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

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Abstract Grazing by large herbivorous mammals is still a structuring force in tropical grassy ecosystems, and cattle grazing is one of the main economic activities carried out in these ecosystems in modern times. 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 tropical grassy ecosystem after cattle removal. For this, we assessed the patterns of dung beetle taxonomic and functional diversity of 14 natural grasslands with distinct cattle grazing removal ages (from 3 months to 22 years) along a chronosequence, applying the space-for-time substitution method. Our results show a strong decrease in dung beetle abundance (93 times) and species richness (6 times) in the first ten years of cattle removal. However, after ten years there is an increase in dung beetle abundance (73 times) and species richness (5 times). Taxonomic composition was also influenced by cattle removal time demonstrating the importance of cattle in the structuring of dung beetle communities in natural grasslands. In contrast, functional composition and diversity were not affected by cattle grazing removal, indicating these metrics are less sensitive to cattle absence than taxonomic diversity and composition. Our results provide evidence that cattle grazing removal, at least in the short term (10 years), may be an inefficient management tool for restoration and conservation of tropical grassy ecosystems. However, we highlight the need to investigate the reintroduction of cattle grazing after different removal times to provide complimentary information to livestock management able to integrate human use and conservation of tropical grassy ecosystems.

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

Introduction

Livestock farming, the largest land-use sector on Earth, occupies more than 30% of the planet's continental surface (FAO 2012). In tropical grassy ecosystems (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 tropical grassy ecosystems (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 (van Klink et al. 2015; Dettenmaier et al. 2017).

There is an increasing debate about the effects of cattle grazing in biodiversity of tropical grassy ecosystems (Parr et al. 2014; Veldmann et al. 2015; Overbeck et al. 2015; Lehmann and Parr 2016). Livestock farming is considered the main driver of natural habitat loss worldwide (Alkemade et al. 2013; Herrero and Thornton 2013). 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 (Kröpfl et al. 2013; Al-Rowaily et al. 2015; Listopad et al. 2018). Although the role of livestock farming as a global agent for the degradation of the ecosystems is recognized (Parr et al. 2014; Overbeck et al. 2015; Veldmann et al. 2015; Lehmann and Parr 2016), cattle grazing in suitable density and frequency may be beneficial for the biodiversity of grasslands ecosystems (Overbeck et al. 2007; Correa et al. 2019a). Cattle grazing affects vegetation heterogeneity, plant succession and forage-plant growth control (Olff and Ritchie 1998; Adler et al. 2001), 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 (Verdú et al. 2007; Fynn et al. 2016; Török et al. 2016). For example, in parts of Europe (Pykälä 2003, Török et al. 2016), African savannas (Fynn et al. 2016) and in 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 tropical grassy ecosystems.

In this sense, the importance of long-term time series (more than 20 years) for analyzing the effects of anthropic actions is widely recognized (Bakker et al. 1996; Rees et al. 2001; Peco et al. 2006), given that ecological processes that lead to functional and biodiversity changes in grassland ecosystems are generally long-term (Peco et al. 2006, 2017; Listopad et al. 2018). However, studies of the successional trajectory of biotic communities in tropical grassy ecosystems are scarce (see Cava et al. 2018), and the impacts of inclusion or exclusion of cattle grazing as a tool for 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; Veldmann et al. 2015; Cava et al. 2018).

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 viable models for functional diversity studies aimed at understanding the effects of anthropogenic actions on ecosystem processes (Barrágan et al. 2011; Audino et al. 2014, 2017; Beiroz et al. 2018). 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), to answer the following questions: (1) Do species richness, number of individuals, diversity, biomass and functional diversity decrease with cattle grazing removal age? (2) Are dung beetle taxonomic and functional composition influenced by time of cattle grazing removal? We expect dung beetle richness, abundance, diversity and 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 composition because the grazing exclusion implies changes in spatial heterogeneity of vegetation (Wallis-de-Vries et al. 2007), also modifying the local microclimate conditions (Edmondson et al. 2016; Ozkan and Gokbulak, 2017) and favoring colonization by a number of habitat specialist dung beetle species (Larsen 2012).

Material and Methods

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).

Sampling sites

The studied area has been historically influenced by livestock farming activities, where we sampled dung beetles in 14 areas of natural grasslands that had been used for cattle grazing in the past. The vegetation of these areas is dominated by a ground layer composed of natural grasses (e.g. *Andropogon* spp. and *Axonopus* spp.), herbs, and small shrubs; and predominantly sandy soil (>70% sand). These areas present 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. 2016a), 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).

Experimental design

For this study, we applied the space-for-time substitution method (SFT). This method is widely applied in ecological modelling which contemporary spatial patterns of biodiversity are used to model temporal processes and project changes through time, either into the future or into the past (Blois et al. 2013; Wogan and Wang 2018; Damgaard 2019). In order to apply SFT, it is important that the sites are ordered into a sequence that reflects the stages of development, for example, the successional age (Blois et al. 2013; França et al. 2016). Thus, it is essential to know the history of the sites to understand if the process is constant or stationary; that is, the random variation of the environment around a fixed mean. In this case, spatial regression models may be used for studying interspecific interactions and successional processes (Damgaard 2019). As such, in our study, this method has been used to evaluate dung beetle diversity in restorating chronosequence in tropical forests (see Audino et al. 2014; Derhé et al. 2016)

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 due to increased 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. 2016b). 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. We performed the same sampling effort in the reference habitat. Dung beetles captured were identified at genus level (Vaz-de-Mello et al. 2011), and then sent to an expert to perform species identification (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).

Dung beetle traits

We analyzed seven functional traits that are directly related to the ecosystem functions performed by dung beetles (Slade et al. 2007; Barrágan et al. 2011; Braga et al. 2013; Griffiths et al. 2015; Audino et al. 2014, 2017): 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 the Supplementary Material. When necessary, we also obtained additional information on dung beetle traits from the literature and specialists.

Data analysis

Species richness, number of individuals and biomass

We tested the effects of cattle grazing removal on total species richness, number of individuals, diversity (Shannon index) 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 2019).

Taxonomic and functional composition

To verify whether dung beetle taxonomic and functional composition are influenced by time since cattle removal, we performed a DistLM analysis (Distance-based Multivariate Analysis for a Linear Model, Legendre and Anderson 1999; McArdle and Anderson 2001). Species and functional composition matrices were used as response variables and cattle removal time as a predictor variable. Matrices were transformed in triangular matrices using Bray-Curtis similarity index. Abundance data of each species and of each trait was standardized and square root transformed (Anderson and Willis 2003). Time since cattle abandonment was also transformed in a similarity matrix, but using Euclidian distance. DistLM analyzes and models the relationship between a multivariate data cloud and one or more independent variables (Anderson et al. 2008).

To determine whether taxonomic and functional composition of dung beetle assemblage is progressing towards or deviating from the reference sites, we performed non-metric multidimensional scaling analysis (NMDS) and a permutational multivariate analysis of variance (PERMANOVA). NMDS 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 NMDS and PERMANOVA were performed using the software PRIMER+ (Anderson et al. 2006; Clarke and Gorley 2006). Finally, we used similarity percentage (SIMPER) analysis (Clarke 1993) to determine the contributions of individual species in terms of distinguishing differences in community structure among categorized groups. This analysis was performed using Past (Hammer et al. 2001).

Functional diversity

To calculate three functional diversity indexes that measure different aspects of functional diversity, we used the “FD” package (R Development Core Team 2019): 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 2019).

Results

Species richness, number of individuals and biomass

We collected 1622 dung beetle individuals from 32 species of 16 genera and six tribes (Table S1). 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 S1).

The identity of dominant species changed over cattle removal age. However, *Canthidium* aff. *viride* was present among the three dominant species in 10 of the 11 cattle removal ages (Fig. 1). Eleven species were no longer present on sites that had experienced no grazing for over 10 years of cattle removal, three have appeared and 18 species were distributed along all cattle removal ages (Fig. 2).

Species richness ($R^2 = 0.46$; $p = 0.03$ – Fig. 2a) and number of individuals ($R^2 = 0.51$; $p < 0.001$ – Fig. 2b) have a significant relationship with cattle removal time, decreasing the dung beetle abundance (93 times) and species richness (6 times) until ten years of cattle removal; and then increasing dung beetle abundance (73 times) and species richness (5 times) until 22 years. However, species diversity (Shannon index) ($R^2 < 0.001$; $p = 0.711$ – Fig. 2c) and biomass were not influenced by time of cattle grazing removal ($R^2 < 0.001$; $p = 0.372$ – Fig. 2d).

Taxonomic and functional composition

Taxonomic composition was significantly influenced by cattle removal time (13.84% of independent effect) (Pseudo-F = 3.53, p = 0.001, *df* = 22), however, functional composition was not (Table 1).

Taxonomic composition in the different categories of cattle grazing removal deviates from the reference sites (cattle-used sites) (Fig. 3a). PERMANOVA analysis revealed that except for reference sites and early-stage removal sites (*t* = 1.21; *p* = 0.13) (Table 2), all other categories were significantly different from each other based on taxonomic composition (Pseudo-F = 2.94; p = 0.001) (Fig. 3a; Table 2). Ten species *Canthidium* aff. *viride*, *Ateuchus* sp., *Canthon conformis*, *Digitonthophagus gazella*, *Uroxys* aff. *corporaali*, *Canthon unicolor*, *Ontherus appendiculatus*, *Deltochilum* aff. *komareki*, *Canthon curvodilatatus* and *Dichotomius opacipennis* contributed to >80% of the observed differences in community composition among all categories (Table S2). For functional composition, PERMANOVA analysis revealed that only mid-stage and late-stage abandonment were significantly different from each other based on functional composition (*t* = 1.65; *p* = 0.04) (Table 2). In contrast, all other categories were not significantly different from each other (Pseudo-F = 1.37; p = 0.16) (Fig. 4b; Table 2).

Functional diversity

The time of cattle grazing removal did not influence the FRic ($R^2 < 0.001$; p = 0.614 – Fig. 5a), FEve ($R^2 = 0.25$; p = 0.10 – Fig. 5b) and FDis ($R^2 = 0.13$; p = 0.18 – Fig. 5c).

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 ten years of cattle grazing abandonment. However, after ten years we observed an increase in dung beetle richness and abundance. Taxonomic composition was influenced by cattle removal time demonstrating the importance of cattle in the structuration of dung beetle communities in natural grasslands. Functional diversity and composition were 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 ten years of cattle grazing removal, with an onset of community recovery of species diversity after ten years, but with a distinct community.

Patterns of dung beetle species distribution across natural grasslands with different cattle removal times

Canthidium aff. *viride* was the dominant in 10 of the 11 ages of cattle removal we examined, demonstrating that, this species is unaffected by the effects of cattle grazing removal on species composition. *Dichotomius bos* and *O. appendiculatus* are among the species that were distributed along all cattle removal ages. These species are also considered important for introduced Brazilian pastures due to their frequency, abundance and wide distribution in pastures (Tissiani et al. 2017), and are dominant in natural grasslands of the Pantanal (Correa et al. 2016a).

Dichotomius nisus, *D. gazella* and *Trichillum externepunctatum* disappeared after ten years of cattle removal. *D. nisus* and *T. externepunctatum* are also considered important for introduced Brazilian pastures (Tissiani et al. 2017). In addition, *D. nisus* is a dominant species in natural grasslands of the Brazilian Pantanal (see Correa et al. 2016a). We found a higher abundance of *D. gazella* in control sites and after 0.4 years of cattle removal. However, this species remained in the sites until three years after cattle removal. It is an African species introduced to Brazil during the 1980s to help control gastrointestinal and parasitic flies. It is a strict coprophage (Miranda et al. 2000) and benefits from cattle presence (Correa et al. 2019a). However, *D. gazella* is a threat to the native dung beetle fauna and could negatively impact local ecosystems (Filho et al. 2018). These results demonstrated that these species are benefited by cattle presence with higher populations on sites where cattle farming is occurring.

Finally, *C. unicolor*, *Canthon* aff. *maldonadoi* and *Phanaeus palaeno* are the species that appeared after then years of cattle removal. These species are frequently found in savannahs (Cerrado *strictu senso*) and the Pantanal biome (Vaz-de-Mello et al. 2017), being adapted to open ecosystems, which may explain their distribution on sites that have been absent of cattle of a long period. Thus, these species demonstrated a positive effect of cattle removal in natural grasslands.

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 10 years; and then increasing from 10 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 10 years. Fadda et al. (2008) studying beetle assemblages in France found similar results to ours. They found a decrease in beetle abundance during the first four year after sheep grazing abandonment; then 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 10 years reveals that the impact of cattle grazing removal is dependent on 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 in dung beetle abundance and species richness after 10 years of cattle removal: presence of wild animals (change in food resource) and vegetation structure. Recently, Macedo et al. (2020) demonstrated that alterations in food resources and vegetation structure played an important role in the dung beetle assemblages in open ecosystems (e.g. exotic pastures). 1) Presence of wild animals: there is a consensus in literature that livestock grazing can have a negative impact on native mammals (Torre et al. 2007; Cao et al. 2016). So, cattle removal can promote the recovery of wild mammals (Madhusudan 2004; Legge et al. 2011). This was also demonstrated by a study performed in the same landscape we conducted our study (Eaton et al. 2017). However, this recovery generally takes a while (years) to happen (Legge et al. 2011; Frank et al. 2013). So, after 10 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 10 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 (herbaceous density and complexity) of our study area; such as an invasion of shrubs, native herbs and increase in plant biomass (native grass). Thus, after ten years of cattle removal, the changes in vegetation structure may have altered the local microclimate conditions (Edmondson et al. 2016; Ozkan and Gokbulak 2017) 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 (Halffter and Arellano 2002; Correa et al. 2019a).

Effects of cattle removal time on taxonomic and functional composition

Although, the functional structure of dung beetle communities was not influenced by cattle grazing removal time, taxonomic structure was, demonstrating the importance of cattle in the structure of dung beetle communities in natural grasslands. Control and early-stage of cattle removal had similar species composition. This is probably happening because in the first three years of removal, environmental conditions and vegetation structure remain similar enough to maintain the same species group as cattle-used sites. Control sites and early-stage cattle removal shared a high number of dung beetle species (17 species, see Fig 1), being some of these species benefited by cattle grazing, such as: *C. curvodilatatus*, *Deltochilum pseudoicarus* and *D. gazella* (Correa et al. 2019a). In contrast, all other categories of cattle removal (mid-stage and late-stage) were different from control and early – stage removal sites. In these sites, a variation in the vegetation structure (mainly vegetation density) occurred due to cattle absence (see Fig. S1). This variation in vegetation structure can happen because cattle grazing can hinder plant succession, enabling forage development (Adler et al. 2001). Despite this, we could not find a statistical relationship between vegetation density and complexity and cattle removal age, it is possible to see a variation in vegetation density over time (see Fig. S1). The modification of the vegetation structure (e.g., herbaceous density and complexity) can influence environmental conditions (e.g.

atmospheric and soil surface luminosity, temperature and humidity) (Edmondson et al. 2016; Ozkan and Gokbulak 2017), directly affecting the biology of dung beetle species (Hanski and Cambefort 1991), and modifying the structure of dung beetle community (Halffter and Arellano 2002; Costa et al. 2017). Indeed, our results show the occurrence of new species that did not occur in the control and early - stage of removal, such as; *C.* aff. *maldonadoi*, *C. unicolor* and *P. palaeno* (see Fig. 2), forming a distinct dung beetle community independent of cattle grazing. In summary, this result demonstrates that taxonomic composition is more sensitive than functional structure to cattle grazing removal.

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 (Rosenfeld 2002; Magnago et al. 2014). Thus, even with species richness reduction in the first ten years of cattle removal, the loss of functionally specialized species may not have occurred, resulting in a lack of reduction in 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 (Mlambo 2014; Beiroz et al. 2018). Thus, high intensity disturbances tend to negatively affect both taxonomic and functional components of the local biodiversity (Mlambo 2014; Magnago et al. 2014; Correa et al. 2019b). 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; Mouillot et al. 2013; Lauretto et al. 2015), our results suggest a possible maintenance of ecological functions performed by dung beetles in tropical grassy ecosystems after cattle grazing removal.

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 (Török et al. 2016; Listopad et al. 2018), in tropical grassy ecosystems this discussion is incipient (Overbeck et al. 2015; Veldmann et al. 2015). So, since the dung beetle is a considerable 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 (10 years), may be an inefficient management tool for restoration and conservation of detritus-feeding insects in tropical grassy ecosystems. We highlight a need for research on the benefit of moderate livestock grazing for the conservation of tropical grassy ecosystems. For example, research on semi-natural grassland in temperate zones (Europa) has led 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 (Török et al. 2016; Tonelli et al. 2018). In the case of Europe where the majority of native grazers have gone extinct, the continuity of grazing by domestic animals is needed (Buse et al. 2015; Tonelli et al. 2018, 2019); but in tropical grassy ecosystems it may be possible that eventually domestic animals will no longer be 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 (Bond and Parr 2010; Veldmann et al. 2015).

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Figure captions

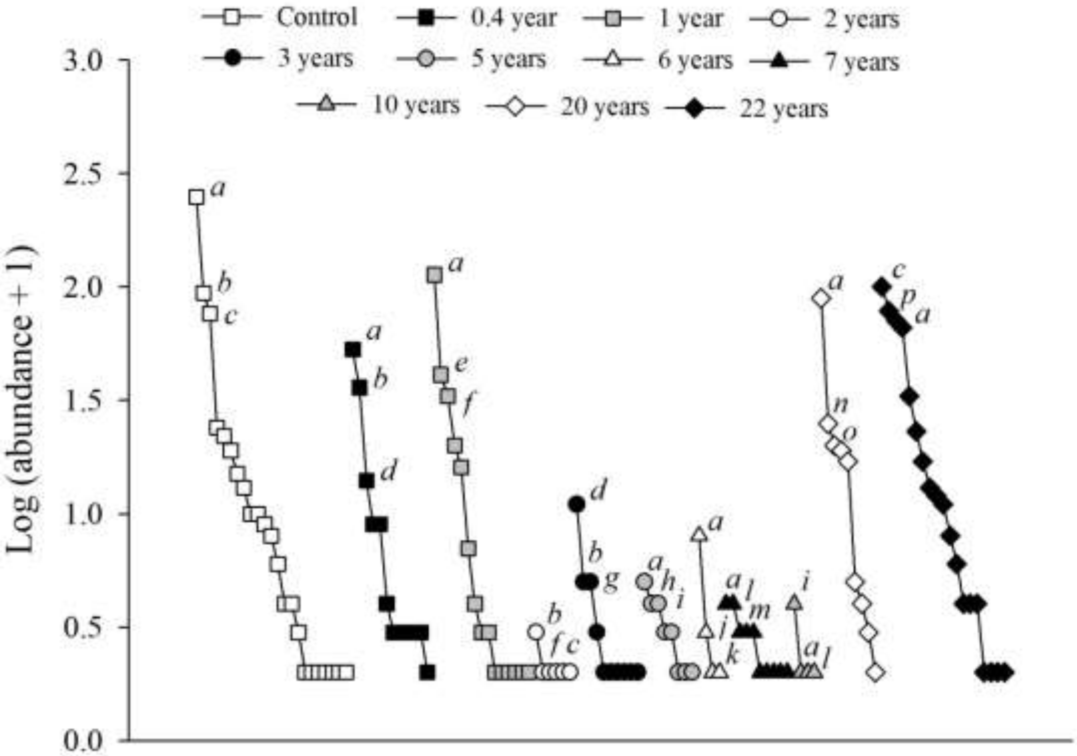
Fig. 1 Rank distribution of dung beetles species across natural grassland with different cattle removal times in a tropical grassy ecosystem. "*a*" = *Canthidium* aff. *viride*; "*b*" = *Ateuchus* sp.; "*c*" = *Canthon conformis*; "*d*" = *Digitonthophagus gazella*; "*e*" = *Genieridium bidens*; "*f*" = *Ontherus appendiculatus*; "*g*" = *Dichotomius opacipennis*; "*h*" = *Canthon cinctellus*; "*i*" = Canthon curvodilatatus; "*j*" = *Eurysternus aeneus*; "*k*" = *Onthophagus aeneus*; "*l*" = *Canthon histrio*; "*m*" = *Canthidium* aff. *refulgens*; "*n*" = *Deltochilum* aff. *komareki*; "*o*" = *Uroxys* aff. *corporaali*; "*p*" = *Canthon unicolor*.

Fig. 2 Variation in the distribution of dung beetle species occurrence (percentage) across natural grasslands with different cattle removal times in a tropical grassy ecosystem. Percentage is based in the dung beetle abundance in each natural grassland.

Fig. 3 Relationship between cattle removal time and (a) species richness, (b) number of individuals, diversity (c) and (d) biomass.

Fig. 4 Non metric multidimensional scaling 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. 5 Relationship between cattle removal time and (a) functional richness, (b) functional evenness and (c) functional dispersion.


Control
0.4 year
1 year
2 years
3 years
5 years
6 years
7 years
10 years
20 years
22 years
Log (abundance + 1)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
a
b
c
a
b
d
a
e
f
b
f c
d
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g
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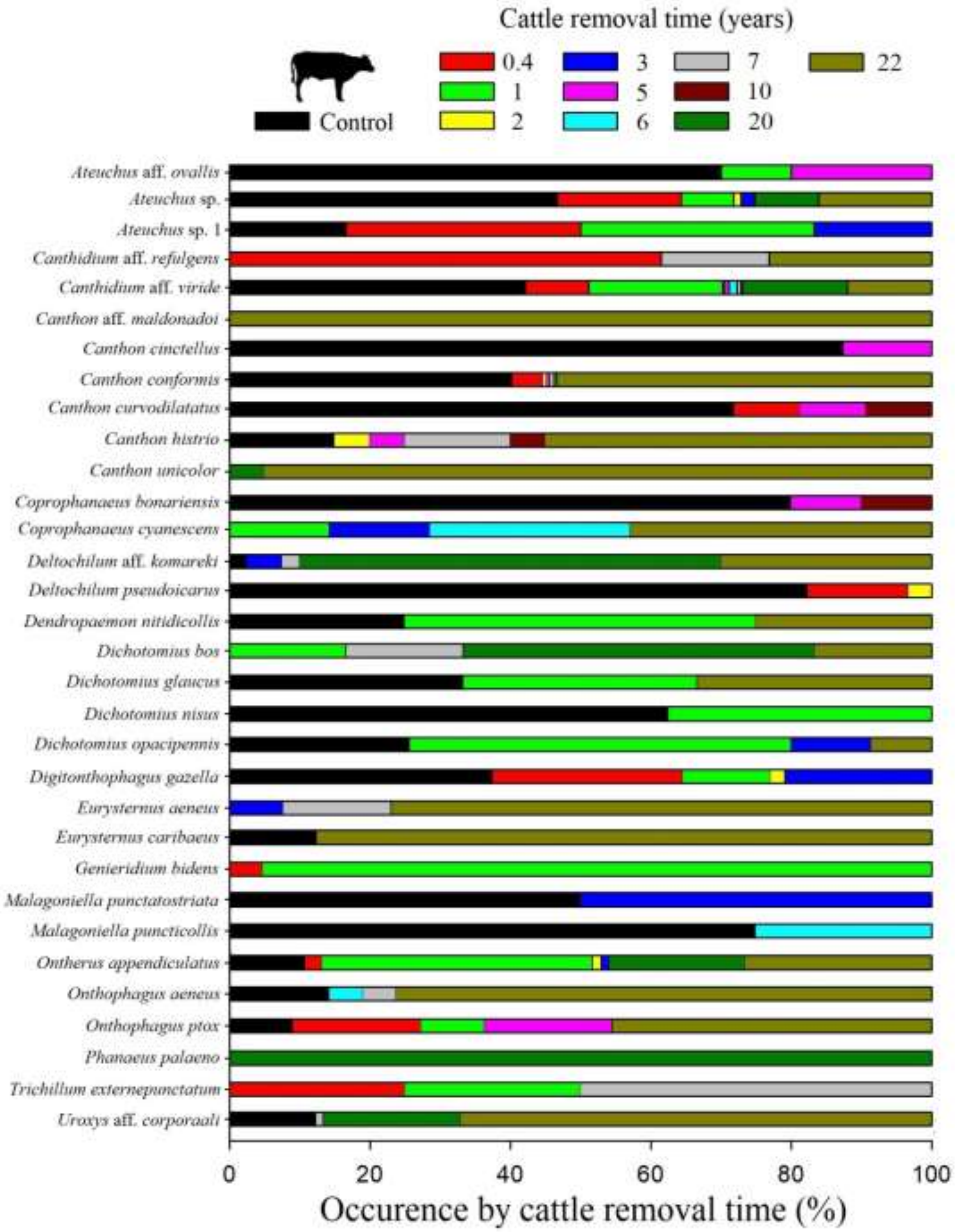
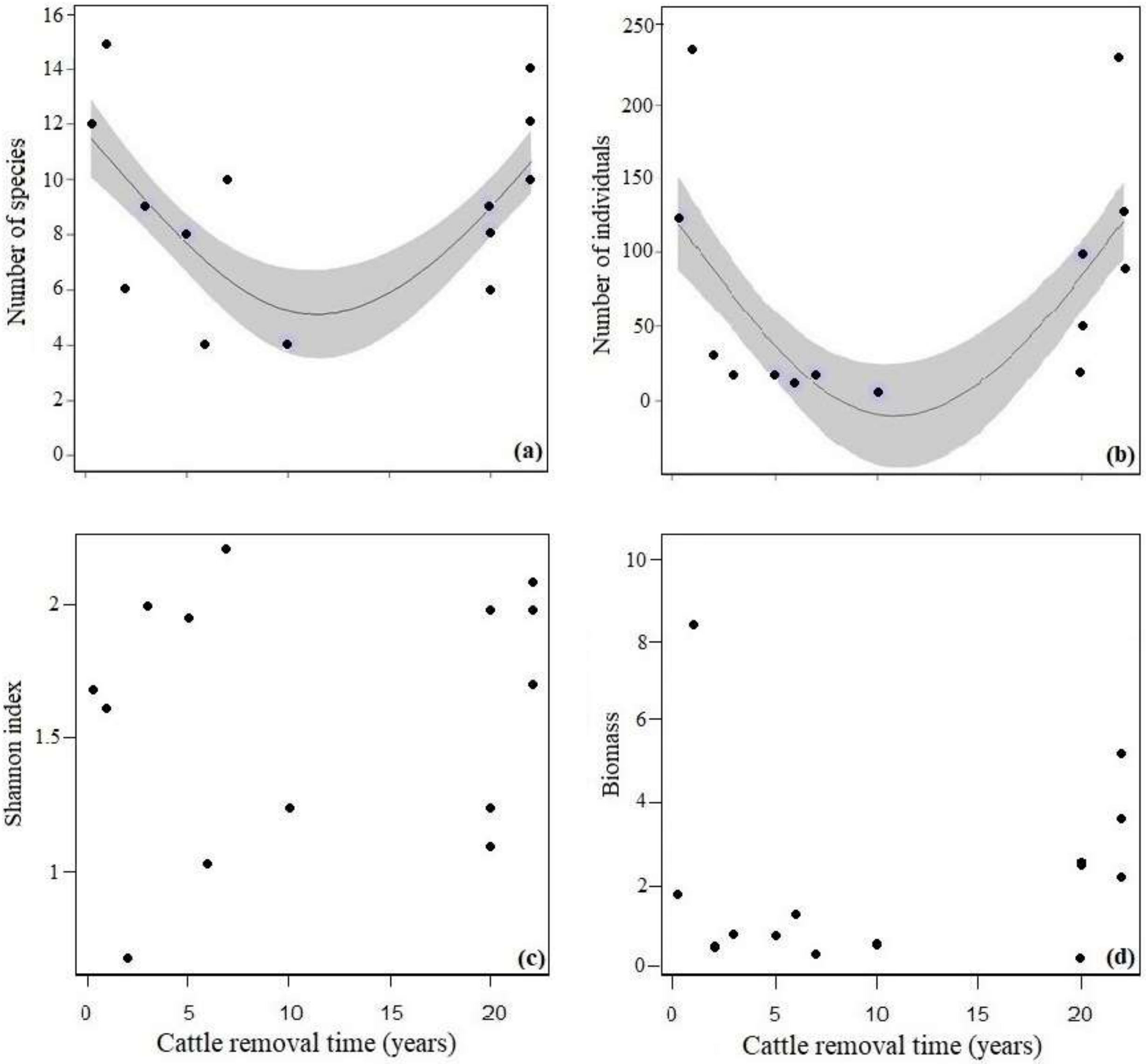
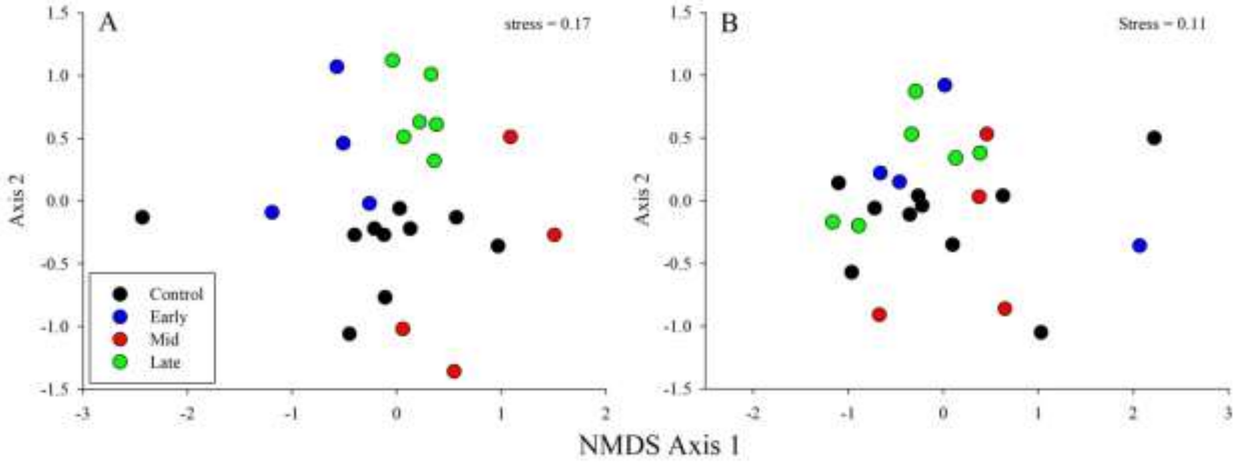
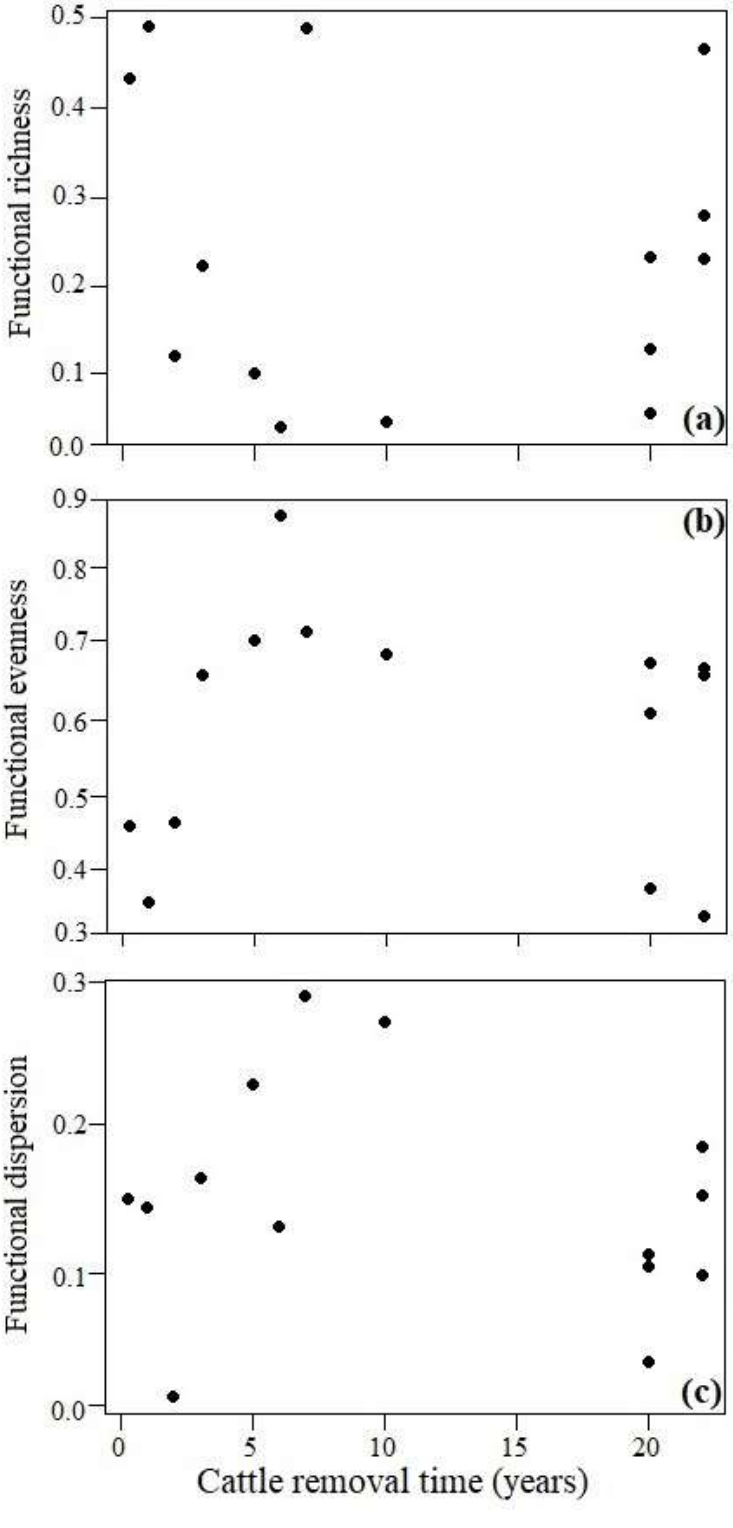

Cattle removal time (years)
Control
0.4
1
2
3
5
6
7
10
20
22
Ateuchus aff. ovallis
Ateuchus sp.
Ateuchus sp. 1
Canthidium aff. refulgens
Canthidium aff. viride
Canthon aff. maldonadoi
Canthon cinctellus
Canthon conformis
Canthon curvodilatatus
Canthon histrio
Canthon unicolor
Coprophanaeus bonariensis
Coprophanaeus cyanescens
Deltochilum aff. komareki
Deltochilum pseudoicarus
Dendropaemon nitidicollis
Dichotomius bos
Dichotomius glaucus
Dichotomius nisus
Dichotomius opacipennis
Digitonthophagus gazella
Eurysternus aeneus
Eurysternus caribaeus
Genieridium bidens
Malagoniella punctatostriata
Malagoniella puncticollis
Ontherus appendiculatus
Onthophagus aeneus
Onthophagus ptox
Phanaeus palaeno
Trichillum externepunctatum
Uroxys aff. corporaali
0
20
40
60
80
100
Occurence by cattle removal time (%)


Number of species
16
14
12
10
8
6
4
2
0
(a)
Number of individuals
250
200
150
100
50
0
(b)
Shannon index
2
1.5
1
(c)
Biomass
10
8
6
4
2
0
(d)
0
5
10
15
20
Cattle removal time (years)
Cattle removal time (years)


A
stress = 0.17
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Axis 2
-3
-2
-1
0
1
2
● Control
● Early
● Mid
● Late
B
Stress = 0.11
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Axis 2
-2
-1
0
1
2
3
NMDS Axis 1


0.5
0.4
0.3
0.2
0.1
0.0
Functional richness
(a)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
Functional evenness
(b)
0.3
0.2
0.1
0.0
Functional dispersion
(c)
0
5
10
15
20
Cattle removal time (years)

718

Table 1 Results of distance based linear models (DistLM). Response variable is dung beetle taxonomic composition and functional composition and predictor variable is cattle removal time (CRT).

	Variable	AICc	SS(trace)	Pseudo-F	P	Prop	Cumulative	res.df
	Marginal tests							
Functional	CRT	-	6599.8	1.243	0.272	0.053	-	22
Taxonomic	CRT	-	7323.5	3.534	0.001	0.138	-	22
	Sequential tests							
Taxonomic	CRT	185.75	7323.5	3.534	0.001	0.138	0.138	22

Note: Prop, Proportion of explained variation

Table 2 Permutational analysis of variance (PERMANOVA) contrasting grassland categories according to taxonomic and 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

	Taxonomic		**Functional**	
Source of variation	**Pseudo-F**	**p**	**Pseudo-F**	**p**
Grassland categories	2.94	0.001*	1.37	0.16
Post hoc comparison of systems				
Grassland categories	**T**	**p**	**T**	**p**
Control vs. late-stage of cattle removal	2.2	0.001*	1.20	0.19
Control vs. mid-stage of cattle removal	1.47	0.02*	1.09	0.28
Control vs. early-stage of cattle removal	1.2	0.12	0.84	0.57
early-stage of cattle removal vs. late-stage of cattle removal	1.68	0.003*	1.19	0.23
early-stage of cattle removal vs. mid-stage of cattle removal	1.63	0.03*	1.24	0.17
mid-stage of cattle removal vs. late-stage of cattle removed	2.05	0.003*	1.65	0.04*