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, five were classified as specialist of cattle-used grasslands, three considered specialist of non-cattle grasslands, eight were habitat generalists and for the 14 species it was not possible to determine their habitat preference due the low number (Table S1).

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).

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 conformis* (Harold), *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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Figure captions

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.

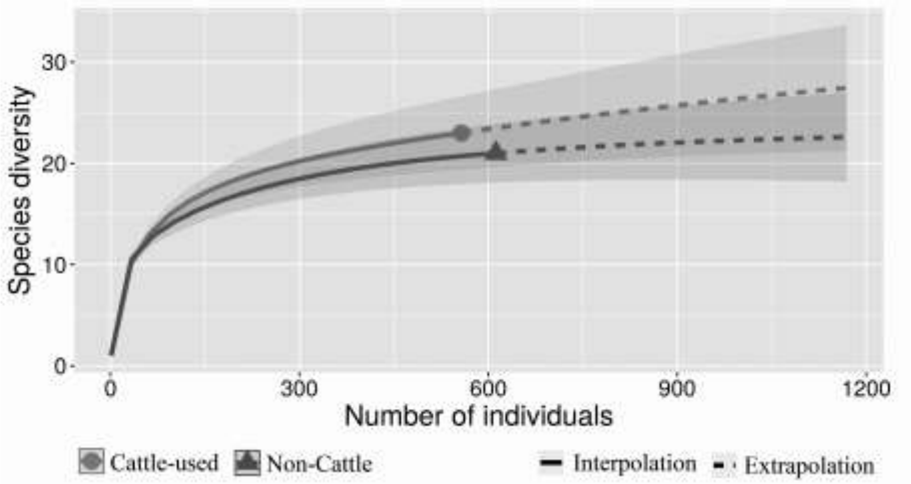
Fig. 2 Average species richness (A), average abundance (B) and biomass (C) of dung beetles sampled in cattle-used and non-cattle grasslands, in the Brazilian Pantanal. Error bars represent ± SE. NS = no significance ($p > 0.05$)

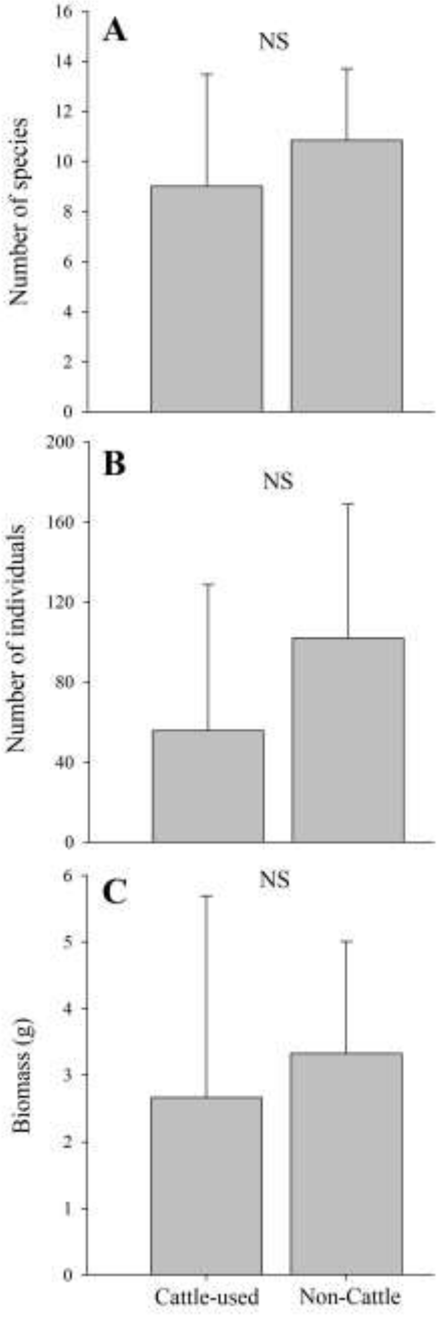
Fig. 3 Non-metric multidimensional scaling results (NMDS), constructed from Jaccard matrices, for dung beetle communities in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Stress = 0.16

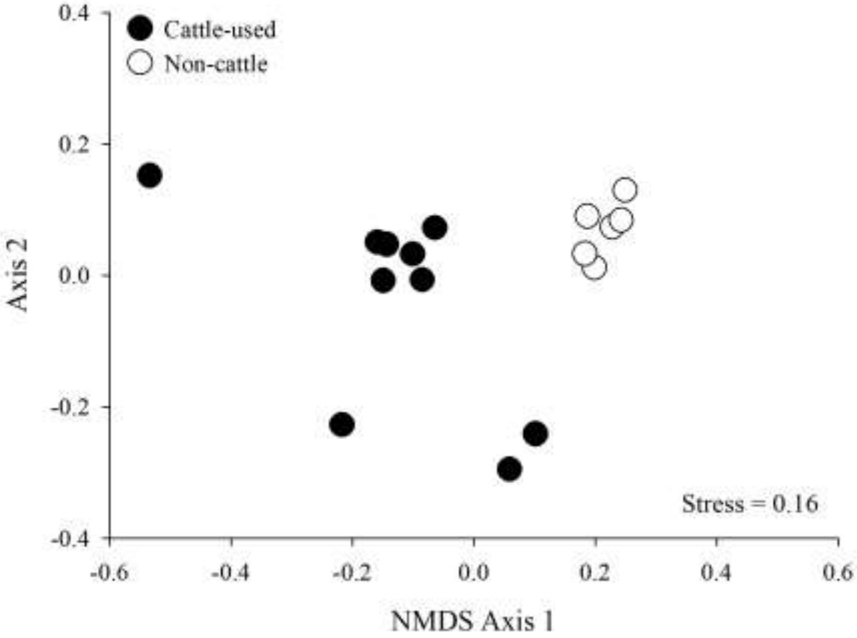
Fig. 4 Proportional change in functional dung beetle groups sampled in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Numbers inside the figure represent the species numbers in each functional group.

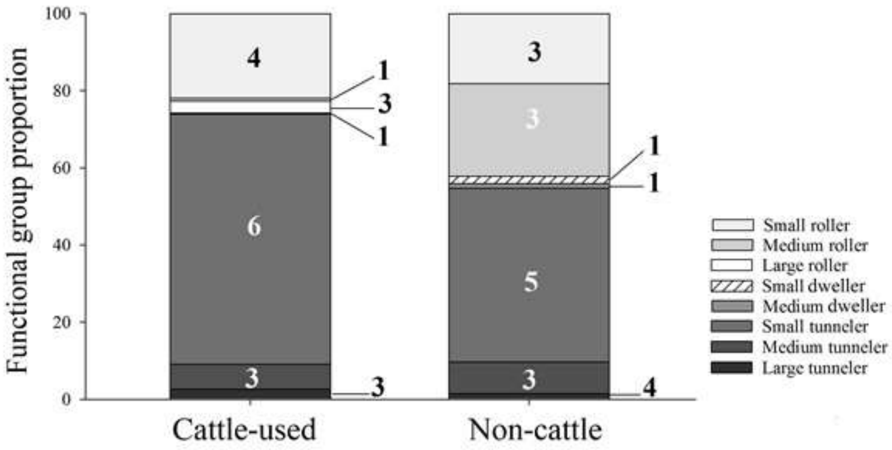
Fig. 5 Average species richness (A), abundance (B) and biomass (C) of dung beetle functional groups sampled in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Error bars represent ± SE. NS = no significance ($p > 0.05$); ** significance ($p < 0.01$); * significance ($p < 0.05$).

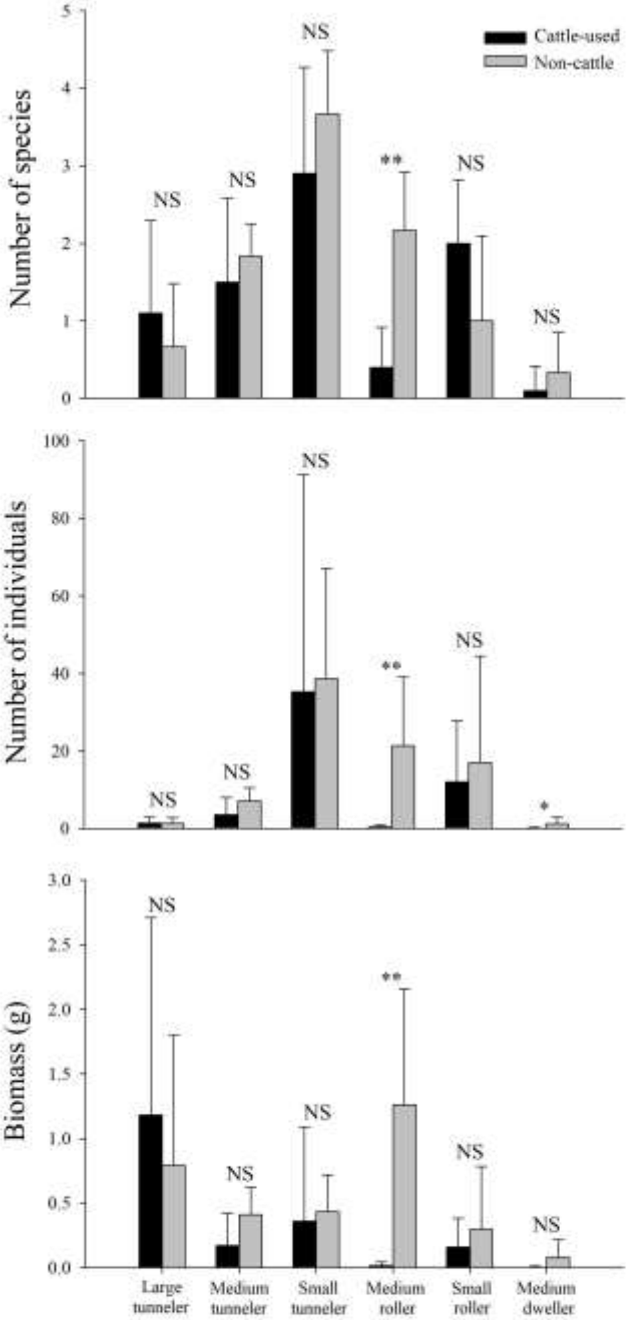
Fig. 6 Ecological functions: (A) dung removed and (B) soil excavation performed by dung beetles in cattle-used and non-cattle grasslands in the Brazilian Pantanal. Error bars represent ± SE. NS = no significance ($p > 0.05$)

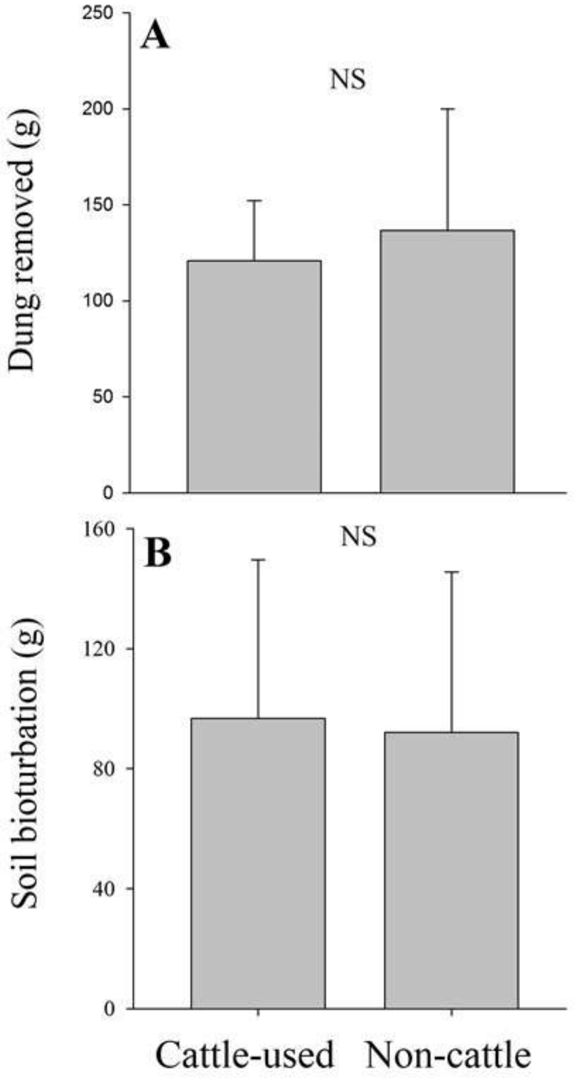

Species diversity
0
10
20
30
0
300
600
900
1200
Number of individuals
Cattle-used
Non-Cattle
Interpolation
Extrapolation


A
NS
Number of species
0
2
4
6
8
10
12
14
16
B
NS
Number of individuals
0
40
80
120
160
200
C
NS
Biomass (g)
0
1
2
3
4
5
6
Cattle-used
Non-Cattle


0.4
0.2
0.0
-0.2
-0.4
Axis 2
● Cattle-used
○ Non-cattle
Stress = 0.16
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
NMDS Axis 1


Functional group proportion
100
80
60
40
20
0
4
1
3
1
6
3
3
3
3
1
1
5
3
4
Cattle-used
Non-cattle
Small roller
Medium roller
Large roller
Small dweller
Medium dweller
Small tunneler
Medium tunneler
Large tunneler


Cattle-used
Non-cattle
Number of species
0
1
2
3
4
5
NS
NS
NS
**
NS
NS
Number of individuals
0
20
40
60
80
100
NS
NS
NS
**
NS
*
Biomass (g)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
NS
NS
NS
**
NS
NS
Large tunneler
Medium tunneler
Small tunneler
Medium roller
Small roller
Medium dweller


250
A
NS
200
Dung removed (g)
150
100
50
0
160
B
NS
120
Soil bioturbation (g)
80
40
0
Cattle-used
Non-cattle

746

747

748