating from the reference sites, we performed a principal coordinates analysis (PCO) and a permutational multivariate analysis of variance (PERMANOVA), using the software PRIMER+ (Anderson et al., 2006; Clarke and Gorley, 2009). PCO was used to graphically express the similarity between sites and PERMANOVA to test for significant differences in taxonomic and functional composition among site groups. To carry out this analysis we categorized the study sites as: control (reference sites; n = 10), early-stage (0.4–3 years; n = 4), mid-stage (5–10 years; n = 4) and late-stage of cattle removal time (20–22 years; n = 6). The cattle removal groups were classified based on vegetation characteristics metrics of each area (e.g. vegetation density and vegetation complexity) (see Gries et al., 2012 for more details on the methodology) (Supplementary Material), since there is no a protocol used for this propose.

2.5.3. Functional diversity

To calculate three functional diversity indexes that measure different aspects of functional diversity, we used the “FD” package (R Development Core Team, 2016): 1) functional dispersion (FDis) the distribution of abundances in the space of functional traits in relation to a weighted centroid in abundance and the volume of space occupied (Laliberté and Legendre, 2010), 2) Functional evenness (FEve) summarizes how species abundances are distributed along the occupied functional space; and 3) Functional richness (FRic) represents the range of traits in a community quantified by the volume of functional trait space occupied (Villéger et al., 2008).

We evaluated the influence of cattle removal time on FDis, FEve and FRic using GAMs. This analysis was implemented using the “mgcv” package in the R v 3.3.1 (R Development Core Team, 2016).

3. Results

3.1. Species richness, number of individuals and biomass

We collected 1622 dung beetle individuals from 32 species of 16 genera and six tribes (Table 1). In the reference sites (cattle-used grasslands) we recorded 23 species and 557 individuals, while in the cattle grazing removal sites; we recorded 32 species and 1065 individuals (Table 1).

Species richness ($R^2 = 0.46$; $p = 0.03$ – Fig. 1a) and number of individuals ($R^2 = 0.51$; $p < 0.001$ – Fig. 1b) have a significant relationship with cattle removal time, decreasing until ten years; and then increasing until 22 years. Biomass was the only variable that was not influenced by time of cattle grazing removal ($R^2 < 0.001$; $p = 0.372$ – Fig. 1c).

Table 1. Abundance of dung beetle species sampled in cattle-used system and areas with different stages of cattle abandonment in Aquidauana, Mato Grosso do Sul, Brazil.

Taxon	Cattle-used	Stage of cattle removal			Total
		Early	Mid	Late	
Ateuchini					
Ateuchus sp.	93	56	0	50	199
Ateuchus sp. 1	1	5	0	0	6
Ateuchus aff. *ovallis*	7	1	2	0	10
Genieridium bidens	0	42	0	0	42
Trichillum externenpunctatum	0	2	2	0	4
Uroxys aff. *corporaali*	12	0	1	84	97
Coprini					
Canthidium aff. *refulgens*	0	8	2	3	13
Canthidium aff. *viride*	248	165	15	158	586
Dichotomius bos (Blanchard)	0	1	1	4	6
Dichotomius glaucus (Harold)	1	1	0	1	3
Dichotomius nisus (Olivier)	5	3	0	0	8
Dichotomius opacipennis (Luederwaldt)	9	23	0	3	35
Ontherus appendiculatus (Manerrheim)	9	36	0	38	83
Deltochilini					
Canthon aff. *maldonadoi*	0	0	0	1	1
Canthon cinctellus Germar	21	0	3	0	24
Canthon conformis Harold	75	9	2	100	186
Canthon curvodilatatus Schimdt	23	3	6	0	32
Canthon histrio (Lepelletier and Serville)	3	1	5	11	20
Canthon unicolor Blanchard	0	0	0	81	81
Deltochilum aff. *komareki*	1	2	1	36	40
Deltochilum pseudoicarus Balthasar	14	3	0	0	17
Malagoniella punctatostriata (Blanchard)	1	1	0	0	2
Malagoniella puncticollis (Blanchard)	2	0	1	0	3
Oniticellini					
Eurysternus carybaeus (Herbst)	1	0	0	7	8
Eurysternus aenaeus Génier	0	1	2	10	13
Onthophagini					
Digitonthophagus gazella (Fabricius)	18	30	0	0	48
Onthophagus aeneus Olivier	3	0	2	16	21
Onthophagus ptox Erichson	1	3	2	5	11
Phanaeini					
Coprophanaeus bonariensis Gory	8	0	2	0	10
Coprophanaeus cyanescens d'Olsoufieff	0	2	2	3	7
Dendropaemon nitidicollis Olsoufieff	1	2	0	1	4
Phanaeus palaeno Blanchard	0	0	0	2	2
Number of species	23	23	17	20	
Number of individuals	557	400	51	614	1622

3.2. Taxonomic and functional composition

Bray-Curtis similarity demonstrated that taxonomic ($R^2 < 0.001$; $p = 0.666$ – Fig. 2a) and functional ($R^2 < 0.001$; $p = 0.605$ – Fig. 2b) composition was not influenced by time of cattle grazing removal. However, taxonomic composition in the different categories of cattle grazing removal is deviating from the reference sites (cattle-used sites) (Fig. 3a). PERMANOVA analysis revealed that except from reference sites and early-stage removal ($t = 1.21$; $p = 0.13$) (Table S2), all other categories were significantly different from each other based on taxonomic composition (Pseudo-F = 2.94; p = 0.001) (Fig. 3a; Table S2). For functional composition, PERMANOVA analysis revealed that just mid-stage and late-stage of abandonment were significantly different from each other based on functional composition ($t = 1.65$; $p = 0.04$) (Table S3). In contrast, all other categories were not significantly different from each other (Pseudo-F = 1.37; p = 0.16) (Fig. 3b; Table S3).

3.3. Functional diversity

The time of cattle grazing removal did not influence the FRic ($R^2 < 0.001$; $p = 0.614$ – Fig. 4a), FEve ($R^2 = 0.25$; $p = 0.10$ – Fig. 4b) and FDis ($R^2 = 0.13$; $p = 0.18$ – Fig. 4c).

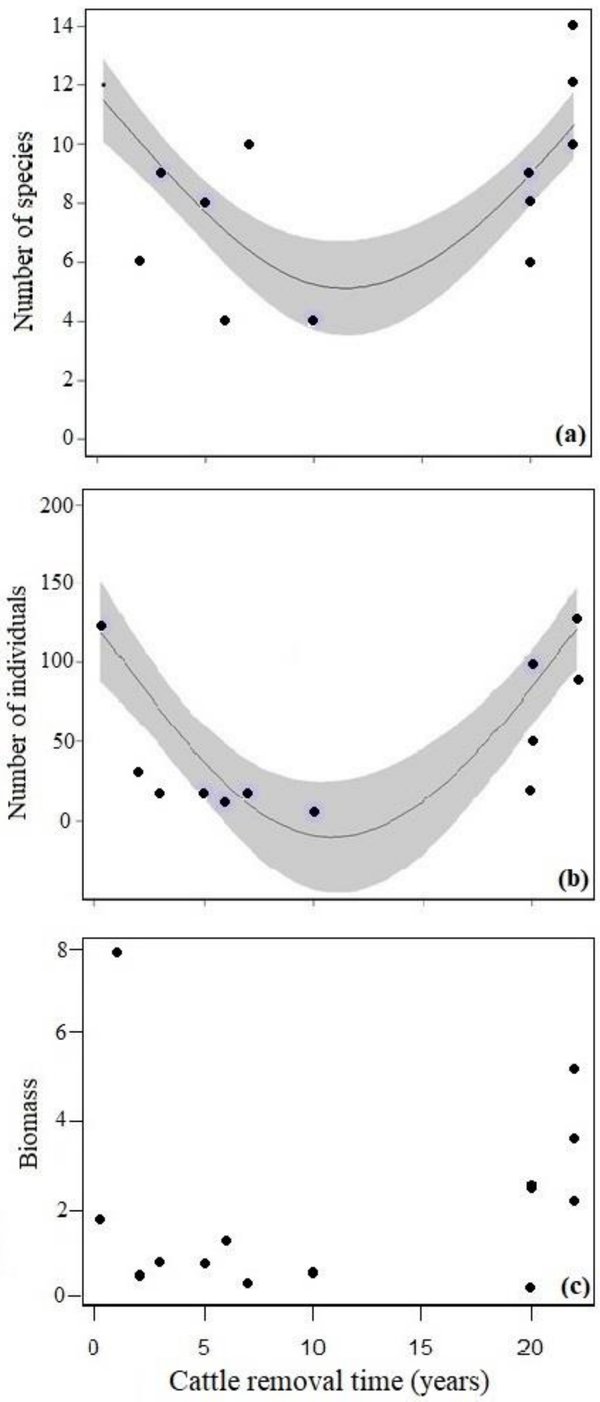

Fig 1. Relationship between time since cattle removal and (a) species richness, (b) number of individuals and (c) biomass.

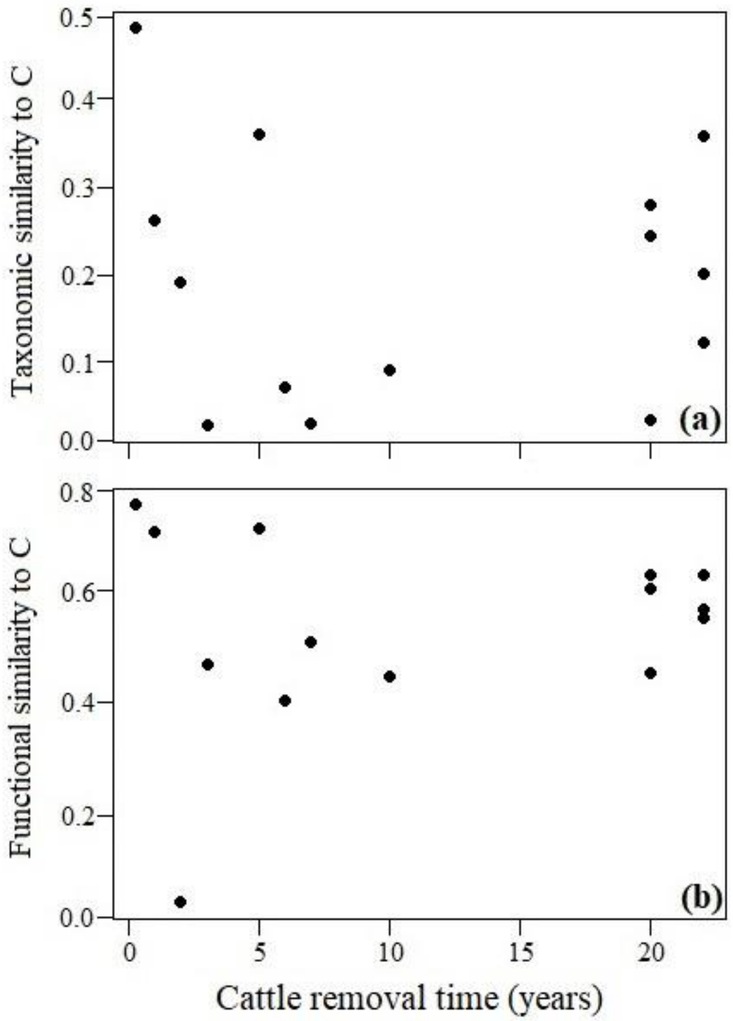

Fig 2. Relationship between time since cattle removal and (a) dung beetle taxonomic diversity and (b) functional diversity, and similarity (Bray-Curtis index) to cattle-used systems (C).

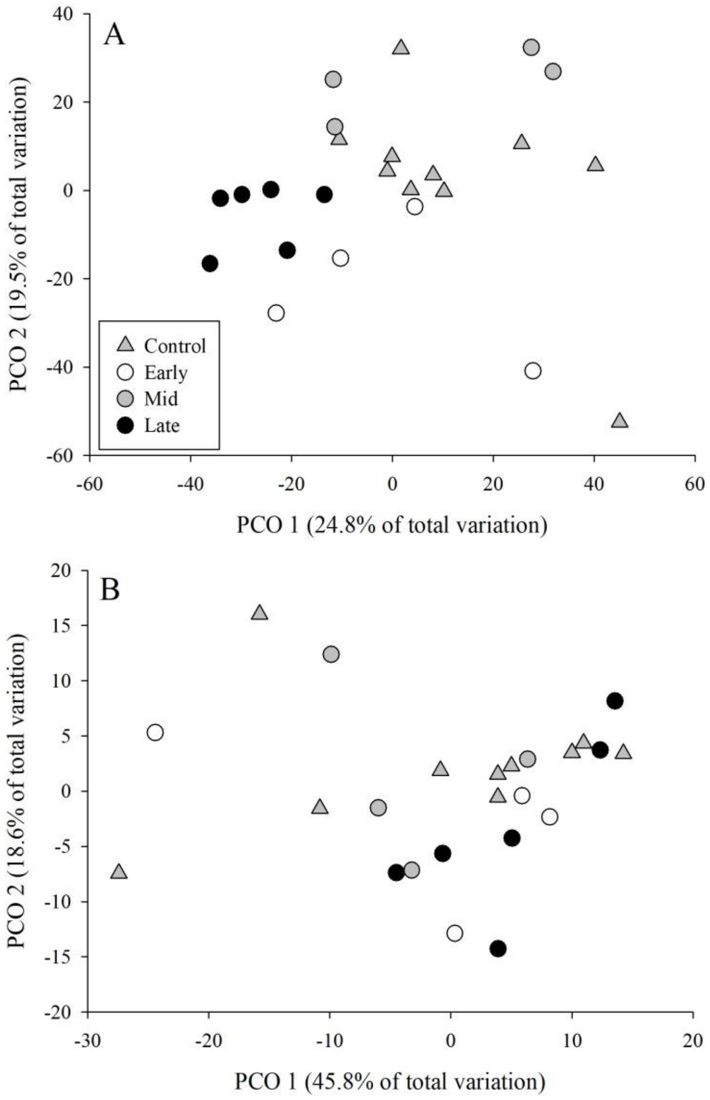

Fig 3. Principal coordinates analysis (PCO) graph exhibiting (A) species composition similarity, and (B) functional composition similarity relationships (based on Bray-Curtis similarity) between areas with different cattle removal times and the control (cattle-used sites). Cattle grazing removal categories are: early-stage (0.4–3 years), mid-stage (5–10 years), and late-stage of removal (20–22 years).

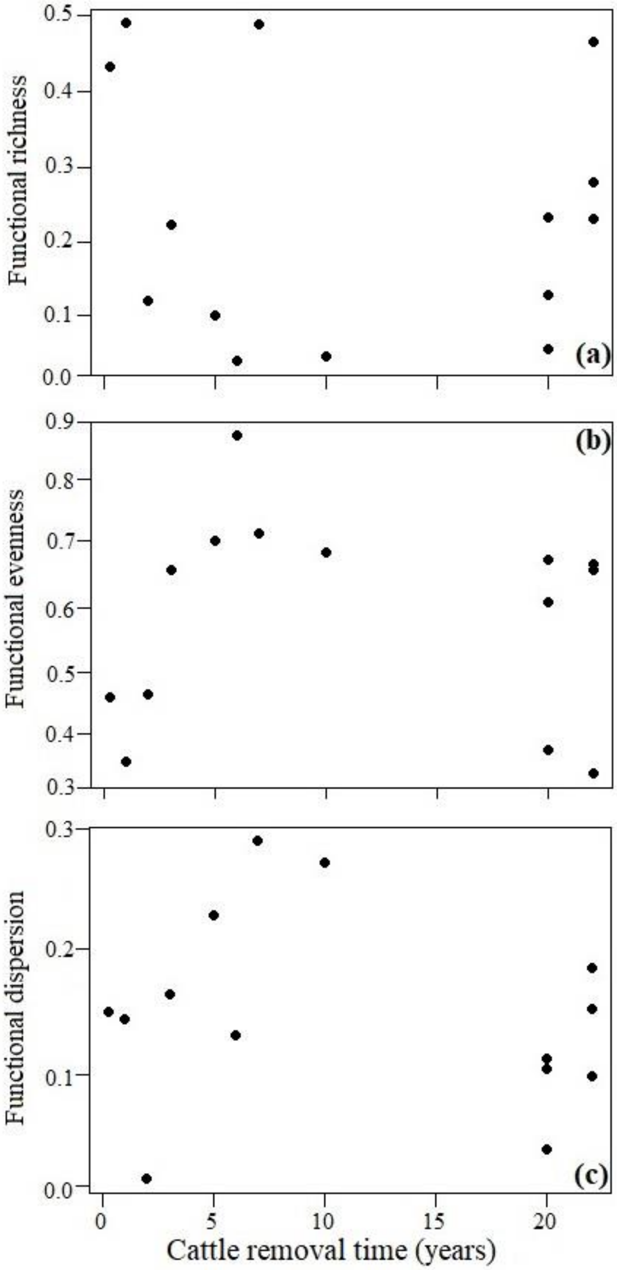

Fig. 4 Relationship between cattle removal time and (a) functional richness, (b) functional evenness (c) and functional dispersion (c).

4. Discussion

This study evaluated the successional trajectory of dung beetle communities in a tropical grassy ecosystem after cattle grazing removal. Our results show a strong decrease of both abundance and species richness of dung beetles in the first twenty years of cattle grazing abandonment. However, after twenty years we observed an increase of dung beetle richness and abundance. Despite taxonomic and functional composition not being related to time of cattle removal, after three years of cattle removal (early – stage of cattle removal) the taxonomic composition is already different from the control, with the establishment of a community deviating in composition from the cattle-used system. Functional diversity was not affected by cattle grazing removal. Thus, we demonstrated that taxonomic but not functional diversity of dung beetles was altered by cattle grazing removal, with a strong negative impact on taxonomic diversity in the first twenty years of cattle grazing removal, with an onset of community recovery of species diversity after ten years, but with a distinct community.

4.1. Effects of cattle removal time on dung beetle community

Contrary to our expectations biomass was not influenced by time of cattle grazing removal. In contrast, we found decreasing dung beetle species richness and abundance until 20 years; and then increasing from 20 to 22 years, showing that the absence of the major resource (cattle dung) causes a strong negative impact on the dung beetle community in the first 20 years. Fadda et al. (2008) found similar results to ours studying beetle assemblages in France. These authors demonstrated a decrease in beetle abundance during the first four years after sheep grazing abandonment. Later, after 23 years of grazing abandonment, there was no significant loss of species. Indeed, the absence, and even the reduction, of grazing and/or the abandonment of previously grazed grasslands has been reported to negatively affect dung beetle communities in

Europe (Buse et al., 2015; Tonelli et al., 2018, 2019), with a strong positive effect of grazing continuity on total species richness being reported (Buse et al., 2015). The fact that the dung beetle community start to recover after 20 years reveals that the impact of cattle grazing removal is dependent of exclusion time, and demonstrates the plasticity of Neotropical dung beetles to adapt in tropical grassy ecosystems.

We propose two main mechanisms to explain the increase of dung beetle abundance and species richness after 20 years of cattle removal. 1) Presence of wild animals: It has been reported that the presence of wild mammals is higher in areas without cattle grazing (Cao et al., 2016; Torre et al., 2007) including tropical grassy ecosystems (Eaton et al., 2017). So, after 20 years of cattle absence, grazing by wild herbivores may reach the level required to provide enough resources to maintain a high dung beetle species richness and abundance (Nichols et al., 2009). However, our results show that this native mammalian fauna was not enough to maintain the dung beetle community during the first 20 years since cattle removal. In this case, it is likely that the native mammalian community was not yet well established in early years of removal, resulting not only in low resource abundance but also spatial distribution of dung diversity (Tonelli et al., 2019). 2) Changes in vegetation structure: grazing by cattle has a direct effect on vegetation by modifying the structure and the composition of plant communities and limiting or excluding ligneous species establishment (Listopad et al., 2018). The absence of livestock leads to changes in the vegetation structure of our study area; such as an invasion of shrubs, native herbs and increase in plant biomass (native grass) (Correa CMA, 2016, personal observation). Thus, after ten years of cattle removal, the changes in vegetation structure may have altered the local microclimate conditions and favored the colonization by a number of habitat specialist dung beetle species (Larsen, 2012). This suggests that greater availability of cattle dung is important, but not mandatory, for the increase in species richness and abundance of the local dung beetle community in tropical grassy ecosystems (Correa et al., 2019a; Halffter and Arellano, 2002).

4.2. Effects of cattle removal time on taxonomic and functional composition

The taxonomic and functional composition was not influenced by increase of cattle grazing removal time. However, taxonomic composition in the different removal categories is deviating from the control. Since control and early-stage of cattle removal had similar species composition, it means that in the first three years of removal, the environmental conditions and vegetation structure are similar enough to maintain the same species group from the cattle-used sites. In addition, this information is confirmed by the high sharing of dung species among these categories (17 species, see Table 1) highlighting some species that are benefited by cattle grazing; *Canthon curvodilatatus* Shimdt, 1920, *Deltochilum pseudoicarus* Balthasar, 1939 and *Digitonthophagus gazella* (Fabricius, 1787) (Correa et al., 2019a). In contrast, all other categories were different from control and early – stage of removal. In this case, an increase of vegetation structural heterogeneity due to cattle absence may have occurred, since cattle control plant succession and forage development (Adler et al., 2001). Structural heterogeneity generally increases the number of ecological niches for species adapted to tall, short or both vegetation types (Debano et al., 2006). Thus, the increase of pasture structural heterogeneity may favor colonization by a greater number of insect species (Krues and Tscharntke, 2002; Wallis-de-Vries et al., 2007). Indeed, our results show the occurrence of new species that did not occur in the control and early - stage of removal, such as; *Canthon* aff. *maldonadoi*, *Canthon unicolor* Blanchard, 1843 and *Phanaeus palaeno* Blanchard, 1846 (see Table 1), forming a distinct dung beetle community independent of cattle grazing.

4.3. Effects of cattle removal time on functional diversity

Functional diversity did not show a relationship with cattle grazing removal. In our study, the decline and subsequent recovery of dung beetle species richness and abundance after 20 years of cattle grazing abandonment was not accompanied by similar functional diversity changes. Differences in taxonomic and functional patterns may be the result of functional redundancy between species in cattle-used systems and different cattle exclusion ages; or replacement by functionally different species that could maintain similar functional diversity values (Magnago et al., 2014; Rosenfeld, 2002). Thus, even with species richness reduction in the first ten years of cattle removal, the loss of functionally specialized species may not have occurred, thus not leading to reduction of functional diversity after cattle removal.

Overall, functional responses have been shown to depend mainly on the intensity of the disturbed and the functional characteristics chosen (Beiroz et al., 2018; Mlambo et al., 2014). Thus, high intensity disturbances tend to negatively affect both taxonomic and functional components of the local biodiversity (Magnago et al., 2014; Mlambo et al., 2014). In contrast, a low intensity disturbance in highly diversified communities does not modify functional structure, but may alter species composition (Magnago et al., 2014). In this sense, the absence of cattle grazing may represent a low disturbance for dung beetle functional diversity in tropical grassy ecosystems. Since functional diversity is directly related to ecosystem functions (Gerisch et al., 2012; Lauretto et al., 2015; Mouillot et al., 2013), our results suggest a possible maintenance of ecological functions performed by dung beetles in tropical grassy ecosystems after cattle grazing removal.

5. Conservation implications

Tropical grassy ecosystems dominate the tropics and account for 20% of the global surface area (Scholes and Archer, 1997), sustaining unique biodiversity and providing valuable ecological services to humankind (Parr et al., 2014). Despite their importance, they have been neglected in terms of conservation and public policies (Overbeck et al., 2015). Although there is still debate about the trade-offs between livestock grazing and/or exclusion and the potential for grassland ecosystem regeneration (Listopad et al., 2018; Török et al., 2016), in TGE this discussion is incipient (Overbeck et al., 2015; Veldmann et al., 2015). So, since the dung beetle is a considerable usefulness indicator for monitoring environmental change across the globe (Nichols et al., 2007), our results suggest that complete cattle grazing removal, at least in a short time (20 years), may be an inefficient management tool for restoration and conservation of detritus-feeding insects in tropical grassy ecosystems. We suggest the need of research of the benefit of moderate livestock grazing for the conservation of TGE. For example, research on semi-natural grassland in temperate zones (Europa) has lead to the recommendations that complete grazing abandonment is not a good management plan for the conservation of this habitats and that moderate grazing is required (Tonelli et al., 2018; Török et al., 2016). In the case of Europe where the majority of native grazers have gone extinct the continuity of grazing by domestic animals is need, but in TGE it may be possible that eventually domestic animals will be no longer required. In addition, studies with reintroduction of cattle after different times of grazing removal are also needed (Listopad et al., 2018), to provide information that may help us to create a livestock management that determines the most appropriate cattle removal interval and reintroduction. Thus, we may integrate human use and conservation of tropical grassy ecosystems efficiently (Veldmann et al., 2015; Bond and Parr, 2010).

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Supplementary Material

Dung beetle trait assignment

Species were characterized in terms of seven ecological attributes: food relocation habitat, diet, diel activity, body mass, body mass-adjusted front leg area, body mass-adjusted pronotum volume, and back:front leg lengths. Protocols for trait assignments are described below.

Food relocation habit: Food relocation habit assignment followed the classificatiom of Hanski and Cambefort (1991) who categorized dung beetle species as rollers (telecoprids), tunnellers (paracoprids) or dwellers (endocoprids). Roller species remove portions of dung, which are rolled various distances and then buried. Tunneler species construct tunnels below or adjacent to the food resource and transport dung into the bottom. Dweller species live within a dung pat and do not exhibit resource allocation;

Diet: Diet preference was investigated using traps baited with cattle dung (n = 72 traps) carrion (n = 72 traps) using the same sampling design described in the Materials and Methods section. We used the proportion of individuals of each species attracted to a certain bait to determine bait specificity. Species was considered as “coprophage or necrophage” when its occurrence was ≥80% on one bait used (cattle dung or carrion), otherwise it was considered “generalist” (Halffter and Arellano 2002). The minimum number of individuals of each species required to calculate diet n = 3.

Diel activity: We obtained information on dung beetle diel activity from the published literature (Pêssoa et al., 2017; Beiroz et al., 2017; Iannuzzi et al., 2016; Audino et al., 2014, Hernández 2002) and personal observations of specialist (Fernando Vaz-de-Mello).

Body mass: To determine the body mass, all individuals of each species were dried at 42°C for 72 hours and weighed using a balance accurate to 0.0001 g

Morphological traits (Body mass-adjusted front leg area; body mass-adjusted pronotum volume; back: front leg lengths): We measured pronotum area, front tibia and femur area, and front and back leg length using a Leica M250 microscope and Life Measurement software (Leica, Wetzlar, Germany); with digital calipers (0.01-mm resolution) we measured pronotum height. 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 (see Griffiths et al., 2015)**.**

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Vegetation measurements

At each trap location, a 140 · 150 cm black panel was placed vertically and photographed four times (at each of the cardinal compass point) at a 3 m distance and at 70 cm above the ground. We used the white pixels percentage of bichromatic pictures as a proxy of herbaceous vegetation density and fractal dimension as a measure of its complexity (Marsden et al., 2002). This was carried out using a Canon PowerShot SX10 IS and the software Sidelook 1.1.01 (Zehm et al., 2003).

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Table S1. Identity and traits for 32 species of dung beetles (Scarabaeinae: Coleoptera) sampled in the Brazilian Pantanal. **NA:** missing data.

Species	Food relocation habitat	Diet	Diel Activity	Body Mass	Body mass-adjusted front leg area	Body mass-adjusted pronotum volume	Back:front leg lengths
Ateuchus aff. *ovallis*	Tunneler	Generalist	Nocturnal	0.0071	56.3809	513.2356	0.667
Ateuchus sp.	Tunneler	Generalist	Nocturnal	0.0079	38.6081	461.7164	0.732
Ateuchus sp. 1	Tunneler	Generalist	Nocturnal	0.0097	43.2716	554.7964	0.8764
Canthidium aff. *refulgens*	Tunneler	Necrophage	Diurnal	0.0032	105.9472	1014.3274	0.7814
Canthidium aff. *viride*	Tunneler	Generalist	Diurnal	0.0254	34.3261	774.5236	0.6113
Canthon aff. *maldonadoi*	Roller	NA	Diurnal	0.0199	19.5980	146.6533	0.6707
Canthon cinctellus	Roller	Necrophage	NA	0.0111	36.0605	457.6623	0.6354
Canthon conformis	Roller	Necrophage	Diurnal	0.0174	35.0137	533.5141	0.584
Canthon curvodilatatus	Roller	Necrophage	NA	0.4601	20.1462	637.0834	0.5299
Canthon histrio	Roller	Generalist	Diurnal	0.0406	46.4894	759.1104	0.5761
Canthon unicolor	Roller	Generalist	Diurnal	0.0549	34.8867	488.5335	0.6378
Coprophanaeus bonariensis	Tunneler	Necrophage	Mixed	1.2786	10.6263	883.9542	0.7369
Coprophanaeus cyanescens	Tunneler	Necrophage	Mixed	0.7619	12.2958	717.7956	0.7265
Deltochilum aff. *komareki*	Roller	Necrophage	NA	0.0889	18.6912	422.339	0.6503
Deltochilum pseudoicarus	Roller	Necrophage	Diurnal	1.2786	10.6263	883.9542	0.7369
Dendropaemon nitidicollis	Tunneler	NA	Diurnal	0.0072	110.723	1158.7351	0.7178
Dichotomius bos	Tunneler	Coprophage	Nocturnal	0.5221	15.9039	648.5058	0.8271
Dichotomius glaucus	Tunneler	Coprophage	Nocturnal	0.2682	17.1766	642.8564	0.7339
Dichotomius nisus	Tunneler	Coprophage	Nocturnal	0.7552	6.8206	228.0884	0.6955
Dichotomius opacipennis	Tunneler	Generalist	Nocturnal	0.0665	36.0232	919.8393	0.6905
Digitonthophagus gazella	Tunneler	Coprophage	Nocturnal	0.0459	68.9821	1131.607	0.8308
Eurysternus aenaeus	Dweller	Coprophage	Mixed	0.009	52.1708	622.504	0.5191
Eurysternus carybaeus	Dweller	Coprophage	Mixed	0.0705	36.7601	785.9048	0.6874
Genieridium bidens	Dweller	Necrophage	NA	0.0055	31.5447	297.3858	0.6546
Malagoniella punctatostriata	Roller	NA	NA	0.1099	40.0471	695.7604	0.6892
Malagoniella puncticollis	Roller	Generalist	NA	0.1094	41.3538	752.458	0.6461
Ontherus appendiculatus	Tunneler	Generalist	Nocturnal	0.0466	31.3303	534.9569	0.7786
Onthophagus aeneus	Tunneler	Coprophage	Mixed	0.0054	63.7901	764.3143	0.7003
Onthophagus ptox	Tunneler	Generalist	Mixed	0.0051	51.7242	676.6979	0.7364
Phanaeus palaeno	Tunneler	NA	Diurnal	0.1829	24.915	991.8123	0.6941
Trichillum externenpunctatum	Dweller	Coprophage	Nocturnal	0.0013	44.6446	456.7207	0.5779
Uroxys aff. *corporaali*	NA	Generalist	NA	0.0029	49.0099	430.5344	0.7972

Table S2. Permutational analysis of variance (PERMANOVA) contrasting grassland categories according to species composition. Pseudo-F and p-value are presented for the main test and test statistic (t) and p-values for each pair-wise comparison. * = p-values < 0.05

Source of variation	**Pseudo-F**	**p**
Grassland categories	2.94	0.001*

Post hoc comparison of systems		
Grassland categories	**T**	**p**
Control vs. late-stage of cattle removal	2.20	0.001*
Control vs. mid-stage of cattle removal	1.47	0.02*
Control vs. early-stage of cattle removal	1.20	0.12
early-stage of cattle removal vs. late-stage of cattle removal	1.68	0.003*
early-stage of cattle removal vs. mid-stage of cattle removal	1.63	0.03*
mid-stage of cattle removal vs. late-stage of cattle removed	2.05	0.003*

Table S3. Permutational analysis of variance (PERMANOVA) contrasting grassland categories according to functional composition. Pseudo-F and p-value are presented for the main test and test statistic (t) and p-values for each pair-wise comparison. * = p-values < 0.05

Source of variation	**Pseudo-F**	**p**
Grassland categories	1.37	0.16
Post hoc comparison of systems		
Grassland categories	**T**	**p**
Control vs. late-stage of cattle removal	1.20	0.19
Control vs. mid-stage of cattle removal	1.09	0.28
Control vs. early-stage of cattle removal	0.84	0.57
early-stage of cattle removal vs. late-stage of cattle removal	1.19	0.23
early-stage of cattle removal vs. mid-stage of cattle removal	1.24	0.17
mid-stage of cattle removal vs. late-stage of cattle removal	1.65	0.04*

3. GENERAL CONCLUSIONS

Until now, there has been very little information on the cattle grazing effects on dung beetle diversity and their ecological functions in Neotropical region. In this thesis, I mitigated this lack of information and presented, for the first time, the successional trajectory of dung beetle communities in a tropical grassy ecosystem after cattle grazing removal.

The results presented in this thesis agree with the view that cattle breeding in natural grasslands of the Brazilian Pantanal can integrate livestock production with the conservation of the dung beetle community and its ecological functions. These results are related to livestock management applied in the natural grasslands of Pantanal with low-use of veterinary drugs and soil fertilizers, and due to the rich local community of native mammals. Indeed, the negative effects of livestock on biodiversity are most related to the conversion of native to exotic vegetation, grazing intensity and land management (e.g., use of fertilizers and veterinary drugs). In our case, it was demonstrated that cattle grazing *per si* did not cause a reduction in dung beetle biodiversity. Since dung beetles are good indicators of anthropic changes, this result indicates that extensive cattle breeding in the Pantanal is carried out in a conservationist way with low impact on biodiversity, at least for our study group.

This thesis has crucial implications for conservation of tropical grassy ecosystems with base data from taxonomic, functional diversity and ecological functions performed by dung beetles. This work provides the first empirical evidence that cattle grazing exclusion represent a low disturbance for dung beetle functional diversity in tropical grassy ecosystems. Thus, another key finding of this thesis is that complete cattle grazing exclusion, at least in a short time (20 years), may be an inefficient management tool for restoration and conservation of tropical grassy ecosystems. However, the debate about the trade-offs between livestock grazing and/or exclusion and the potential for tropical grassy ecosystem regeneration is still an incipient, and more studies are needed.

Additionally, the use of native grasslands for livestock, besides economically helping the farmers, may provide opportunities to maintain or restore native fields that could be converted into introduced pastures, mechanized agriculture or other land uses, that are detrimental to dung beetle biodiversity and their ecological functions. Finally to contributing to our knowledge of the cattle grazing consequences on both dung beetle biodiversity and ecosystem functioning, this thesis also highlights several key research priorities in which future work may further our comprehension of the impacts of livestock farming on tropical grassy ecosystems; such as: cattle grazing reintroduction and cattle exclusion interval time and grazing intensity (moderate livestock grazing). Thus, we may integrate human use and improve the sustainable use of tropical grassy ecosystems.