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Funções ecossistêmicas realizadas por besouros coprófagos na melhoria da qualidade do solo e de gramíneas forrageiras através da remoção de fezes bovinas

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O presente trabalho em nível de mestrado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Florianópolis, 2022.

Este trabalho é dedicado:

às incríveis criaturas, objetos de estudo deste trabalho;

aos colegas pós-graduandos e pós-graduandas que insistem. E resistem.

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RESUMO

Os escarabeíneos coprófagos estão entre os organismos edáficos que promovem funções e serviços ecossistêmicos que melhoram a fertilidade do solo e desenvolvimento das plantas, evidenciando sua importância em ambientes agropecuários. O grupo funcional da espécie, se telecoprídea (roladora) ou paracoprídea (construtora de túneis), influencia sua eficiência em remover matéria orgânica. Portanto, a hipótese do presente trabalho é que rola-bostas melhoram as características do solo como consequência da remoção superficial do esterco bovino, resultando em uma melhoria no desenvolvimento das plantas, podendo se aproximar do efeito de fertilizantes minerais. Essas melhorias vão depender dos grupos funcionais envolvidos, com melhores resultados na presença de diferentes grupos, devido à complementaridade funcional. Os objetivos do trabalho foram: 1) comparar o efeito da ação de espécies de diferentes grupos funcionais, entre si, e com a aplicação de fertilizante mineral sobre a melhoria das características do solo e das gramíneas; 2) analisar o papel da remoção de fezes na melhoria das características do solo e das plantas. Para tanto, durante o verão/outono de 2021, um experimento em mesocosmos foi realizado em Florianópolis, SC, sul do Brasil, onde a gramínea *Urochloa brizantha* foi semeada com adição posterior dos tratamentos: T1) telecoprídeos + fezes, T2) paracoprídeos + fezes, T3) telecoprídeos + paracoprídeos + fezes, T4) fertilizante mineral, e C) controle com fezes bovinas. As espécies utilizadas foram *Dichotomius sericeus* (paracoprídea) e *Canthon rutilans cyanescens* (telecoprídea). A remoção de fezes foi quantificada semanalmente ao longo do experimento (12 vezes) e, ao final do mesmo, foram analisadas as características físicas, químicas e microbiológicas do solo dos vasos, além da biomassa seca e nutrientes (NPK) das folhas e raízes, e pigmentos fotossintéticos. Os dados foram analisados por meio de Modelos Lineares Generalizados. Os resultados mostram que paracoprídeos reduziram a densidade do solo em comparação com telecoprídeos, e melhoraram a agregação do solo comparados ao tratamento com fertilizante mineral. Também tiveram influência sobre o pH, teores de Mg, diminuição das concentrações e a saturação por Al e melhoria na soma e saturação de bases. Além disso, paracoprídeos foram tão eficientes quanto o fertilizante mineral na incorporação de K ao solo. Tratamentos com os insetos se destacaram no aumento do NT e da matéria orgânica, com destaque para as frações particuladas de C e N. Em relação às plantas, os tratamentos com besouros tiveram valores semelhantes ao fertilizante mineral nas concentrações foliares de P, e paracoprídeos promoveram aumentos nos conteúdos de K nas folhas e raízes da gramínea. A espécie paracoprídea foi mais eficiente na remoção das fezes bovinas, não diferindo quando sozinha ou em tratamento misto, e esta função ecossistêmica foi positivamente relacionada às quantidades de N, matéria orgânica e suas frações particuladas de C e N, P, macroagregados e à capacidade de troca de cátions do solo. Apesar de a hipótese da sinergia entre os grupos funcionais não ter sido corroborada, os resultados mostram a eficiência dos escarabeíneos, principalmente da espécie paracoprídea, na incorporação de nutrientes e na modificação de características físicas do solo, indicando a melhoria na qualidade do mesmo. Conclui-se que a remoção de fezes pode ser associada à melhoria no solo, reforçando a importância das funções ecossistêmicas realizadas por estes organismos em ambientes agropecuários, onde podem contribuir para o aumento da ciclagem de nutrientes com consequente diminuição do uso de fertilizantes minerais.

Palavras-chave: Coleoptera. Ecologia. Serviços ecossistêmicos. Matéria orgânica particulada. Scarabaeinae.

ABSTRACT

Coprophagous dung beetles are among the edaphic organisms that promote ecosystem functions and services that improve soil fertility and plant development, evidencing their importance in agricultural environments. The functional group of the species, whether telecoprid (roller) or paracoprid (tunnel builder), influences its efficiency in removing organic matter. Therefore, the hypothesis of present work is that dung beetles improve soil characteristics as a consequence of superficial removal of cattle manure, resulting in an improvement in plant development, which may approach the effect of mineral fertilizers. This improvement will depend on the functional groups involved, with better results in the presence of different groups, due to functional complementarity. The objectives of this study were: 1) to compare the effect of the action of species from different functional groups, among themselves, and with the application of mineral fertilizer on the improvement of soil and grass characteristics; 2) analyze the role of dung removal in improving soil and plant characteristics. Thus, during the summer/autumn of 2021, a mesocosm experiment was carried out in Florianópolis, SC, southern Brazil, where the *Urochloa brizantha* grass was sown with subsequent addition of the treatments: T1) telecoprids + dung, T2) paracoprids + dung, T3) telecoprids + paracoprids + dung, T4) mineral fertilizer, and C) control with cattle dung. The species used were *Dichotomius sericeus* (paracoprid) and *Canthon rutilans cyanescens* (telecoprid). Dung removal was quantified weekly throughout the experiment (12 times) and, at the end, physical, chemical, and microbiological characteristics of the soil in the pots were analyzed, in addition to the dry biomass and nutrients (NPK) of the leaves and roots, and photosynthetic pigments. Data were analyzed using Generalized Linear Models. The results show that paracoprids reduced soil bulk density compared to telecoprids, and improved soil aggregation compared with mineral fertilizer treatment. They also had an influence on pH, Mg contents, decrease in concentrations and Al saturation and improvement in the sum and saturation of bases. In addition, paracoprids were as efficient as mineral fertilizers in the incorporation of K into the soil. Treatments with insects stood out in the increase of TN and organic matter, with emphasis on the particulate fractions of C and N. Regarding plants, treatments with beetles had similar values to mineral fertilizer in leaf P concentrations, and paracoprids promoted increases in K contents in grass leaves and roots. The paracoprid species was more efficient in the removal of cattle dung, not differing when alone or in mixed treatment, and this ecosystem function was positively related to the amounts of N, organic matter and its particulate fractions of C and N, P, macroaggregates and the cation exchange capacity of the soil. Although the hypothesis of synergy between the functional groups has not been supported, the results show the efficiency of dung beetles, mainly of the paracoprid species, in nutrient incorporation and modification of physical characteristics of the soil, indicating an improvement in its quality. It is concluded that dung removal can be associated with soil improvement, reinforcing the importance of ecosystem functions performed by these organisms in agricultural environments, where they can contribute to the increase in nutrient cycling with a consequent decrease in the use of mineral fertilizers.

Keywords: Coleoptera. Ecology. Ecosystem services. Particulate organic matter. Scarabaeinae.

SUMÁRIO

1 INTRODUÇÃO

Besouros da subfamília Scarabaeinae (Coleoptera: Scarabaeidae), popularmente conhecidos como “rola-bostas”, nidificam e se alimentam, tanto adultos como larvas, em fezes (principalmente de mamíferos) e/ou carcaças (HALFFTER; MATTHEWS, 1966), auxiliando na decomposição da matéria orgânica. Devido a esses comportamentos, os besouros rola-bostas são responsáveis pela realização de várias funções e serviços ecossistêmicos, cuja eficiência varia conforme o hábito de alocação do recurso (NIERO; BATILANI-FILHO; HERNÁNDEZ, 2022; SLADE *et al.*, 2007). Paracoprídeos cavam túneis abaixo do alimento, telecoprídeos fazem bolas com o alimento e rolam até certa distância da fonte, e endocoprídeos permanecem no recurso (HALFFTER; EDMONDS, 1982). Os serviços ecossistêmicos são processos ecológicos, ou funções, que têm o potencial de gerar bens e serviços ao ser humano (DE GROOT *et al.*, 2010; DE GROOT; WILSON; BOUMANS, 2002; MEA, 2003). A economia, a saúde e o bem-estar humano são dependentes das funções e processos dos ecossistemas, que têm suporte na diversidade biológica, que, por sua vez, é importante na resiliência e resistência dos ambientes (MEA, 2005). Uma perspectiva mais recente dessa relação engloba as contribuições da natureza para as pessoas, incluindo contribuições positivas e negativas, contexto-dependentes, para a qualidade de vida do ser humano (DÍAZ *et al.*, 2018). Assim, a valorização das contribuições e dos serviços ecossistêmicos prestados pelos organismos deve ser incluída nas tomadas de decisão e nas políticas que afetam os ecossistemas, principalmente se tiverem um valor monetário direto (ARMSWORTH *et al.*, 2007; NICHOLS *et al.*, 2008). No entanto, apesar de sua importância, o papel dos rola-bostas é frequentemente ignorado nas decisões políticas e de gestão (BEYNON; WAINWRIGHT; CHRISTIE, 2015; NICHOLS *et al.*, 2008).

Uma das funções ecossistêmicas realizada pelos rola-bostas mais bem estudada é a remoção de fezes (ou seja, a taxa com a qual as fezes são removidas da superfície do solo), tanto pela facilidade de ser medida quanto por ser uma função primária e base para as demais (AMÉZQUITA; FAVILA, 2010, 2011; BATILANI-FILHO; HERNÁNDEZ, 2017; BRAGA *et al.*, 2013; DANGLES; CARPIO; WOODWARD, 2012; RAINE; SLADE, 2019; SLADE *et al.*, 2007). Ambientes agropecuários fornecem abundância de recursos a esses besouros que, por meio das atividades de alimentação e nidificação, reciclam os nutrientes (ANDUAGA, 2004; ANDUAGA; HUERTA, 2007; MENÉNDEZ; WEBB; ORWIN, 2016; ORTEGA-MARTÍNEZ; MORENO; ESCOBAR, 2016), promovendo melhorias químicas, físicas e biológicas no solo e no desenvolvimento das plantas (BANG *et al.*, 2005; BARRIOS, 2007; BEYNON; WAINWRIGHT; CHRISTIE, 2015; FINCHER; MONSON; BURTON, 1981; PENTTILÄ *et al.*, 2013; SLADE *et al.*, 2016; YAMADA *et al.*, 2007). Porém, o amplo uso de antiparasitários em bovinos têm afetado negativamente as comunidades de escarabeíneos (VERDÚ *et al.*, 2015, 2018), e, consequentemente, as funções que estes insetos realizam (CORREA *et al*., 2022; VERDÚ *et al*., 2018). Além disso, várias características influenciam nas taxas de remoção de fezes e na incorporação de matéria orgânica ao solo. Essas características podem ser da comunidade de rola-bostas, como riqueza (SARMIENTO-GARCÉS; HERNÁNDEZ, 2021), abundância (DANGLES; CARPIO; WOODWARD, 2012) e grupo funcional das espécies (BATILANI-FILHO; HERNÁNDEZ, 2017; SLADE *et al.*, 2007), características dos indivíduos, como biomassa (BRAGA *et al.*, 2013) e morfologia (DECASTRO-ARRAZOLA et al., 2020), ou do ambiente, como classe de solo (DE FARIAS; HERNÁNDEZ, 2017), tipo de recurso (AMÉZQUITA; FAVILA, 2010), e grau de perturbação do habitat (DECASTRO-ARRAZOLA *et al.*, 2020; NERVO *et al.*, 2014; ORTEGA-MARTÍNEZ; MORENO; ESCOBAR, 2016; SLADE; MANN; LEWIS, 2011). As comunidades de escarabeíneos e as funções realizadas por eles são negativamente afetadas pelas mudanças nas propriedades físicas e químicas do solo e pela intensidade de uso do mesmo (ALVARADO; DÁTTILO; ESCOBAR, 2019; BRAGA *et al*., 2013; BROWN *et al*., 2010; DE FARIAS *et al.*, 2015; DE FARIAS; HERNÁNDEZ, 2017). A perda e conversão de habitats naturais diminui a abundância, riqueza e biomassa desses organismos (BRAGA *et al*., 2013; CORREA; PUKER; ABOT, 2020; MACEDO *et al.*, 2020; SARMIENTO-GARCÉS; HERNÁNDEZ, 2021). Sendo assim, a redução dos escarabeíneos em ambientes de pastagem pode ter efeitos adversos na economia pecuária pela perda dos serviços ecossistêmicos prestados, que chegam a valores anuais de £ 367 milhões no Reino Unido (BEYNON; WAINWRIGHT; CHRISTIE, 2015) e USD 380 milhões nos EUA (LOSEY; VAUGHAN, 2006).

A pecuária é um importante setor socioeconômico no Brasil (MAPA, 2022), que tem destaque na produção e exportação de carne bovina (IBGE, 2018a). A demanda crescente por áreas de pastagem para o rebanho bovino tem levado ao aumento da conversão de ecossistemas naturais em vários biomas do país (IBGE, 2018b), homogeneizando as paisagens com a plantação de gramíneas. No estado de Santa Catarina, na região sul do Brasil, a produção pecuária é significativamente caracterizada por pequenas propriedades com predomínio de criação extensiva (GIEHL *et al*., 2019), normalmente rodeadas por fragmentos florestais em menor ou maior grau de conservação (RIBEIRO *et al*., 2009). Santa Catarina detém 22,8% de sua vegetação original de Mata Atlântica (FUNDAÇÃO SOS MATA ATLÂNTICA; INPE, 2021) formando uma paisagem em mosaico que permite a manutenção de muitas espécies nativas. Algumas destas espécies, mais tolerantes, podem se deslocar entre as manchas de mata ao atravessarem e/ou utilizarem recursos na matriz agropecuária, como é o caso das comunidades de rola-bostas (DE FARIAS *et al.*, 2015; SARMIENTO-GARCÉS; HERNÁNDEZ, 2021).

As gramíneas forrageiras do gênero *Urochloa* (*Brachiaria*) spp. são frequentemente utilizadas nesses ambientes como fonte de alimentação para os bovinos (ALVIM; BOTREL; XAVIER, 2002; CRISPIM; BRANCO, 2002). No entanto, as espécies de braquiária utilizadas são exóticas, naturais do continente africano, e algumas possuem um alto potencial invasor, principalmente em campos rupestres e cerrados (ALVIM; BOTREL; XAVIER, 2002; CRISPIM; BRANCO, 2002). Além disto, há registros de algumas delas serem tóxicas para o gado (ALVIM; BOTREL; XAVIER, 2002; GAVA *et al.*, 2010), e não se sabe como os besouros rola-bostas podem ser afetados por essa interação. Em relação ao manejo, a aplicação de fertilizantes minerais é uma prática comum para o desenvolvimento das gramíneas (BARCELOS *et al.*, 2011; COSTA; OLIVEIRA; FAQUIN, 2006; PRIMAVESI *et al.*, 2003), mesmo que a utilização desse tipo de adubação seja insustentável (SANTOS *et al.*, 2022). As plantas assimilam a maioria dos nutrientes necessários das reservas do solo, de fertilizantes minerais ou adubos orgânicos adicionados (ISHERWOOD, 2000). O uso de fertilizantes minerais pode solucionar a falta de nutrientes perdidos por lixiviação, forma gasosa ou por competição com a população microbiana do solo. Porém, fertilizantes podem causar o esgotamento e perda de nutrientes por erosão, poluição das águas por escoamento, inibição de fixação de nitrogênio atmosférico e aumento da mineralização da matéria orgânica do solo por microrganismos (ISHERWOOD, 2000).

A fertilização do solo com o uso de fezes de animais pode ser uma alternativa ao uso de fertilizantes minerais, pois possuem macro e micronutrientes essenciais ao desenvolvimento de plantas como as gramíneas (LOSS *et al.*, 2022). Além da melhoria na produtividade das culturas, a utilização de fezes animais promove a ciclagem de nutrientes, redução de custos e melhoria na qualidade do solo (LOSS *et al.*, 2022; SANTOS; NOGUEIRA, 2012). Também pode diminuir a quantidade de dejetos estocados, uma vez que parte deles pode ser usada como fonte de nutrientes para adubação de pastagens e/ou lavouras, diminuindo os prejuízos à produção agropecuária (FINCHER; MONSON; BURTON, 1981; LOBO; VEIGA, 1990;

MARIATEGUI *et al.*, 2001). Invertebrados de solo, como os rola-bostas, podem auxiliar o processo de fertilização com fezes ao transportar a matéria orgânica abaixo da superfície. Um solo saudável, rico em nutrientes, suficientemente poroso e com alta biodiversidade pode regular processos ambientais tanto em ecossistemas naturais quanto em agroecossistemas (ALTIERI; NICHOLLS, 2003; BARRIOS, 2007). Mas a conversão de sistemas naturais, como florestas nativas, em sistemas de uso da terra com a intensificação da agropecuária, modifica as características do solo, podendo diminuir sua biodiversidade. Isso leva a uma capacidade reduzida de autorregulação do agroecossistema, com menor capacidade dos ambientes naturais de fornecer serviços ecossistêmicos e, portanto, a uma dependência maior de insumos externos e a uma menor resiliência (BARRIOS, 2007).

A importância dos rola-bostas se traduz na eficiência de incorporação de nutrientes, que pode rivalizar com determinadas concentrações de aplicação de fertilizante mineral sobre a produtividade de gramíneas (FINCHER; MONSON; BURTON, 1981; MIRANDA; DOS SANTOS; BIANCHIN, 2000). As melhorias nas condições do solo e de pastagens promovidas por esses organismos são bem documentadas (BANG *et al.*, 2005; BARRIOS, 2007; BEYNON; WAINWRIGHT; CHRISTIE, 2015; FINCHER; MONSON; BURTON, 1981; YAMADA *et al.*, 2007; YOKOYAMA *et al.*, 1991), e podem amplificar os efeitos da fertilização por fezes, uma vez que a fauna edáfica participa de vários processos importantes no solo (BARRIOS, 2007; MUMMEY; RILLING; SIX, 2006; SALTON *et al.*, 2008). Desta forma, e diante da problemática do uso de fertilizantes minerais, levando-se em conta o potencial que os rola-bostas possuem de fertilizar o solo e causar melhorias nas plantas, o presente trabalho buscou mensurar o efeito da ação dos besouros, ao utilizarem as fezes bovinas, na fertilização do solo, e relacionar a remoção superficial de fezes com a incorporação e absorção de nutrientes por gramíneas forrageiras.

1.1 OBJETIVOS

1.1.1 Objetivo Geral

Avaliar e comparar a eficiência entre grupos funcionais distintos de besouros rola-bostas, e com fertilizante mineral, sobre a melhoria de características do solo e de gramíneas, relacionando essa possível melhoria com a incorporação de matéria orgânica realizada pelos besouros.

1.1.2 Objetivos Específicos

1. Avaliar e comparar a eficiência na realização de funções ecossistêmicas de telecoprídeos e paracoprídeos entre si, quando em conjunto, e com fertilizante mineral, sobre a melhoria de características do solo e desenvolvimento de gramíneas.

2. Relacionar a quantidade de fezes incorporadas pelos besouros com as características físicas, químicas e biológicas do solo e desenvolvimento das gramíneas.

2 CAPÍTULO 1

Artigo formatado de acordo com as normas da revista *Agriculture, Ecosystems and Environment*

The efficiency of dung beetles in improving soil and forage grasses by incorporating nutrients through the removal of cattle dung

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ABSTRACT

Coprophagous dung beetles provide important ecosystem services in improving the quality of soil and plant development in agricultural environments due to the availability of nutrients from the dung removal. Our objective was to compare the effect of dung removal performed by two species of different functional groups, among themselves and with the application of mineral fertilizer, on the improvement of soil and forage grasses characteristics. We hypothesized that 1) dung beetles improve soil characteristics as a consequence of dung removal, improving plant development, which may approach the effect of mineral fertilizers, 2) this increase varies according to the functional group, with better results when they act together, due to functional complementarity. To test the hypotheses, an experiment in mesocosms was conducted in Florianópolis, SC, southern Brazil, during the summer/autumn of 2021, with the sowing of *Urochloa brizantha* in the treatments: 1) telecoprid species (*Canthon rutilans cyanescens*), 2) paracoprid species (*Dichotomius sericeus*), 3) the two species together, 4) mineral fertilizer, and a control with cattle dung only. Dung removal was quantified weekly, and, at the end of the experiment, the soil's physical, chemical, and microbiological characteristics were analyzed, in addition to the dry biomass and macronutrients (NPK) of the leaves and roots, and photosynthetic pigments of grasses. The results show that the paracoprid species decreased the soil bulk density and improved its aggregation, influencing the pH and Mg contents, with a reduction in Al levels and consequent increase in the sum and saturation of bases. Paracoprids were also as efficient as mineral fertilizer in incorporating K into the soil. The dung beetles, in general, stood out in the increase in TN and organic matter contents and its particulate fractions of C and N. Concerning the plants, treatments with beetles had values similar to mineral fertilizer in the foliar concentrations of P, and paracoprids promoted increases in the K contents in the leaves and roots of the grass. The paracoprid species was more efficient in removing cattle dung, which was positively related to the amounts of N, organic matter, and its particulate fractions, P, macroaggregates, and the CEC of the soil. We can conclude that the dung removal can be associated with improvement in the soil, mainly by the action of paracoprids, reinforcing the importance of the ecosystem functions performed by these organisms in agricultural environments, where they can contribute to the increase in nutrient cycling with a consequent decrease in the use of mineral fertilizers.

Keywords: Nutrient incorporation. Dung removal. Ecosystem functions. Scarabaeinae.

1. Introduction

Livestock is an important socioeconomic sector in Brazil, having reached, in 2021, a production of R$ 381 billion, of which R$ 158 billion with cattle breeding (MAPA, 2022). Currently, the country is the main exporter and the world's second-largest cattle meat producer (IBGE, 2018a). Forage grasses of the genus *Urochloa* (*Brachiaria*) sp. have been used as food for cattle herds for their nutritional content and good adaptation to Brazilian soils. Brazil has 112 million hectares of planted pastures (IBGE, 2017), which require fertilization due to low natural fertility soils and excessive grazing and pest incidence (Barcelos et al., 2011; Costa et al., 2006; Primavesi et al., 2003). Nonetheless, the applications of mineral fertilizers are often carried out inefficiently (mainly due to inappropriate use and in large quantities), besides being unsustainable, as they do not self-regulate, depend on constant external factors, and do not respond to environmental changes (Barrios, 2007; Isherwood, 2000; Primavesi, 1994). The use of animal manure as a source of nutrients in agricultural crops is an alternative or complement to mineral fertilizers, promoting nutrient cycling, cost reduction, and improvement in soil quality (Loss et al., 2022; Santos and Nogueira, 2012). Cattle dung is rich in macro and micronutrients (Loss et al., 2022), essential for the productivity of forage grasses. It is estimated that about half of cattle's ingested returns to the soil surface as dung, composed of vegetable matter, metabolism by-products, and large amounts of dead microorganisms with high moisture content (Lobo and Veiga, 1990). The use of animal dung is also a way to use the excess pasture waste because the large production of dung by cattle (which can reach 28 kg/day/animal; Mariategui et al., 2001), if not incorporated into the soil, causes a rejected area of cattle feeding, in addition to a direct impediment to the growth of grasses (Fincher et al., 1981). This can cause ecological and economic problems, with loss of pasture areas, the incidence of pests, and higher spending on mineral fertilization (Lobo and Veiga, 1990). Besides plant productivity, dung fertilization improves several physical, chemical, and microbiological aspects of the soil, such as the increase in organic matter and its organic carbon (C) and nitrogen (N) fractions, which reflects the increase in biological activity and soil aggregation, with consequent decrease in soil bulk density (Loss et al., 2021; Santos et al., 2022; Yagüe et al., 2012). The nutrients in dung are transferred to the soil in a water-soluble state by the action of rain or transported as dung pellets by the soil fauna (Yamada et al., 2007). In this process, edaphic organisms, like earthworms and many insect orders perform ecological processes essential for maintaining ecosystems (Barrios, 2007).

Soil is the regulatory center of nutrient cycling processes, and soil invertebrates perform this activity mainly through the fragmentation and reallocation of organic matter below the surface, causing biological, physical, and chemical changes and contributing to the process of nutrient mineralization by microorganisms (Barrios, 2007; Nichols et al., 2008). Among the soil invertebrates contributing to dung fertilization are the beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). The introduction of cattle in the Americas allowed some dung beetles to use cattle dung as a food resource, even in exotic pastures (Huerta et al., 2018; Louzada and Silva, 2009). These beetles nest and feed adults and larvae in dung (mainly mammals) and/or carcasses (Halffter and Matthews, 1966), assisting in the decomposition of organic matter. They are divided into functional groups according to the type of food allocation: paracoprids bury the resource in tunnels or galleries below the source, telecoprids form balls with the food, which can be buried near or rolled up to a certain distance from the source, and endocoprids feed and nest directly at the source (Halffter and Edmonds, 1982). Dung removal, the rate at which dung is removed from the soil surface, is one of the most beneficial ecological functions of dung beetles in livestock landscapes and may reduce dung degradation time by more than 80% (Cruz et al., 2012). Thus, dung beetles are part of nature's contributions to people, economically contribute to livestock in maintaining clean areas, besides incorporating nitrogen as a fertilizer (Díaz et al., 2018; Lopez-Collado et al., 2017). Some studies even indicate that dung beetles can rival the application of mineral fertilizers in grass productivity due to dung incorporation (Fincher et al., 1981; Miranda et al., 2000). Although dung removal is not always a good proxy for other ecosystem functions, such as soil excavation and seed dispersal (Carvalho et al., 2020), dung beetles present in livestock environments provide crucial contributions, ecosystem functions and services when feeding on cattle dung and recycling nutrients (Anduaga, 2004; Anduaga and Huerta, 2007; Díaz et al., 2018; Menéndez et al., 2016; Ortega-Martínez et al., 2016). They promote bioturbation and improvement of soil fertility and aeration (Bang et al., 2005; Barrios, 2007), increase pasture productivity (Bang et al., 2005; Beynon et al., 2015; Fincher et al., 1981; Yamada et al., 2007), decrease of nitrogen loss by volatilization (Yokoyama et al., 1991a), biological pest control in cattle (Braga et al., 2012), and modification of flows and reduction of livestock greenhouse gases (Penttilä et al., 2013; Slade et al., 2016).

The growing demand for pasture areas for livestock has led to an increase in the conversion of natural ecosystems in several biomes in the country (IBGE, 2018b). The state of Santa Catarina, in southern Brazil, is historically characterized by small properties with extensive cattle ranching (Giehl et al., 2019) with fragments of Atlantic Forest remnants corresponding to 22.8% of the original cover (Fundação SOS Mata Atlântica and INPE, 2021; Ribeiro et al., 2009). The loss and conversion of natural habitats negatively affects dung beetle communities, decreasing the richness, abundance, and rates of dung removal (Alvarado et al., 2019; Anduaga, 2004; Braga et al., 2013; Correa et al., 2020; De Farias et al., 2015; De Farias and Hernández, 2017; Horgan, 2008; Macedo et al., 2020; Sarmiento-Garcés and Hernández, 2021; but see Ortega-Martínez et al., 2021). The lower diversity found in pastures compared to forest environments indicates that, despite the abundance of food, this environment is unsuitable for most native species since many of them are evolutionarily adapted to forest conditions (Anduaga, 2004). The replacement of natural pastures with exotic ones also has effects on dung beetle communities, with changes in species composition and diversity (Almeida et al., 2011; Correa et al., 2021; Macedo et al., 2020). The decrease in environmental complexity and the increase in the intensity of the management practice negatively affect the richness of these organisms (Almeida et al., 2011; De Farias et al., 2015). Thus, environmental filters in pastures favor species that consume herbivorous dung or are habitat generalists (Almeida et al., 2011; Macedo et al., 2020), limiting the carrying capacity of these environments. Brazilian pastures have 76 dung beetle species, 42 paracoprids, and 15 telecoprids (Tissiani et al., 2017), but this number may be higher. Paracoprid species of large body size and that occur in abundance are responsible for removing large amounts of dung in pastures (Ortega-Martínez et al., 2021). Still, the intensification of management in agricultural environments reduces the biomass of dung beetles, which affects the dung removal function (Alvarado et al., 2019; Sarmiento-Garcés and Hernández, 2021). This is mainly due to the loss of these larger species (Braga et al., 2013; Dangles et al., 2012). Thus, changes in dung beetle assemblages can alter the functioning of ecosystems (Alvarado et al., 2019; Buse and Entling, 2020; Slade et al., 2007) and may harm the livestock economy by the loss of contributions and ecosystem services provided by these organisms (Beynon et al., 2015; Díaz et al., 2018; Losey and Vaughan, 2006).

Besides the influence of habitat on performance in carrying out ecosystem functions by dung beetles, the wide use of antiparasitics in cattle also has negative effects on beetle communities (Verdú et al., 2018, 2015), decreasing the richness, abundance, and biomass of beetles in pastures (Kavanaugh and Manning, 2020; Sands and Wall, 2018; Verdú et al., 2018, 2015). Paracoprids are more sensitive than other functional groups (Sands and Wall, 2018; Verdú et al., 2018), and given their importance in livestock environments, there may be a significant loss of ecosystem functions that support agricultural production (González-Tokman et al., 2017; Kavanaugh and Manning, 2020).

Habitat disturbance is one of several extrinsic factors that affect the performance of ecosystem functions by dung beetles (Amézquita and Favila, 2010; Batilani-Filho and Hernández, 2017; Braga et al., 2013; Dangles et al., 2012; De Farias and Hernández, 2017; deCastro-Arrazola et al., 2020; Nervo et al., 2014; Ortega-Martínez et al., 2016; Slade et al., 2007, 2011). Other factors are soil class (Davis, 1996; De Farias et al., 2015; De Farias and Hernández, 2017), resource type (Amézquita and Favila, 2010), seasonality (Amore et al., 2018), and environmental variables (Davis, 1996; Sarmiento-Garcés and Hernández, 2021). Among the intrinsic factors are identity (Piccini et al., 2019), richness (Sarmiento-Garcés and

Hernández, 2021) and abundance of species (Dangles et al., 2012), size and biomass of individuals (Braga et al., 2013; Carvalho et al., 2018; Dangles et al., 2012; Davis, 1996), morphological characteristics (deCastro-Arrazola et al., 2020), and functional group (Amézquita and Favila, 2011, 2010; Batilani-Filho and Hernández, 2017; Braga et al., 2013; Dangles et al., 2012; Niero et al., 2022; Slade et al., 2007). As already mentioned, nocturnal and larger body size paracoprids are important in carrying out ecosystem functions (Nervo et al., 2014; Piccini et al., 2019; Slade et al., 2007), including in livestock environments (Almeida et al., 2011; De Farias et al., 2015; Ortega-Martínez et al., 2021; Tissiani et al., 2017). Nevertheless, several studies have shown that heterogeneous communities have greater functional capacity (Menéndez et al., 2016) by increasing (Yoshihara and Sato, 2015) or decreasing competition (De Oca and Halffter, 1995) as the presence of different groups promotes greater facilitation and division of resources (Nervo et al., 2014).

Considering the importance of livestock activity in Brazil, it is important to understand how the components of biodiversity affect the functioning of the ecosystem and can contribute to the natural fertilization of environments. Studies have shown that paracoprids and telecoprids play important roles in pasture environments, improving soil characteristics and plant development and productivity, including comparing their efficiency with mineral fertilizer. However, we are unaware of a study comparing the performance of the two functional groups, either alone or together, with the effect of mineral fertilizer application. Thus, this study aimed to compare the efficiency between distinct functional groups of dung beetles, among themselves and with mineral fertilizer, in improving soil physical, chemical, and microbiological conditions and in grasses development, and measure the role of dung removal in these ecosystem functions. Through an experiment in mesocosms, we sought to test the hypothesis that dung beetles of different functional groups have different efficiencies in removing cattle dung, unequally contributing to the improvement of soil conditions and plant development. Nonetheless, acting together and by functional complementarity, the action of both groups could approach the effect of mineral fertilizer, a product of the incorporation of organic matter by dung removal.

2. Material and Methods

2.1. Experimental design

To evaluate the action of dung beetles on physical, chemical and microbiological characteristics of the soil and on the development of grasses, an experiment in mesocosms was carried out from December 2020 (beginning of summer) to June 2021 (end of autumn) at the Center of Biological Sciences of the Federal University of Santa Catarina (CCB/UFSC), in Florianópolis, SC, southern Brazil (27°35’52.824”S; 48°30’53.929”W). According to the Köppen classification, the climate of the region is Cfa, humid subtropical (mesothermic), with hot summers (mean of 25 °C), without a dry season and with well-distributed rainfall throughout the year with an annual mean of around 1500 mm (Veloso et al., 1991). The experiment initially consisted of 50 pots, in which soil and grass seeds were added and, subsequently, treatments with beetles and mineral fertilizer. The plastic pots had a capacity of 11 l (27 cm in diameter and 24 cm in height), with lower openings protected with double tulle fabric internally and externally, avoiding the exit of soil and beetles but allowing the flow of surplus water (Fig. S1). Each pot was filled with soil up to 5 cm from the upper edge using samples of Typic Hapludult soil (Soil Survey Staff, 2014), with a loamy texture (Teixeira et al., 2017). The soil was collected in the county of Paulo Lopes/SC, Brazil, from the mixture of horizons A and B, sieved at 4 mm, and homogenized. The granulometric analysis indicated 20.6% of clay, 43.24% of sand, and 36.13% of silt. The other physicochemical characteristics of the initial soil are shown in Table S1. The parameters to be measured were based on the literature, whether those already measured by other works, or those with potential to be explored, but still with few studies on. Initial soil bulk density and aggregation analyses were obtained from the mean of four subsamples collected from each soil horizon (Table S1). Chemical analyzes (pH, Al, Ca, Mg, K and P) were performed according to the methodology described in Tedesco et al. (1995). Subsequently, the sum of bases, aluminum and base saturation and cation exchange capacity were calculated as described in CQFS RS/SC (2016). The physical, microbiological, and granulometric fractionation of organic matter were performed as described in item 2.3.

The forage grasses of the species *Urochloa* (*Brachiaria*) *brizantha* (cv. Marandu, 2017/2018 harvest) were sown in two stages: first, 20 seeds in December 2020, and, as the seedlings had difficulty germinating, another 15 g of seeds per replicate in January 2021

(Table S1). To assist in the emergence of seedlings, all pots had the application of 100 ml of Hoagland and Arnon's solution (1950). Due to the differences in sowing dates and the number of plants per pot, they were categorized as larger or smaller than 10 cm. The plants were transplanted between the pots, so each container had five larger plants and three smaller ones when the other components were added. In each pot a nylon screen with 16 x 16 mm mesh and 31 BWG thread was placed, sewn with string, fastened with elastic to the pot, and supported by three metal rods to prevent colonization by other insects and prevent the beetles from escaping, being removable for handling (Fig. S1). The pots were kept in open and outdoor conditions, with a transparent plastic tarp as a cover against the incidence of rain and were watered as needed by the plants. The average daily temperature during the experiment was 23.18 ^{o}C, ranging from 7.86 ^{o}C to 33.90 ^{o}C, with an accumulated precipitation of 1267.47 mm, ranging from 0 to 116.21 mm daily (Epagri, 2020). When all plants had a minimum height of 10 cm, the treatments were drawn, randomized, and received the other components (Table S2).

The number of replicates analyzed varied according to the survival of the plants at the end of the experiment (Fig. S1). The treatments consisted of: T1) telecoprid beetles + dung (n = 9), T2) paracoprid beetles + dung (n = 6), T3) telecoprid beetles + paracoprid beetles + dung (mixed; n = 5), T4) mineral fertilizer (n = 4) and control with dung only (C; n = 8). Due to the ease of collection in the study region and laboratory maintenance, the dung beetle's species used as models were *Canthon rutilans cyanescens* (Harold 1868), representing the telecoprids, and *Dichotomius sericeus* (Harold 1867), representing the paracoprids. Both are coprophagous and without evident sexual dimorphism, the first diurnal and small-sized (less than 1 cm), and the second nocturnal and medium-sized (between 1 and 2 cm; Hernández et al., 2019). Individuals of these species are abundant in Atlantic Forest areas in southern Brazil nevertheless can be found in agricultural environments (De Farias and Hernández, 2017). The beetle sampling for the experiments were conducted in Florianópolis, SC, between January and May 2021. Pitfall traps for live insects were baited with domestic dog feces from the UFSC Central Animal Research Facility. The beetles were kept in the laboratory under constant temperature and relative humidity conditions until they were used in the experiment, fed on domestic dog feces every four or five days. The mean wet weight of *D. sericeus* is 0.46 g, and of *C. rutilans cyanescens*, 0.17 g. That is, in terms of biomass, 1 individual of *D. sericeus* corresponds to 2.7 individuals of *C. rutilans cyanescens*. Based on these data and to exclude the interference of biomass between treatments, 16 telecoprids (2.72 g) were used in each T1 replicate, 6 paracoprid individuals (2.76 g) in each T2 replicate, and 8 telecoprids + 3 paracoprids (2.74 g) in each T3 replicate, totaling a mean of 2.74 g of beetles per mesocosm. Individuals found dead on the soil surface during the experiment were replaced. There was no increase in the number of individuals per replicate during the period.

To provide a common resource in livestock environments, the dung provided for the treatments was cattle dung from the UFSC Experimental Ressacada Farm. The dung was collected fresh and without beetles from January to May 2021 from animals not treated with ivermectin to reduce the effect of this antiparasitic on the dung beetle behavior. After dung collection, they were homogenized and frozen in individual portions of 150 g, completely thawed before being added to the treatments. A dung sample was collected in October 2021 for physical and chemical characterization, with the following parameters being verified, according to the methodology described in Tedesco et al. (1995): pH = 7.4, humidity (65 ºC) = 80.69, P_2O_5 = 0.64%, K_2O = 0.59%, Ca = 0.1%, Mg = 0.08%, C = 37.73%, N = 1.41%. The Farm's bovine herd consists of 58 animals fed during the evaluated period with pasture (forage grasses) and mineral supplementation in the trough.

The chemical fertilizer followed the regional recommendations (CQFS RS/SC, 2016), with an application of 1.1 g of KCl + 1.53 g of triple superphosphate (TSP)/pot and three applications of 0.24 g of urea (CH_4N_2O)/pot (Table S2). Thirteen weeks after adding the beetles to the treatments, soil and plant samples were collected for physical, chemical and microbiological analyzes (Table S2). The plants did not sprout during this period of time.

2.2. Dung removal

Weekly, 150 g of cattle dung was supplied to each replicate of the treatments with beetles (T1, T2, and T3), always placed in the same location of the container, on a plastic screen with 2 x 2 cm mesh opening. In pots with more than 10 individuals, dung was divided into two portions on two 7 x 9 cm mesh, while in pots with less than 10 individuals, a single portion was added to the 10 x 11 cm mesh. Dung removal was quantified during dung exchange once a week (except in the first one), totaling 12 independent measurements. The removal calculation was made by the difference between the wet mass initially supplied to the treatments and the final mass remaining on the soil surface. The eight control pots received the same weekly amounts of dung and served to estimate the loss of dung moisture due to evaporation, whose weekly mean was deducted in the removal calculation (Slade et al., 2007).

2.3. Soil analyses

At the end of the experiment, in each pot, physical, chemical, and microbiological characteristics of the soil were analyzed to understand how these characteristics can be modified by the entry of organic matter from the action of beetles in the dung removal. Soil bulk density, related to total porosity and mean organic and mineralogical composition, was evaluated using the volumetric ring method (Teixeira et al., 2017), using a 50 cm^3 Kopeck ring. The analysis of the size and stability of wet aggregates was performed according to Teixeira et al. (2017). After the collection of soil bulk density and microbiology samples, the remainder of the soil up to 10 cm deep in the pots was used to analyze aggregates, an unmeasured variable when it comes to dung beetles. The samples were air dried and manually pounded to break up clods, passing through 8.0 mm and 4.0 mm sieves to obtain the aggregates. The soil aggregates retained in the 4.0 mm sieve were separated for later stability evaluation. The remaining material that passed through the 4.0 mm sieve was macerated and passed through a 2.0 mm mesh to carry out chemical analysis of the soil, according to the methodology of Tedesco et al. (1995). From the samples of aggregates retained on the 4.0 mm sieve, 25 g were weighed and transferred to a set of sieves with decreasing mesh diameter, being 2.0, 1.0, 0.50, 0.25, 0.105 and 0.053 mm. Subsequently, the set of sieves was subjected to vertical wet sieving for 15 minutes in the Yoder apparatus (Yoder, 1936). After this time, the material retained in each sieve was removed, separated with a water jet, placed in previously weighed and identified aluminum crucibles, and taken to a forced air circulation oven at 105 °C until a constant dry mass was obtained. With these data, the weighted mean diameter (WMD) and geometric mean diameter (GMD) aggregation indices of aggregates were calculated (Claessen et al., 1997), as well as the distribution of aggregates in the mean diameter classes: $8.0 > Ø \geq 2.0$ mm (macroaggregates), $2.0 > Ø \geq 0.25$ mm (mesoaggregates) and $Ø < 0.25$ mm (microaggregates) (Costa Junior et al., 2012). The higher the percentage of aggregates retained in sieves with larger meshes, the greater the WMD is, and the GMD represents an estimate of the size of the most frequent class of aggregates (Loss et al., 2022).

The methods used for the chemical analysis of soil samples were those described in Tedesco et al. (1995). The pH was measured by the potentiometric method in 1:1 water (v:v) and organic matter (OM) and total organic carbon (TOC) by sulfochromic digestion (Walkley and Black, 1934) and titration. The available phosphorus (P) was determined by Mehlich I solution extraction for later determination by colorimetry, according to Murphy and Riley (1962). Potassium (K) was extracted by Mehlich I and determined by flame photometry (Analyser 910M). The exchangeable cations aluminum (Al), calcium (Ca), and magnesium (Mg) were quantified by extraction with KCl 1 mol L^{-1} solution and the reading of extracts made by atomic absorption spectrophotometry. Potential acidity (H + Al) was estimated by the SMP method using the buffer solution performed according to Raij and Quaggio (1983). The cation exchange capacity (CEC) at pH 7.0 was estimated by the sum of cations (Ca + Mg + K + H + Al) and the effective CEC by the sum of the cations, with the absence of H^{+}. The aluminum saturation was obtained by dividing (Al^{+3} x 100) by the effective CEC (Teixeira et al., 2017). The base saturation was calculated by dividing the sum of bases (SB = Ca + Mg + K) and $CEC_{pH7.0}$. Total nitrogen (TN) was determined by the Kjeldahl method (1883). The granulometric fractionation of OM, another analysis little related to dung beetles, was carried out according to Cambardella and Elliott (1992) by stirring in sodium hexametaphosphate solution 5 g L^{-1} and further sieving at 53 μm to separate the OM retained in the sand fraction from the silt and clay fraction. After drying at 50 °C, the material that was retained on the 53 μm sieve, which consists of particulate organic carbon and nitrogen (POC and PON) were ground in porcelain gral, sieved at 100 mesh (150 μm), and determined in an elementary dry combustion analyzer (FlashEA 1112 Thermo Finnigan model) at the Carbon and Nitrogen Biotransformation Research Laboratory (LABCEN) – Santa Maria, RS. The material that passed through the 53 μm sieve contains silt and clay minerals and is called mineral organic matter (MOM < 53 μm). The difference between the total levels of TOC/TN and POC/PON was measured to obtain the levels of MOM-C and MOM-N.

The microbiological attributes analyzed consisted of basal soil respiration (BSR) and microbial biomass carbon (MBC). Samples from each pot were collected with a 10 cm diameter by 10 cm height PVC cylinder. The determination of BSR followed the protocol of Jenskinson and Powlson (1976), where three soil subsamples undergo NaOH 0.2 mol L^{-1}. After the incubation period, NaOH was titrated with HCl 0.2 mol L^{-1}. The MBC was determined by the fumigation-extraction method (Vance et al., 1987), where the soil is previously incubated, and the carbon is determined by the $K_2Cr_2O_7$ oxidation.

2.4. Plant analysis

To quantify and compare the development of the plants between treatments, the content of chlorophylls and carotenoids in the leaves was determined at the end of the experiment. The analysis was performed by extraction with dimethyl sulfoxide in a water bath at 65 ºC for two hours, without maceration, and with determination by spectrophotometry (Hiscox and Israelstam, 1979). Calculations for determining the concentration of chlorophylls *a*, chlorophyll *b*, total chlorophyll, and carotenoids were performed using the formulas of Wellburn (1994).

At the end of the experiment, the root and aerial parts of the plants were separated and collected to determine the dry mass of the shoot (DMS) and root (DMR), and nitrogen (N), phosphorus (P), and potassium (K) content and accumulation of DMS and DMR. For this, the biomass was subjected to washing and drying in a forced air circulation oven at 60 ºC until it reached constant weight. The material was then ground in a Wiley mill with a 1 mm sieve. To quantify and compare dry and ground DMS and DMR, they were subjected to sulfur digestion (Tedesco et al., 1995) for subsequent determination of N, P, and K. Nitrogen was determined by the Kjeldahl method (1883), P by nitro-perchloric digestion and later spectrophotometry, and K by flame photometry (Analyser 910M).

2.5. Data analysis

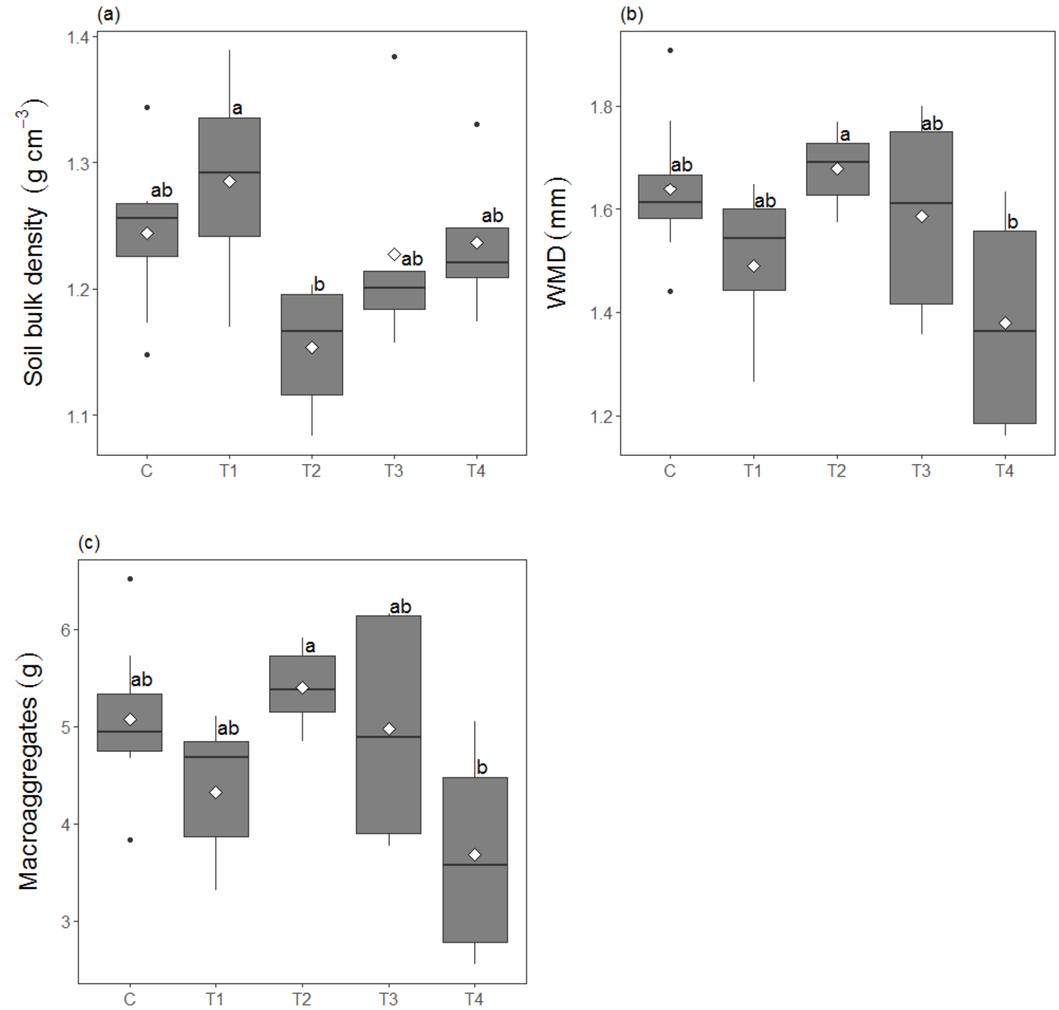
To compare the data obtained from the initial soil sample with the final data from the experiment, One Sample t-test was performed. Generalized Linear Models (GLM) were performed to compare the soil's physical, chemical, and microbiological variables and the pigments, biomass, and macronutrients of the plants between treatments. Therefore, the treatments entered the models as a factor while the other variables as responses. A likelihood ratio test (Wald Type II chi-square test) was applied to each model to test all significance (Deviation Analysis Table) using the *car* package (Fox and Weisberg, 2019). Tukey's post hoc tests were performed using the *multcomp* package (Hothorn et al., 2008) in models whose alpha was less than 0.05. The combined removal data of the T1, T2, and T3 treatments were included as a factor in the GLMs and the other variables as responses to evaluate the relationship between dung removal and the other response variables. When the normality of the data was not followed, the Gamma distribution family (link = *identity*) was used. The graphics were generated with the *ggpubr* package (Kassambara, 2020). All statistical analyses were performed using the RStudio program (RStudio Team, 2021).

3. Results

Regarding soil characteristics, at the end of the experiment, there was an increase of MCB in the treatment with mineral fertilizer in comparison with the results obtained in the initial soil sample (Table S1). In all treatments with beetles, there was an increase in the concentrations of K, P, OM, POC and PON. On the other hand, treatments with paracoprids (T2 and T3) increased soil TN contents (Table S1).

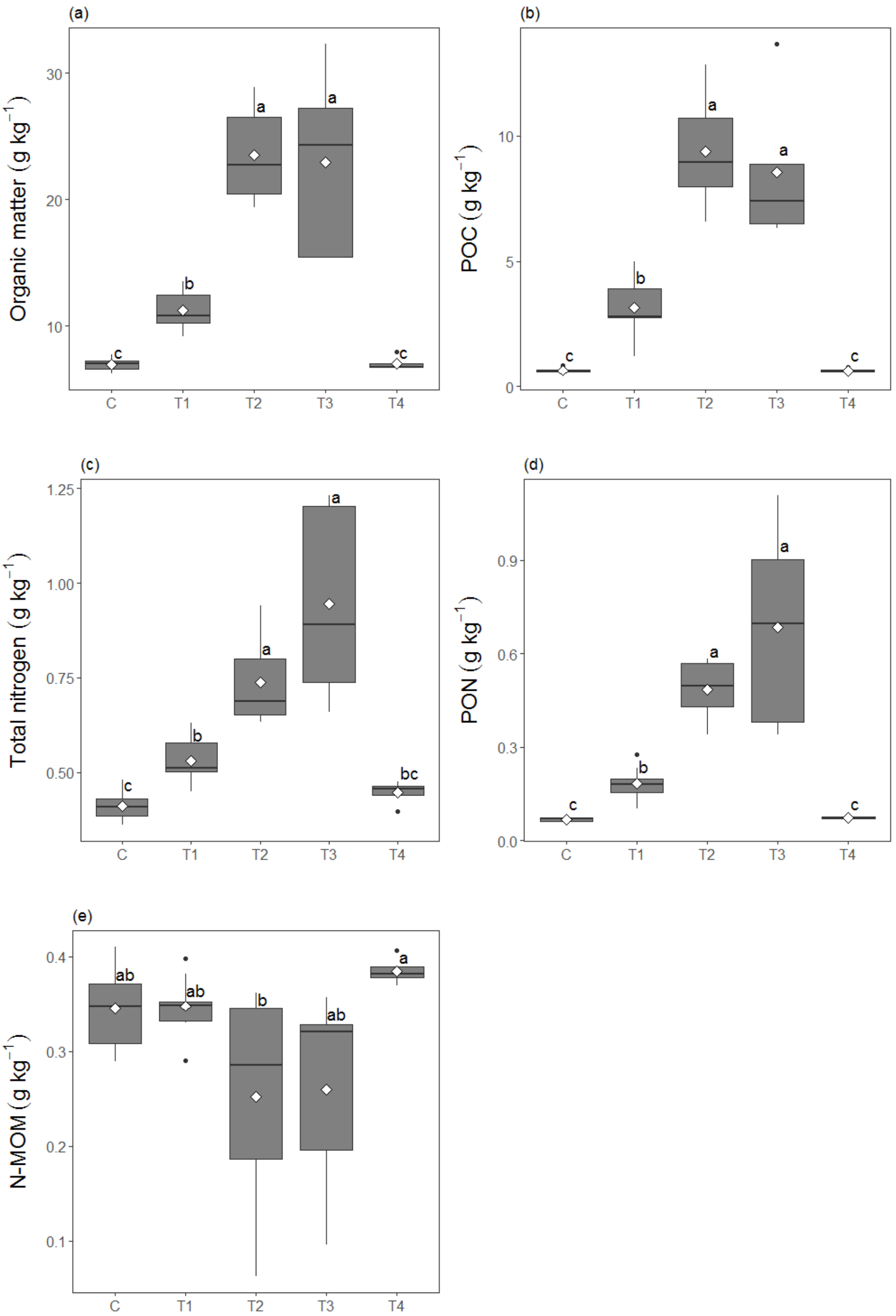
Comparing between treatments at the end of the experiment, the soil bulk density did not differ with the presence of dung beetles and the use of mineral fertilizer, but the treatment with *D. sericeus* only decreased the bulk density by about 10% compared to *C. rutilans cyanescens* only (LR = 12.950, DF = 4, p = 0.011; Fig. 1a). The importance of paracoprid activity in relation to treatment with mineral fertilizer was more evident in the analysis of soil aggregation, with higher values of weighted mean diameter (WMD; LR = 12.803, DF = 4, p = 0.012; Fig. 1b), and amounts of macroaggregates (LR = 14.136, DF = 4, p = 0.007; Fig. 1c), the latter with great variation in the data. Paracoprids only had 18% higher values of WMD and 32% more macroaggregates than treatment with mineral fertilizer, not differing from the control. The variables of GMD, meso, and microaggregates did not differ between treatments (Table S3).

Fig. 1. Comparison of the action of coprophagous dung beetles and mineral fertilizer use on the soil's physical characteristics in a mesocosm experiment. C: control, T1: treatment with telecoprids only, T2: treatment with paracoprids only, T3: mixed treatment, with both functional groups, T4: treatment with mineral fertilizer. Equal letters do not differ significantly according to Tukey's HSD test at $p < 0.05$. The diamonds represent the average per treatment. WMD: weighted mean diameter.



Paracoprids had a greater influence on the total and fractional C and N variables, mainly increasing organic matter and its particulate fractions in the soil. Paracoprid treatments had higher OM values (LR = 303.800, DF = 4, $p < 0.001$; Fig. 2a), and particulate organic C (POC; LR = 434.810, DF = 4, $p < 0.001$; Fig. 2b), with high variability in the data. These treatments had OM contents 52% higher than that of telecoprids only and 70% higher than the treatment with mineral fertilizer and control. POC levels were 65% higher compared to telecoprids only and 93% compared to mineral fertilizer and control. Treatments with paracoprids also obtained higher TN contents (LR = 121.680, DF = 4, $p < 0.001$; Fig. 2c), 36.5% higher than telecoprids only and 51% higher than the control. The same pattern was observed for particulate organic N (PON; LR = 344.320, DF = 4, $p < 0.001$; Fig. 2d), with values 69% higher than telecoprids only and 88% higher than the use of mineral fertilizer and control. Treatment with the paracoprid species only had 34% less MOM-N compared to mineral fertilizer (LR = 14.128, DF = 4, $p < 0.007$; Fig. 2e), with high variation in the data. The variable MOM-C did not differ between treatments (Table S3).

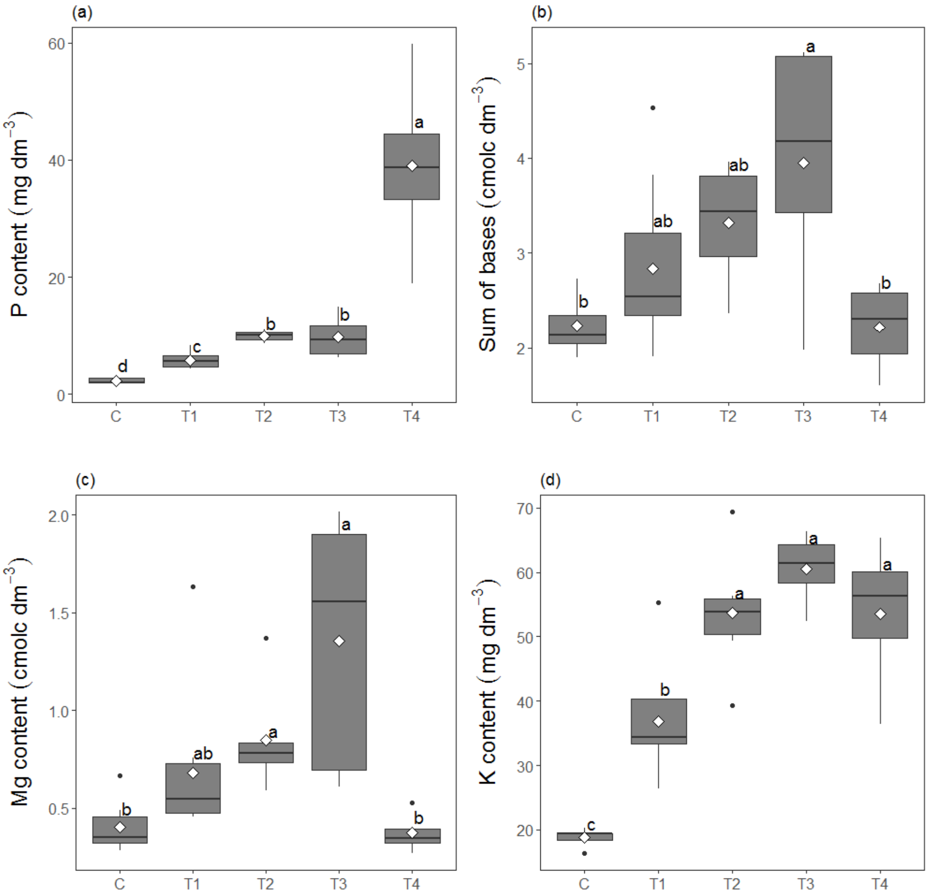
Fig. 2. Comparison of the action of coprophagous dung beetles and mineral fertilizer use on the dynamics of soil organic matter in a mesocosm experiment. C: control, T1: treatment with telecoprids only, T2: treatment with paracoprids only, T3: mixed treatment, with both functional groups, T4: treatment with mineral fertilizer. Equal letters do not differ significantly according to Tukey's HSD test at $p < 0.05$. The diamonds represent the average per treatment. POC: particulate organic carbon, PON: particulate organic nitrogen, MOM-N: mineral organic matter nitrogen.

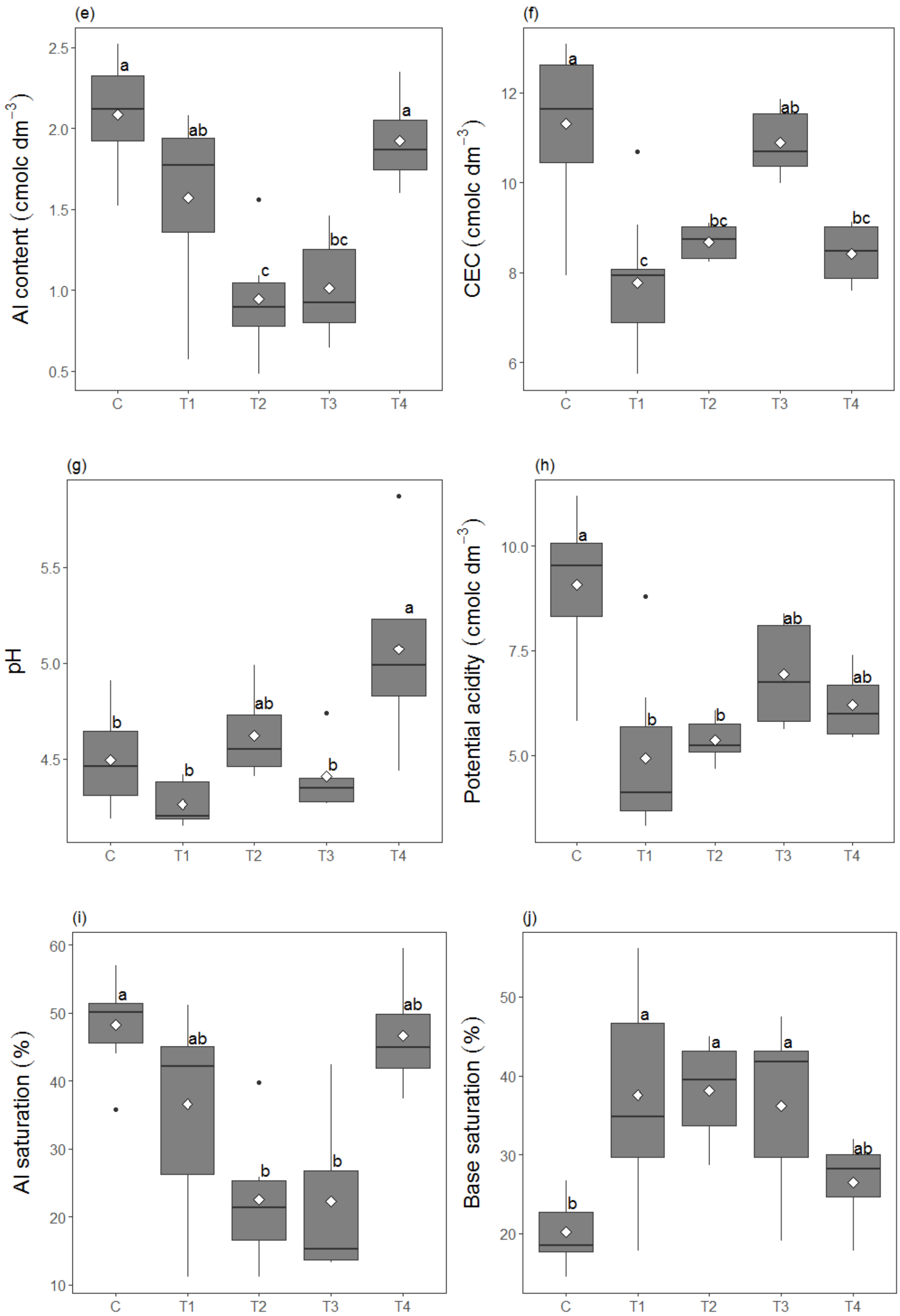


As for the other soil variables, the treatments had different influences. Phosphorus values were higher with the application of mineral fertilizer (LR = 354.790, DF = 4, $p < 0.001$; Fig. 3a), with levels 75% higher than the treatments with paracoprids, 85% higher than telecoprids only, and 94% higher than the control, with great variation in the data. The presence of both species had the highest values of sum of bases in soil (SB; LR = 20.087, DF = 4, $p < 0.001$; Fig. 3b), 44% higher than the treatments with mineral fertilizer and control, which did not differ from each other. Paracoprid treatments had the highest concentrations of Mg (LR = 35. 377, DF = 4, $p < 0.001$; Fig. 3c), 65% higher compared to mineral fertilizer and control. Potassium values did not differ between mixed treatment, paracoprids only and mineral fertilizer (LR = 184.320, DF = 4, $p < 0.001$; Fig. 3d), having great variability in the data. Telecoprids only incorporated 34% lower concentrations of this nutrient into the soil, and control, 66%, showing similar efficiency of paracoprids and mineral fertilizer. Treatments with beetles had a corrective action on the soil by decreasing Al concentrations. Paracoprids only decreased soil Al contents (LR = 41.482, DF = 4, $p < 0.001$; Fig. 3e), 53% lower than treatments with mineral fertilizer and control. Aluminum highly influenced the cation exchange capacity ($CEC_{pH7.0}$) since the control, which had the highest means, did not stand out in the measurements of the other cations (LR = 39.990, DF = 4, $p < 0.001$; Fig. 3f). The control had $CEC_{pH7.0}$ values 32% higher than telecoprids only. The pH also differed between treatments (LR = 28.830, DF = 4, $p < 0.001$; Fig. 3g), 13.5% higher in the treatment with mineral fertilizer compared to the control, with telecoprids only and together with paracoprids (T1 and T3). Treatments with telecoprids only and paracoprids only reduced the potential acidity (H + Al) of the soil by 43% when compared to the control (LR = 32.135, DF = 4, $p < 0.001$; Fig. 3h). Aluminum saturation varied widely in the data, but the paracoprid treatments resulted in values almost 54% lower than the control with dung only (LR = 24.393, DF = 4, $p < 0.001$; Fig. 3i). The base saturation was higher in beetle treatments (LR = 30.863, DF = 4, $p < 0.001$; Fig. 3j), having great variation in the data. This variable in beetle treatments was 46% higher than control. Calcium and effective CEC did not differ between treatments and control.

Basal soil respiration (BSR) and microbial biomass carbon (MBC) were not different between treatments but had great variability in the data (Table S3).

Fig. 3. Comparison of the action of coprophagous dung beetles and use of mineral fertilizer on the chemical characteristics of the soil in a mesocosm experiment. C: control, T1: treatment with telecoprids only, T2: treatment with paracoprids only, T3: mixed treatment, with both functional groups, T4: treatment with mineral fertilizer. Equal letters do not differ significantly according to Tukey's HSD test at $p < 0.05$. The diamonds represent the average per treatment. CEC: cation exchange capability at pH 7.0.





Regarding plant biomass, there was no difference between treatments, whether shoot, root, or total biomasses (Table S4). The values were low and with great variability. The same was observed for chlorophyll *a*, chlorophyll *b*, total chlorophyll, and carotenoids, which also did not differ between treatments. The absorption of most nutrients did not differ between treatments either. Nonetheless, in the leaves, the K was approximately 30% lower in the treatment with mineral fertilizer compared to telecoprids and paracoprids only, but the latter did not differ from the control (LR = 13.544, DF = 4, $p = 0.008$; Fig. 4a). Foliar P was about

55% higher in all treatments compared to the control (LR = 62.710, DF = 4, $p < 0.001$; Fig. 4b). Foliar N did not differ between treatments. In the roots, the K was 45% higher in the treatment with paracoprids only in relation to the presence of the two species (LR = 10.916, DF = 4, $p = 0.027$; Fig. 4c). Both P and root N had no differences between treatments.

As for the amount of dung removed, the paracoprid species *D. sericeus* was more efficient than the telecoprid *C. rutilans cyanescens* (LR = 13.079, DF = 2, $p = 0.001$; Fig. 5). Of the 150 g initially offered to treatments, *D. sericeus* only (T2) removed, on average, 48.2 ± 11.42 g of dung per week. Unlike our predictions, paracoprids only did not differ significantly from mixed treatment (T3) for the removal of cattle dung, having a weekly mean of 53.82 ± 8.23 g. The dung removal of treatment with *C. rutilans cyanescens* only (T1) was 35.42 ± 8.74 g, that is, 34.2% lower than T3.

The relationships between dung removal and the other variables show that the activity of dung beetles in performing this ecosystem function can influence many soil characteristics. Thus, dung removal was positively related to the amounts of macroaggregates (t = 2.519, DF error = 18, $p = 0.021$; Fig. 6a; Table S5) and, consequently, with lower values of soil mesoaggregates (t = -3.599, DF error = 18, $p = 0.002$; Fig. 6b). Higher amounts of dung removal were also related to higher P levels in the soil (t = 2.422, DF error = 18, $p = 0.026$; Fig. 6c), in addition to greater $CEC_{pH7.0}$ (t = 2.410, DF error = 18, $p = 0.026$; Fig. 6d) and potential acidity (t = 2.748, DF error = 18, $p = 0.013$; Fig. 6e). The TN of the soil also increased with dung removal (t = 3.669, DF error = 18, $p = 0.001$; Fig. 6f), as well as OM (t = 3.013, DF error = 18, $p = 0.007$; Fig. 6g), and its particulate fractions of C (t = 2.558, DF error = 18, $p = 0.019$; Fig. 6h) and N (t = 3.834, DF error = 18, $p = 0.001$; Fig. 6i). There was a negative relationship between the amount of dung removed and foliar N (t = -2.225, DF error = 18, $p = 0.039$; Fig. 6j; Table S6).

Fig. 4. Comparison of the action of coprophagous dung beetles and use of mineral fertilizer on the nutritional characteristics of *Urochloa* (*Brachiaria*) *brizantha* in a mesocosm experiment. C: control, T1: treatment with telecoprids only, T2: treatment with paracoprids only, T3: mixed treatment, with both functional groups, T4: treatment with mineral fertilizer. Equal letters do not differ significantly according to Tukey's HSD test at $p < 0.05$. The diamonds represent the average per treatment.

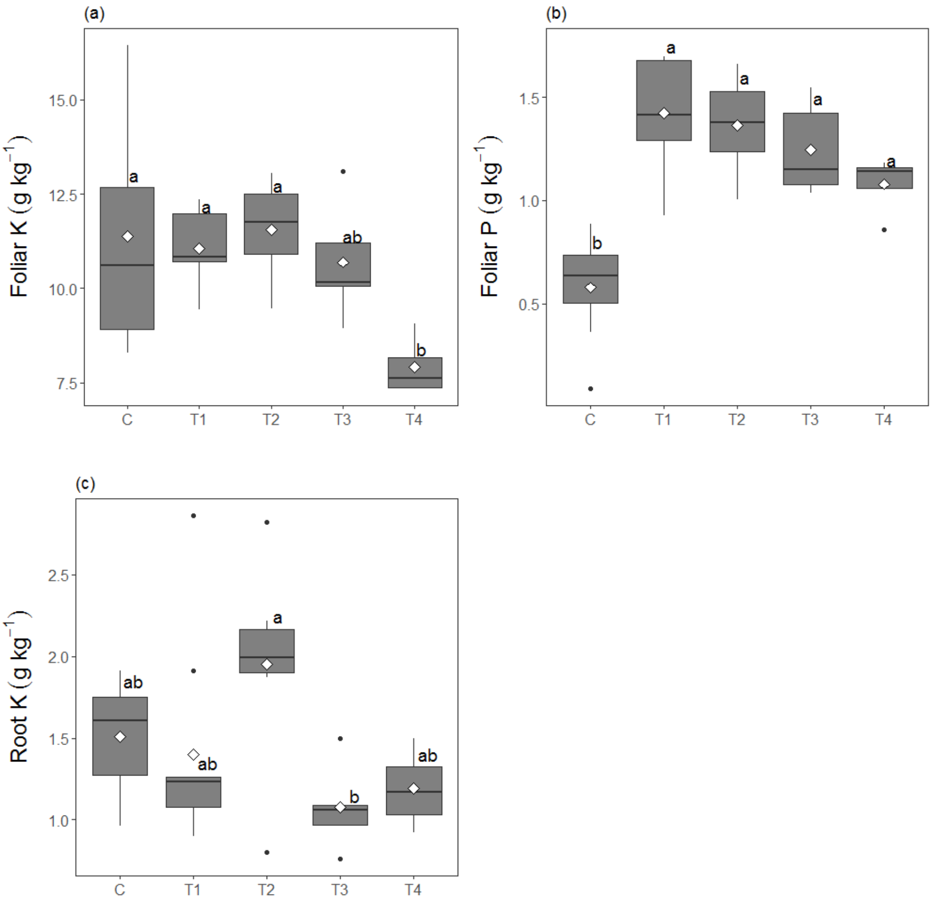


Fig. 5. Cattle dung removal performed weekly by dung beetles in a mesocosm experiment. T1: treatment with telecoprids only, T2: treatment with paracoprids only, T3: mixed treatment, with both functional groups. Equal letters do not differ significantly according to Tukey's HSD test at $p < 0.05$. The diamonds represent the average per treatment.

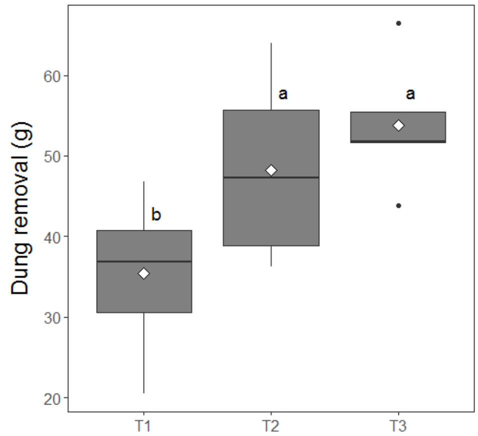
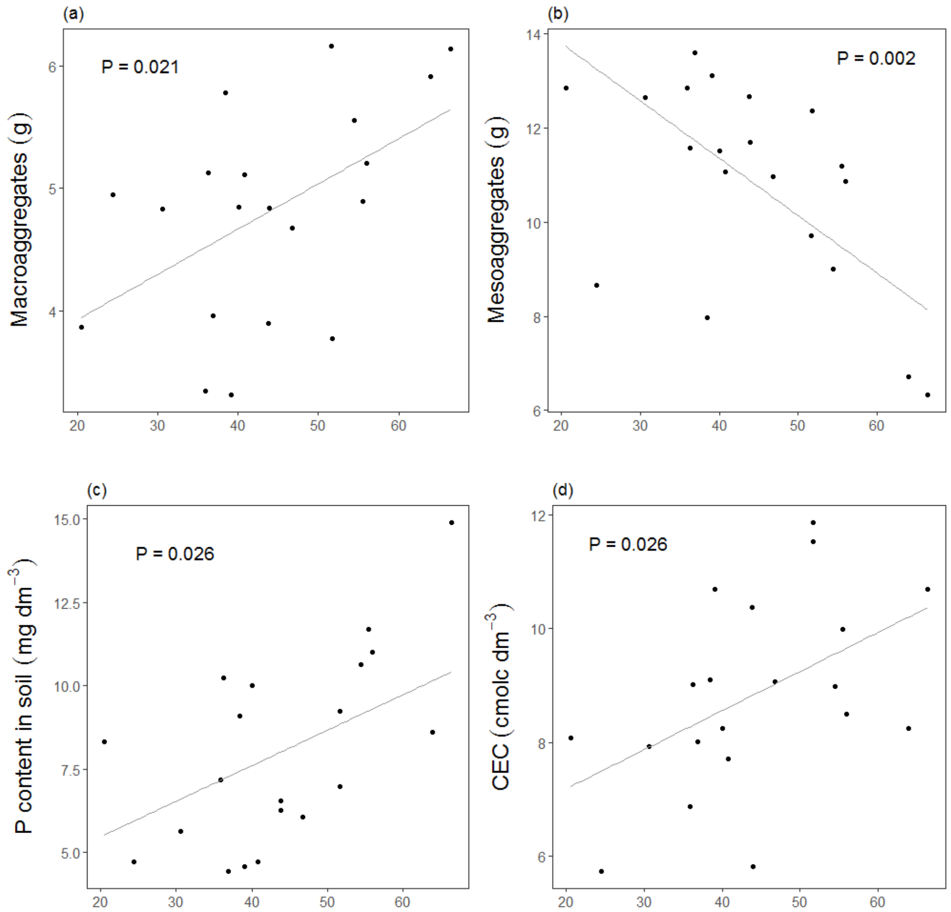
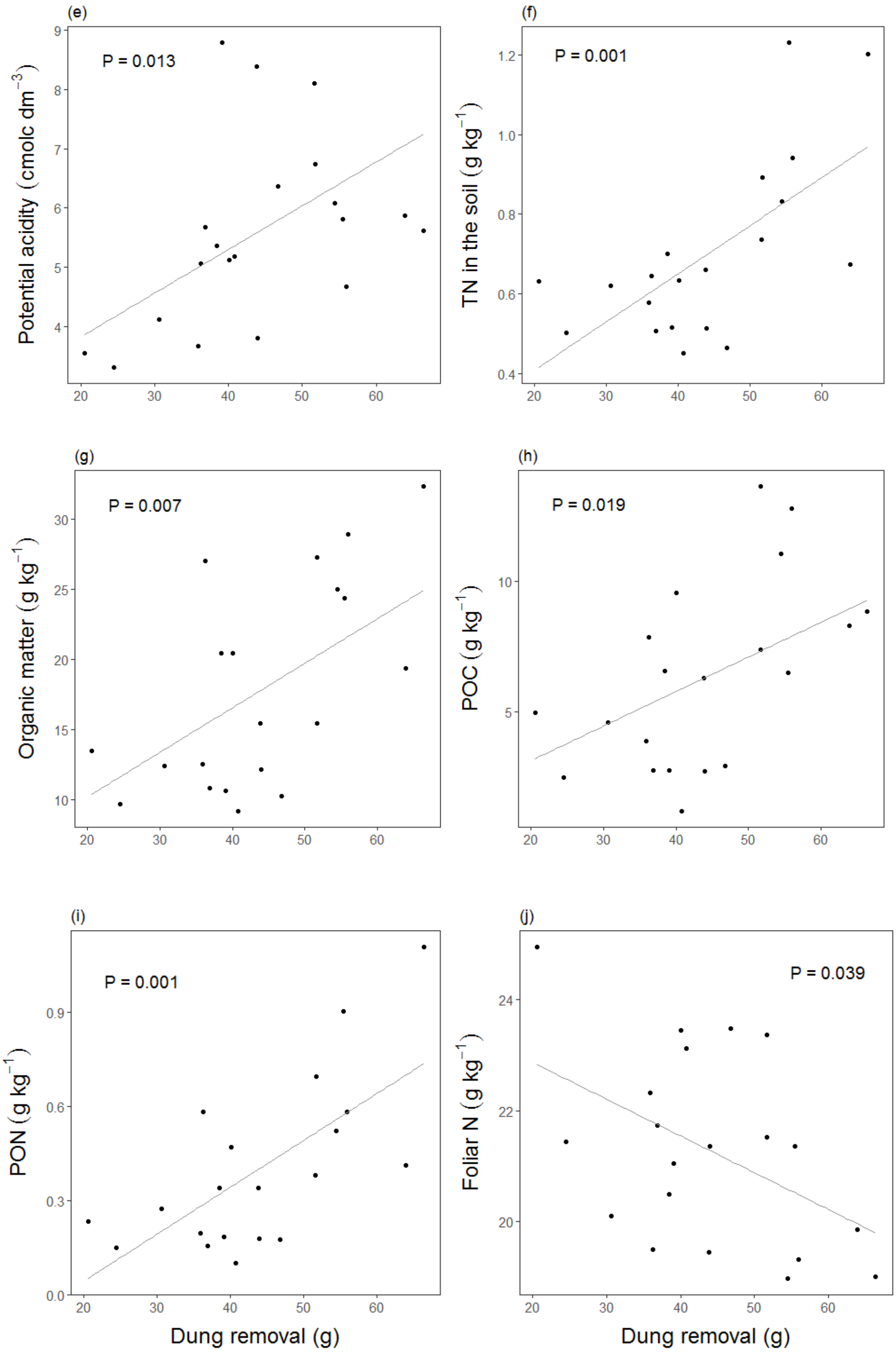


Fig. 6. Relationship between the amount of cattle dung removed by dung beetles and soil and grass *Urochloa* (*Brachiaria*) *brizantha* variables in a mesocosm experiment. CEC: cation exchange capability at pH 7.0, TN: total nitrogen, POC: particulate organic carbon, PON: particulate organic nitrogen.




(e)
P = 0.013
Potential acidity (cmolc dm^{-3})
(f)
P = 0.001
TN in the soil (g kg^{-1})
(g)
P = 0.007
Organic matter (g kg^{-1})
(h)
P = 0.019
POC (g kg^{-1})
(i)
P = 0.001
PON (g kg^{-1})
(j)
P = 0.039
Foliar N (g kg^{-1})
Dung removal (g)
Dung removal (g)

4. Discussion

The results of the present study show that by feeding on cattle dung and transporting them to the soil, dung beetles provide essential contributions and ecosystem services in agroecosystems. These organisms contribute to the quality and fertility of the soil and may be more efficient in incorporating many nutrients into the soil than the use of NPK-based mineral fertilizer. Furthermore, may also be equivalent in the productivity of *Urochloa brizantha* under experimental conditions without associated environmental damage, mainly due to the higher content of carbon and nitrogen in the soil, in addition to the decrease in aluminum content. Dung beetles, especially the paracoprid species under study, were efficient in removing organic matter from the soil. The increase in cattle dung removal was responsible for improving the soil's physical and chemical characteristics, such as the aggregation and dynamics of phosphorus, nitrogen, and organic matter. However, contrary to our initial hypothesis, the presence of distinct functional groups rarely provided synergy in the positive soil or grass results. Still, the relationship between dung removal and improvement in soil conditions reinforces the importance of the ecosystem functions performed by these organisms in livestock environments (Beynon et al., 2015; Cruz et al., 2012; Menéndez et al., 2016).

Dung removal is the initial step of most of the beneficial functions of dung beetles (Alvarado et al., 2019; Arellano, 2016; Noriega et al., 2021), which can lead to ecosystem dynamics, mainly through the removal of mammalian dung (Ortega-Martínez et al., 2016). The results of dung removal observed in the experiment are in line with other studies, which demonstrated the better functional capacity of nocturnal and larger body-sized paracoprids in removing organic matter mainly due to their underground activity (Anduaga, 2004; Anduaga and Huerta, 2007; Basto-Estrella et al., 2016; Batilani-Filho and Hernández, 2017; Buse and Entling, 2020; Nervo et al., 2014; Slade et al., 2007). This is because telecoprids and endocoprids disintegrate and disperse dung, removing them less efficiently. Moreover, telecoprids are limited by the amount of dung that they can roll, while paracoprids tend to return several times to the resource (Davis, 1996). Another factor that may have led to lower efficiency of the telecoprid species may be the dung offered, which dries up quickly since the type of resource affects the ability to remove and make the balls (Amézquita and Favila, 2010; Correa et al., 2020, Hernández et al., 2020). The genus *Dichotomius* sp. has stood out in the dung removal in the Neotropical region (Anduaga and Huerta, 2007; De Farias and

Hernández, 2017; Galbiati et al., 1995; Horgan, 2001; Monteiro et al., 2020; Niero et al., 2022; Ortega-Martínez et al., 2016; Tissiani et al., 2017), as well as some *Canthon* sp. species (Anduaga, 2004; Niero et al, 2022; Ortega-Martínez et al., 2016), despite their lower biomass, which tend to be less efficient (Carvalho et al., 2018; Davis, 1996). There is evidence of functional equivalence between the two species used as a model in this study, suggesting that when *C. rutilans cyanescens* and *D. sericeus* are compared by standardized biomass under experimental conditions, they have similar efficiencies in dung removal (Niero et al., 2022). Nevertheless, in the present study, treatments with similar biomasses of functional groups did not influence the efficiency of performing ecosystem functions (Slade et al., 2007), the functional group being the most important characteristic. Dung removal has been a well-studied ecosystem function and previous works show a strong relationship with the abundance of dung beetles (Manning and Cutler, 2018). In addition, contrary to our predictions, the functional complementarity of the species, with the presence of diurnal and nocturnal, did not present synergy with this ecosystem function, unlike other results (Slade et al., 2007).

The underground activity of dung beetles, especially paracoprids, relocating nutrient-rich organic matter, promotes physical, chemical, and biological changes in the upper layers of the soil (Nichols et al., 2008), having indirect effects on the decomposition of organic matter. In our experiment, there was an evident decrease in soil bulk density in the treatment containing paracoprids only compared to telecoprids only, which makes sense from the point of view of the functional group to which they belong. Paracoprids, when burying large portions of dung for feeding and nesting, dig tunnels (Halffter and Edmonds, 1982), positively altering the soil structure due to greater aeration promoted by the galleries. Paracoprids, when increasing the organic matter (OM) contents, decrease the soil bulk density, either by the change in the structure or by the low density of the OM (Aragón et al., 2000; Braida et al., 2006; Loss et al., 2022). However, unlike other studies (Brown et al., 2010; Kaleri et al., 2020), dung beetle treatments were not very efficient in decreasing the bulk density of the surface soil when compared to other treatments. The decrease in soil bulk density is related to other changes caused by dung beetles, such as the increase in permeability in surface layers (Bang et al., 2005; Manning et al., 2016), besides the improvement in soil hydrological properties (Brown et al., 2010). The difference between our results and those of other authors can be explained by the reduced number of paracoprid individuals in replicates since the contribution of species in the performance of ecosystem functions is highly dependent on abundance (Dangles et al., 2012; Manning and Cutler, 2018; Piccini et al., 2019).

Nevertheless, the number of paracoprids in mesocosms does not seem to have interfered with the efficiency of nitrogen incorporation into the soil. Dung removal activity increased total nitrogen (TN) levels, which were higher in *D. sericeus* treatments. Nitrogen is a limiting element in the productivity of many plants, such as grasses (Loss et al., 2022), and the participation of dung beetles in the transfer of N from the dung to the soil is well documented (Hanafy and El-Sayed, 2012; Kaleri et al., 2020; Maldonado et al., 2019; Sitters et al., 2014; Yamada et al., 2007). Paracoprids stood out in the incorporation of this nutrient into the soil (Maldonado et al., 2019; Yamada et al., 2007), with no synergy between species in the mixed treatment, in contrast to other results, where the increase in the number of species increased the incorporation efficiency (Nervo et al., 2017; Yoshihara and Sato, 2015). It is important to emphasize that the telecoprid species under study was able to incorporate an amount of nitrogen equivalent to the mineral fertilizer. Some telecoprid species, such as *Scarabaeus sacer*, may be highly efficient in increasing soil N content (Hanafy and El-Sayed, 2012). Nevertheless, in addition to being a species larger than *C. rutilans cyanescens*, intra-specific variations in size in *S. sacer* influence incorporation efficiency, which is greater the larger the individuals.

Nitrogen fertilizers are expensive, do not self-regulate, and can cause environmental problems (Barrios, 2007; Vendramini et al., 2007). Fertilization with animal dung improves several physical, chemical, and microbiological aspects of the soil and can be used in a complementary or alternative way to mineral fertilizers (Loss et al., 2022). However, both lose N by volatilization and leaching, reducing crop productivity and contaminating groundwater and surface water (Barrios, 2007). Thus, the activity of dung beetles can aid dung fertilization by rapidly incorporating N (Nichols et al., 2008; Yamada et al., 2007). Nitrogen volatilization and mineralization are bacterial-mediated processes, and dung beetles alter the fauna of microorganisms in dung and brood balls during feeding and nesting (Yokoyama et al., 1991a, 1991b). By burying the dung, dung beetles decrease the gaseous loss by volatilizing NH_3 and increase soil fertility by increasing the labile N available for plant absorption through the processes of ammonification, nitrification, denitrification, and N_2 fixation (Yokoyama et al., 1991b).

Dung removal also positively influenced the increase in organic matter in dung beetle treatments, corroborating other studies (Galbiati et al., 1995; Maldonado et al., 2019). Again, the highest levels were in the presence of paracoprids, which play an important role in the release and transfer of C along the soil profile (Menéndez et al., 2016; Sitters et al., 2014).

However, the treatment with telecoprids only had higher values than the mineral treatment and the control, being behind only the treatments with paracoprids. The lower efficiency of telecoprids only may be due to the size of individuals (Maldonado et al., 2019), even with higher abundance and similar biomass between treatments, and to the functional group itself, which naturally buries smaller amounts of dung. Organic matter influences soil structure, nutrient availability, water retention capacity, and cation exchange capacity (Barrios, 2007; Loss et al., 2022).

The paracoprid treatments, followed by telecoprids only, had large participation in the incorporation of C and N from the OM particulate fractions to the soil due to the dung removal. The particulate portion of the OM is more labile, has a higher cycling rate, and its changes are perceived in the short term (Loss et al., 2014). The mineral fraction is more stable, playing a significant role in the stabilization of smaller aggregates (Cambardella and Elliott, 1992), being less sensitive to changes in the short term. Mineral organic matter C and N have a greater influence on the stabilization of soil microaggregates, especially when comparing soils with contrasting textures and mineralogies, with a greater correlation in clayey textured soils (Bayer et al., 2004; Braida et al., 2011). In our study, the soil has a sandier texture (20.6% clay and 43.24% sand), which leads to a greater participation of the more labile OM fractions together with the improvement of physical and chemical attributes (Loss et al., 2009; Ventura et al., 2020). Our results showed a greater variation of OM particulate fractions (POC and PON) between treatments compared to the more stable fractions (MOM-C and MOM-N). Differences between treatments were found only for MOM-N, this being only between paracoprids (lower value) compared to mineral fertilizer (higher value). These results indicate that paracoprids alone or together with telecoprids increased labile N in the soil (PON), since most of TN is in the more labile fraction (PON) compared to the more stable fraction (MOM-N). For the other treatments, most of the TN is in the most stable fraction (MOM-N). These results are due to the greater dung removal in the treatments with paracoprids, which also corroborates with greater amounts of larger aggregates, results that are opposite to the treatment with mineral fertilizer.

Organic matter and particulate organic carbon, with the root system, are the main soil cementing agents in the formation and stability of aggregates (Salton et al., 2008; Six et al., 1998); with emphasis on the formation of macroaggregates, directly reflecting the increase in the weighted average diameter (WMD) of the aggregates (Francisco et al., 2021). The edaphic fauna, microorganisms, roots, inorganic agents, and environmental variables also influence this process (Salton et al., 2008). The increase in the size of the aggregates is directly linked to the amount of total organic carbon in the soil (Loss et al., 2022; Salton et al., 2008), which may explain why the treatments with dung beetles had large amounts of macroaggregates, which positively related to dung removal, and WMD values. Soil macrofauna, like paracoprid dung beetles, has an essential role in forming macroaggregates (Mummey et al., 2006). Furthermore, the greater aggregate stability causes a better structure in the soil, with porous spaces for root development and air and water circulation (Loss et al., 2022; Salton et al., 2008). However, the presence of dung beetles does not seem to be the only explanation for the amount of macroaggregates and WMD values since the only treatment that differed from mineral fertilizer was that of paracoprids only. The application of dung as fertilizer by itself causes physical, chemical, and biological changes in the soil, favoring the aggregation process (Loss et al., 2022), which could explain the high control values. Moreover, the duration of the experiment (three months) may not have been sufficient for a more evident aggregation in treatments with higher contents of OM and particulate fractions. As the formation of aggregates suggests that macroaggregates are formed by smaller ones (Tisdall and Oades, 1982), it makes sense that mesoaggregates have been negatively related to dung removal since the macroaggregates had a positive relationship with the removal function. It is noteworthy that the treatment with paracoprids alone showed a reduction of 23.2% in the amount of mesoaggregates compared to the treatment with mineral fertilizer, corroborating that mesoaggregates joined to form macroaggregates, as paracoprids showed a 32.85% increase in macroaggregates in relation to NPK treatment.

The formation of aggregates related to particulate organic matter can be measured by the activity of macrofauna and microorganisms (Six et al., 1998). The bioturbation process performed by dung beetles can alter decomposition that occur above and below the soil by transferring bacteria through the soil-dung interface, resulting in greater similarity in the structure and functioning of the microbial community (Slade et al., 2016). Dung beetles modify the communities of soil microorganisms, even though in our results, treatments were homogeneous concerning the microbiological variables measured, perhaps due to the high variation in data. Studies suggest that aerobic dung conditions and increased C and N levels in the upper soil layers, which can be stimulated by dung beetle activity, alter bacterial growth (Hatch et al., 2000; Slade et al., 2016; Yokoyama et al., 1991a, 1991b). Dung beetles reduce the C lost by microbial respiration in mesocosm by removing dung, increasing the values of basal respiration and microbial biomass carbon in superficial soil layers, and there may be complementarity between functional groups, but without differing from treatment with dung only (Menéndez et al., 2016).

The entry of OM into the soil by the activity of beetles also leads to an increase in other macronutrients in the soil (Bertone et al., 2006; Galbiati et al., 1995; Maldonado et al., 2019; Yamada et al., 2007). Incorporation efficiency is usually related to the number and size of individuals present, species identity, abundance, and functional group, with most studies involving paracoprid species (but see Hanafy and El-Sayed, 2012). Animal dung has high levels of P and K, the latter present in the form of K^+, being quickly released and made available (Loss et al., 2022). Dung beetles increase the rate of P release (Sitters et al., 2014) and its concentration in the soil in relation to treatment with dung only since mechanical or biological incorporation is necessary given the limited mobility of this element (Bertone et al., 2006; Galbiati et al., 1995; Hanafy and El-Sayed, 2012; Kaleri et al., 2020; Maldonado et al., 2019; Yamada et al., 2007). Phosphorus has been an important predictor of dung beetle abundance in natural environments (De Farias et al., 2015). In the results of the present study, it was positively related to dung removal, and treatments with dung beetles were better than control. However, none of the treatments had concentrations as high as those with mineral fertilizer. It is known that high concentrations of P released by mineral fertilizers can lead to eutrophication problems by leaching this nutrient (Vendramini et al., 2007). Although treatments with dung beetles have considerably increased the P levels in the initial soil sample, the levels are still considered low (CQFS RS/SC, 2016). However, most Brazilian soils are very weathered and have acidic pH and oxidic mineralogy, which causes specific adsorption of P to soil colloids, causing the absence of available P in the soil solution (Rheinheimer et al., 2008). Therefore, even if P levels are low in treatments with dung beetles, the values are two to four times higher than the control values, which makes this ecosystem function very important, especially when we consider this effect in an environment of pasture for a long time. Potassium is another nutrient that commonly increases in the presence of dung beetles (Bertone et al., 2006; Galbiati et al., 1995; Hanafy and El-Sayed, 2012; Kaleri et al., al., 2020). The action of paracoprids was as efficient in incorporating K into the soil as the use of fertilizer based on this element, resulting in mean concentrations (CQFS RS/SC, 2016). Telecoprids also stood out with higher values than the control, but both treatments had low values (CQFS RS/SC, 2016).

Bivalent cations are also essential agents in soil aggregation (Demarchi et al., 2011), with different dynamics in the present study. Calcium values were similar to those found in other studies, in which there are no differences in the presence of dung beetles (Bertone et al., 2006) but differ from others (Galbiati et al., 1995; Hanafy and El-Sayed, 2012; Kaleri et al., 2020). The results may be due to the low nutritional quality of the dung used, whose nutrients, except for C, were below the general mean (CQFS RS/SC, 2016; Loss et al., 2022). Although there were no significant differences between the treatments, it is worth mentioning that the activity of the dung beetles led to the achievement of mean values of concentration of this nutrient in the soil (CQFS RS/SC, 2016), while control and mineral fertilizer had low values, even the STP containing Ca. Magnesium usually increases in the presence of dung beetles (Bertone et al., 2006; Galbiati et al., 1995; Hanafy and El-Sayed, 2012), being higher in treatments with paracoprids in our results. These increases are significant because they were independent of the leaching of dung since the control had lower values. Treatments with dung beetles were the only ones that could reach mean values of Mg in the soil, and the mixed treatment reached high values (CQFS RS/SC, 2016).

Besides the cations K^{+}, Ca^{+2}, and Mg^{+2}, organic matter also influences the cation exchange capacity ($CEC_{pH7.0}$) due to the high content of negative charges present on its surface. This explains why dung removal was positively related to $CEC_{pH7.0}$, as it also influenced OM. Higher dung removal values favored the increase of OM in the soil of the treatments with dung beetles, generating more negative charges in the soil, attracting cations and causing the soil to have higher $CEC_{pH7.0}$, influencing fertility and the ability to provide nutrients to plants (Ronquim, 2010). Thus, these beetles mediate the effects of environmental stress through the improved incorporation of K, Ca, and Mg (Bertone et al., 2006), that benefit from the increase in OM. Other results show that dung beetles can increase the CEC of the soil, but with no difference between treatment with dung only (Bertone et al., 2006). The highest $CEC_{pH7.0}$ values in control must have been highly influenced by Al, which had the highest concentrations in the control and mineral fertilizer. The mixed treatment, on the other hand, indicates a different soil condition, having a high CEC due to the higher SB. Still, the low $CEC_{pH7.0}$ of telecoprids only in relation to the control should indicate a poorer soil since this treatment had lower values of Ca, Mg, and K compared to the other treatments with dung beetles. The treatments with dung beetles, mainly paracoprids, decreased the levels of Al in the soil, also due to the entry of OM into the soil and increase in POC, whose negative charges neutralize Al. Very high $CEC_{pH7.0}$ values, inflated by Al^{+3} and H^{+} resulting from the potential acidity of the soil and with consequent decrease of basic cations (Ca, Mg and K), can be harmful to soil and plants, limiting the development of plant roots (Ronquim, 2010). In general, the soil of the experiment is considered of low fertility and acidic (Ronquim, 2010).

Dung beetles can promote pH increases in the soil (Bertone et al., 2006; Galbiati et al., 1995). However, the low pH observed in treatments with weekly intake of fresh dung compared to mineral fertilizer can be explained by the formation of humic substances as fulvic acid in the initial stage of decomposition of cattle dung (Senesi, 1989). The positive relationship of dung removal and the potential acidity of the soil can also be explained by this factor. The potential acidity of the soil was lower in the treatments with beetles compared to the control, and since the effective CEC had no significant differences between treatments, the difference is due to Al concentrations or SB. By decreasing Al concentrations and potential acidity, by increasing the sum of bases and decreasing Al saturation, the beetles would be promoting a balance in the mineral nutrition of plants (CQFS RS/SC, 2016). Finally, base saturation was higher in beetle treatments, corroborating other results (Bertone et al., 2006), where this variable was increased by the activity of dung beetles in sandy soils. Nevertheless, it is still considered low (Ronquim, 2010). A longer experiment time, with consequent increase of exchangeable cations, could lead to increased pH and saturation of bases in the soil.

By removing dung and digging tunnels, dung beetles allow plants to use soil resources more efficiently and perform better with increasing concentrations of many nutrients (Galbiati et al., 1995; Yamada et al., 2007). In cultivation and pasture areas, bioturbation caused by dung beetles promotes greater efficiency in using plant nutrients (Bang et al., 2005; Hanafy, 2012). Nevertheless, despite the increase in many nutrients and the improvement in soil's physical conditions, the presence of dung beetles did not differ from treatment with mineral fertilizer or control in several aspects measured in grasses. The dry weight of some plants react well to the presence of dung beetles compared to the control (Bang et al., 2005; Hanafy, 2012), and may rival some concentrations of mineral fertilizer (Fincher et al., 1981), including in a species of forage grass similar to that used in our study, *Brachiaria decumbens* (Miranda et al., 2000). Nevertheless, in our results, foliar and root biomass were not significantly different between treatments, corroborating other studies (Nervo et al., 2017). The plants, in general, had a low development during the experiment. Experimental conditions with little incident solar radiation and high humidity may have affected development and productivity. One solution for future works is to conduct the experiment in two parts: letting the beetles act on the soil and then inserting the plants (Kaleri et al., 2020). As our goal was to measure the soil's physical variables, dividing the work into phases was impossible. Other studies show that paracoprids, by digging tunnels, can lead to greater root development due to greater soil porosity (Brown et al., 2010). Grass roots are considered important in forming soil aggregates and thus favor the highest values of WMD (Loss et al., 2014; Salton et al., 2008), and their constant decomposition promotes an increase in OM in the soil (Demarchi et al., 2011; Rossi et al., 2012). Besides biomass, dung beetles can increase chlorophyll contents under experimental conditions (Kaleri et al., 2020). The concentrations of these photosynthetic pigments have a positive relationship with the N contents in the soil (Costa et al., 2008; Morais et al., 2016), but the high variation in the data may have masked this effect.

Dung beetles can promote nutrient cycling by removing dung in pasture environments, but the flow of nutrients to plants can vary in the presence of these insects (Yamada et al., 2007; Yoshihara and Sato, 2015). Studies show that plant macronutrients can be positively influenced by the action of dung beetles (Galbiati et al., 1995), including telecoprids (Hanafy, 2012), with increases in nutritional contents. Nonetheless, despite increasing the N content of the soil, dung beetle treatments had no better results than the application of mineral fertilizer or than the control in the absorption of this nutrient by grasses, corroborating other studies (Nervo et al., 2017). The soil N dynamics for plants are controversial in other studies and may increase with larger intraspecific individuals (Hanafy, 2012) or be higher in treatment with dung only (Galbiati et al., 1995). Soil N increases with dung removal, but N in plants does not follow the same pattern, as absorption occurs up to critical values (CQFS RS/SC, 2016), which may help to understand why removal was negatively related to foliar N. Other authors, in studies with grasses, also observed higher levels of N and P in the soil in the presence of dung beetles (Yamada et al., 2007), but the subsequent effect on plant growth was also not very clear. Even if the species *Urochloa brizantha* is tolerant to acidic soils and high levels of toxic Al (Meirelles and Mochiutti, 1999), these characteristics can impair the general macronutrient absorption capacity (CQFS RS/SC, 2016; Ronquim, 2010), homogenizing the results between treatments. The experiment time may also not have been sufficient to show differences between treatments, as some studies point out that the positive impacts of the activity of dung beetles on biomass and nutrients in plants may take several months to manifest (Bang et al., 2005; Fincher et al., 1981; Miranda et al., 2000).

Dung beetles were as efficient as mineral fertilizer in the absorption of P by grasses, increasing their foliar contents (Galbiati et al., 1995; Hanafy, 2012), maintaining mean concentrations of this nutrient in leaves (CQFS RS/SC, 2016), even if the soil has much higher contents with the use of mineral fertilizer. This means that the mechanical incorporation performed by the dung beetle was important to complement the fertilization with dung only, with the difference that beetles need to use fresh dung. The amounts of K were higher in treatments with beetles than in mineral fertilizer. Still, as they did not differ from the control, the efficiency cannot be credited to dung beetles, including the conflicting results in root contents between treatments with paracoprids (which can be explained by the number of individuals between treatments). Perhaps this is due to low leaching in dung treatments, with gradual release of this element as dung were removed and decomposed. Despite the good results of this nutrient in the soil, the plants could not absorb enough to reach mean values (CQFS RS/SC, 2016). Given the loss and inefficiency in the mean absorption of mineral fertilizers by crops (Isherwood, 2000; Vendramini et al., 2007), the use of fertilization by dung or with the presence of dung beetles can be viable alternatives since they provide productivity at least, similar to mineral fertilizers. It should also be borne in mind that the increase in plant productivity does not always accompany the improvement of all soil attributes, and conservation practices should aim at good management focused on the quality of the soil as a whole (Loss et al., 2022).

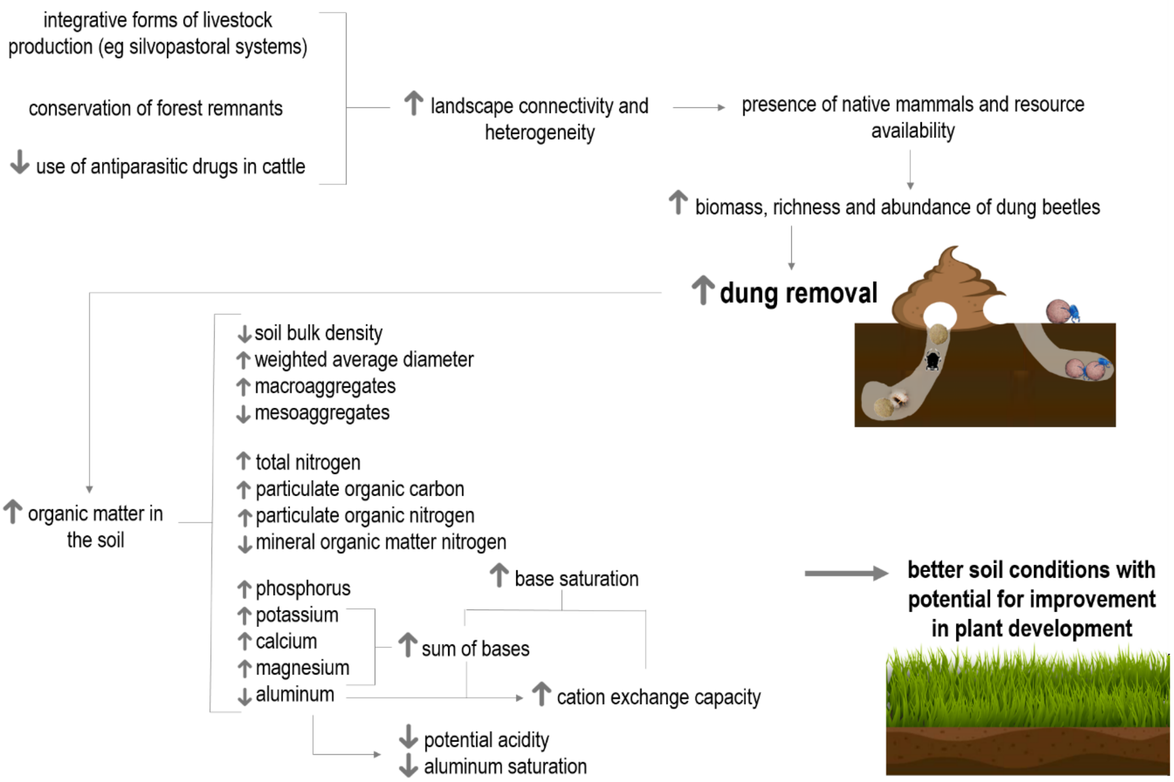
Most of the functions analyzed in this study show the efficiency of paracoprids in improving soil and grass conditions in an experiment simulating livestock environment, without the complementarity between functional groups, initially expected. The species contribute unequally to the performance of different ecosystem functions (Nervo et al., 2014; Piccini et al., 2019; Slade et al., 2007; Slade and Roslin, 2016), which could explain why the telecoprid species did not stand out in the measured variables. Nevertheless, the relationship between paracoprids and the performance of carrying out contributions and ecosystem functions from their functional group needs to be analyzed with caution. First, because dung removal, where this group stands out, is not always a good predictor of other functions (Carvalho et al., 2020; Kavanaugh and Manning, 2020). Our results showed that the dung removal was not always positively related to the other characteristics influenced by dung beetles. Secondly, because no species can provide maximum performance in performing various ecosystem services (Manning et al., 2016; Slade et al., 2011; Yoshihara and Sato, 2015), then ensuring the sustainment of several functions simultaneously requires a greater number of species than any function analyzed individually (Slade et al., 2017; Yoshihara and Sato, 2015). Thus, a high diversity of functional groups can ensure the continuity of ecosystem functioning, depending on the composition of the community and the function considered (Amore et al., 2018; Buse and Entling, 2020; Manning et al., 2016; Ortega-Martínez et al., 2021; Rosenlew and Roslin, 2008; Slade et al., 2017), especially when systems are disturbed (Slade and Roslin, 2016). Although highly efficient, increases in disorders resulting from human activities can lead to the loss of large species (Alvarado et al., 2019; Gardner et al., 2008), such as large paracoprids, and hyperabundance of few smaller species in tropical areas (Alvarado et al., 2019). However, there is a controversy between the studies on the functional compensation of the loss of larger species by the greater abundance of smaller ones, with concordant (Alvarado et al., 2019; Amézquita and Favila, 2010; Correa et al., 2019) and discordant (Buse and Entling, 2020; Piccini et al., 2019) results in different environments. The loss of function performed by a dominant species could be maintained by the complementarity of the others (Slade et al., 2017). Nonetheless, our study shows that complementarity between species not always occur and, besides that, although species may appear functionally redundant, many species would be needed to maintain ecosystem functioning at multiple temporal and spatial scales (Dangles et al., 2012; Nervo et al., 2017).

Thus, despite the best results found in the presence of paracoprids in the experiment in mesocosms, and so that dung beetles can act in real conditions, livestock management needs to aim at alternatives that maintain the greatest diversity of habitats and, consequently, of organisms. Conventional livestock, with low plant diversity and high dependence on chemical fertilizers and herbicides, simplifies ecosystems and negatively affects their functioning (Giraldo et al., 2011). Also, treating domestic grazing ruminants with antiparasitics of the macrocyclic lactone family causes adverse effects on edaphic fauna associated with manure, regardless of the route of administration of the drugs and the doses used (Pérez-Cogollo et al., 2018). Contact with drug residues can cause lethal (Beynon et al., 2012) and sublethal consequences (González-Tokman et al., 2017; Martínez et al., 2017; Verdú et al., 2015) in some species already studied. This can cause an intense and continuous dung accumulation, with cascade effects on functional diversity, resilience, and the effective functioning of the ecosystem in pasture environments (González-Tokman et al., 2017; Kavanaugh and Manning, 2020). Management also affects physicochemical properties (Demarchi et al., 2011), altering processes such as incorporating OM and fractionating aggregates (Rossi et al., 2012; Six et al., 1998). Furthermore, the management intensification decreases dung beetle biomass (Alvarado et al., 2019), whose species have different thermal tolerances (Verdú et al., 2006). Open-site species need adaptations to solar radiation (Halffter and Arellano, 2002; Lobo et al., 1998), in addition to dealing with the rapid desiccation of the resource (Anduaga, 2004;

Correa et al., 2020). Changes in plant structure modify microclimatic factors such as radiant heat (Halffter et al., 1992), light intensity, and air and soil temperature and humidity (Davis et al., 2002).

Such conditions lead us to consider more integrative forms of cattle breeding, such as silvopastoral systems (Fig. 7). In tropical regions, livestock systems that use forage trees and shrubs along with grasses offer a useful landscape management tool that can contribute to the conservation of biodiversity and the stability of ecological processes (De Farias et al., 2015; Giraldo et al., 2011). The most complex vegetation, with more favorable microhabitats to dung beetles, prevents the loss of species, functional groups, and ecosystem services (De Farias and Hernández, 2017; Favila, 2012; González-Tokman et al., 2018; Macedo et al., 2020; Sarmiento-Garcés and Hernández, 2021). Silvopastoral systems increase landscape heterogeneity, improve connectivity and promote the conservation of dung beetles in the productive matrix, enhancing ecological functions in pastures (Montoya-Molina et al., 2016). These conditions, among other forms of management, such as the non-use of antiparasitic of the macrocyclic lactone group, allow the maintenance of dung beetles and enable them to perform ecosystem functions that promote similar or greater improvements than the use of mineral fertilizers in soil and grasses in livestock environments.

Fig. 7. Scheme of ecosystem functions and services that can be provided by dung beetles in agricultural environments, through the removal of cattle dung, in soil improvement and potential improvement in plants.



5. Conclusion

This study compared the efficiency of dung beetles of two functional groups to the use of mineral fertilizer in soil and forage grasses variables under experimental conditions, simulating a livestock environment. Our results suggest that telecoprid and paracoprid species have different efficiencies in performing ecosystem functions. Paracoprids were more efficient, in general, and, unlike our predictions, the complementarity between the species was not responsible for better conditions in the soil or the plants. Although dung beetles were superior to the use of mineral fertilizer in improving physical and chemical conditions in the soil, the effects of this improvement were slight on plant productivity. Most of the variables positively influenced by dung beetles were related to dung removal, mainly in relation to the increase in the contents of total C and N in the soil and in the particulate fractions of OM, macroaggregates and P in the soil, as well as the decrease in exchangeable Al. Our results reinforce the importance of these beetles in livestock environments, where they play a crucial role in nutrient cycling and can perform ecosystem services that assist mineral fertilizer and can be used as a more sustainable form of fertilization.

Declaration of Competing Interest

The authors declare that they do not have financial and personal relationships that may have influenced the work reported in this article.

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Supplementary Material

Figure S1

Illustration of the experiment developed to measure the efficiency of dung beetles in improving soil and forage grasses conditions. (a) schematic representation of the experiment, with the components and number of replicates in each treatment (C: control, T1: treatment with telecoprids only, T2: treatment with paracoprids only, T3: mixed treatment, with both functional groups, T4: treatment with mineral fertilizer); (b) preparation of the mesocosms before the addition of the experiment components; (c) experiment in open and outdoor conditions.

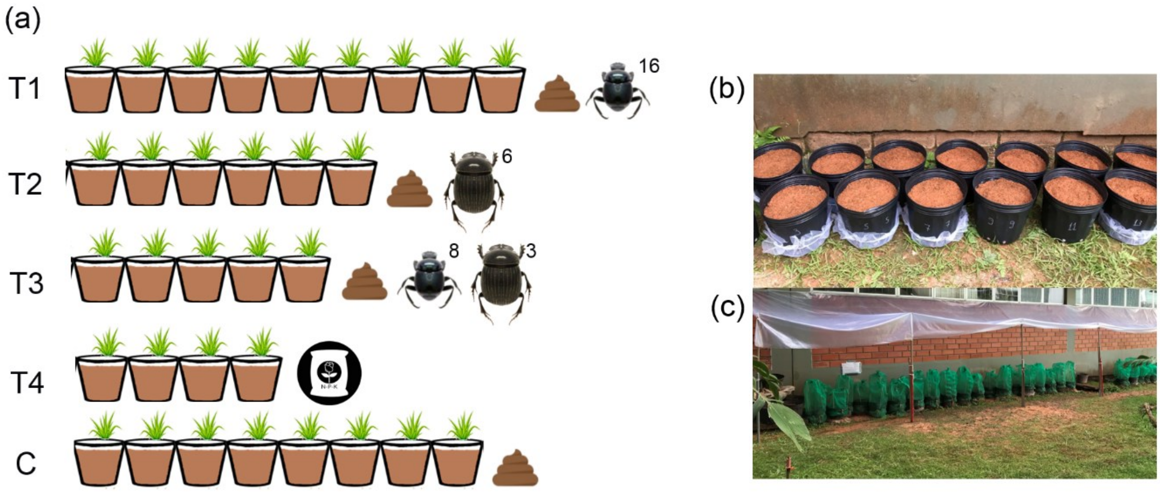

Table S1

One Sample t-test for comparison between the initial and final characteristics of the soil by treatment in mesocosm experiment to evaluate the action of dung removal by dung beetles in the incorporation of nutrients into the soil and absorption by forage grasses. T1 (t): treatment with telecoprids, T2 (p): treatment with paracoprids, T3 (t+p): mixed treatment, with both functional groups, T4 (NPK): treatment with mineral fertilizer. * indicates a significant difference between the initial and final samples, with $p < 0.05$.

Soil variables	Initial	Control	T1 (t)	T2 (p)	T3 (t+p)	T4 (NPK)
Soil bulk density (g cm^{-3})	1.35	t = -4.935, DF = 7, p = 0.001*	t = -2.555, DF = 8, p = 0.034*	t = -9.403, DF = 5, p < 0.001*	t = -3.046, DF = 4, p = 0.038*	t = -3.415, DF = 3, p = 0.042*
WMD (mm)	2.41	t = -15.399, DF = 7, p < 0.001*	t = -19.531, DF = 8, p < 0.001*	t = -24.228, DF = 5, p < 0.001*	t = -9.415, DF = 4, p < 0.001*	t = -8.687, DF = 3, p = 0.003*
GMD (mm)	0.80	t = -7.765, DF = 7, p < 0.001*	t = -13.049, DF = 8, p < 0.001*	t = -6.805, DF = 5, p = 0.001*	t = -9.759, DF = 4, p < 0.001*	t = -6.953, DF = 3, p = 0.006*
Macroaggregates (g)	9.29	t = -15.145, DF = 7, p < 0.001*	t = -21.141, DF = 8, p < 0.001*	t = -23.068, DF = 5, p < 0.001*	t = -8.341, DF = 4, p = 0.001*	t = -9.488, DF = 3, p = 0.002*
Mesoaggregates (g)	7.72	t = 6.444, DF = 7, p < 0.001*	t = 8.233, DF = 8, p < 0.001*	t = 2.284, DF = 5, p = 0.071	t = 2.365, DF = 4, p = 0.077	t = 10.209, DF = 3, p = 0.002*
Microaggregates (g)	5.95	t = 1.629, DF = 7, p = 0.147	t = 0.659, DF = 8, p = 0.528	t = 1.553, DF = 5, p = 0.181	t = 1.363, DF = 4, p = 0.245	t = 2.337, DF = 3, p = 0.101
pH	4.2	t = 3.441, DF = 7, p = 0.011*	t = 1.797, DF = 8, p = 0.110	t = 4.548, DF = 5, p = 0.006*	t = 2.409, DF = 4, p = 0.073	t = 2.947, DF = 3, p = 0.060
H + Al ($cmol_c$ dm^{-3})	21.3	t = -19.641, DF = 7, p < 0.001*	t = -27.426, DF = 8, p < 0.001*	t = -73.483, DF = 5, p < 0.001*	t = -25.127, DF = 4, p < 0.001*	t = -32.990, DF = 3, p < 0.001*
K (mg dm^{-3})	30	t = -26.425, DF = 7, p < 0.001*	t = 2.427, DF = 8, p = 0.041*	t = 5.933, DF = 5, p = 0.002*	t = 12.424, DF = 4, p < 0.001*	t = 3.814, DF = 3, p = 0.032*
P (mg dm^{-3})	2.7	t = -2.457, DF = 7, p = 0.043*	t = 6.865, DF = 8, p < 0.001*	t = 19.262, DF = 5, p < 0.001*	t = 4.486, DF = 4, p = 0.011*	t = 4.357, DF = 3, p = 0.022*
Ca ($cmol_c$ dm^{-3})	0.2	t = 15.551, DF = 7, p < 0.001*	t = 9.875, DF = 8, p < 0.001*	t = 10.020, DF = 5, p < 0.001*	t = 5.911, DF = 4, p = 0.004*	t = 7.919, DF = 3, p = 0.004*

Mg ($cmol_c$ dm^{-3})	0.1	t = 6.689, DF = 7, p < 0.001*	t = 4.659, DF = 8, p = 0.001*	t = 6.802, DF = 5, p = 0.001*	t = 4.221, DF = 4, p = 0.013*	t = 4.959, DF = 3, p = 0.016*
Al ($cmol_c$ dm^{-3})	3.9	t = -15.858, DF = 7, p < 0.001*	t = -13.663, DF = 8, p < 0.001*	t = -19.890, DF = 5, p < 0.001*	t = -19.259, DF = 4, p < 0.001*	t = -12.402, DF = 3, p = 0.001*
SB ($cmol_c$ dm^{-3})	0.39	t = 16.611, DF = 7, p < 0.001*	t = 8.455, DF = 8, p < 0.001*	t = 11.455, DF = 5, p < 0.001*	t = 6.095, DF = 4, p = 0.003*	t = 7.439, DF = 3, p = 0.005*
$CEC_{pH\ 7.0}$ ($cmol_c$ dm^{-3})	21.69	t = -16.982, DF = 7, p < 0.001*	t = -27.004, DF = 8, p < 0.001*	t = -79.268, DF = 5, p < 0.001*	t = -30.726, DF = 4, p < 0.001*	t = -35.296, DF = 3, p < 0.001*
Effective CEC ($cmol_c$ dm^{-3})	4.29	t = 0.249, DF = 7, p = 0.810	t = 0.672, DF = 8, p = 0.521	t = -0.169, DF = 5, p = 0.872	t = 1.442, DF = 4, p = 0.223	t = -0.998, DF = 3, p = 0.392
Aluminum saturation (%)	90.90	t = -18.824, DF = 7, p < 0.001*	t = -12.429, DF = 8, p < 0.001*	t = -16.789, DF = 5, p = < 0.001*	t = -12.200, DF = 4, p < 0.001*	t = -9.4809, DF = 3, p = 0.002*
Base saturation (%)	1.82	t = 11.657, DF = 7, p < 0.001*	t = 9.095, DF = 8, p < 0.001*	t = 13.660, DF = 5, p < 0.001*	t = 6.609, DF = 4, p = 0.002*	t = 8.027, DF = 3, p = 0.004*
TN (g kg^{-1})	0.57	t = -11.212, DF = 7, p < 0.001*	t = -1.793, DF = 8, p = 0.111	t = 3.345, DF = 5, p = 0.020*	t = 3.193, DF = 4, p = 0.033*	t = -7.278, DF = 3, p = 0.005*
OM (g kg^{-1})	7.0	t = -0.408, DF = 7, p = 0.695	t = 8.711, DF = 8, p < 0.001*	t = 10.130, DF = 5, p < 0.001*	t = 4.808, DF = 4, p = 0.008*	t = -0.039, DF = 3, p = 0.971
POC (g kg^{-1})	0.73	t = -2.400, DF = 7, p = 0.047*	t = 6.296, DF = 8, p < 0.001*	t = 9.281, DF = 5, p < 0.001*	t = 5.780, DF = 4, p = 0.004*	t = -2.017, DF = 3, p = 0.137
MOM-C (g kg^{-1})	3.32	t = 0.681, DF = 7, p = 0.518	t = 0.252, DF = 8, p = 0.8074	t = 1.166, DF = 5, p = 0.296	t = 0.874, DF = 4, p = 0.431	t = 0.469, DF = 3, p = 0.671
PON (g kg^{-1})	0.07	t = -0.697, DF = 7, p = 0.508	t = 6.889, DF = 8, p < 0.001*	t = 10.491, DF = 5, p < 0.001*	t = 4.160, DF = 4, p = 0.014*	t = 1.387, DF = 3, p = 0.259
MOM-N (g kg^{-1})	0.51	t = -10.177, DF = 7, p < 0.001*	t = -15.799, DF = 8, p < 0.001*	t = -5.312, DF = 5, p = 0.003*	t = -5.074, DF = 4, p = 0.007*	t = -15.902, DF = 3, p < 0.001*
BSR (μg C-CO_2 g dry $soil^{-1}$ h^{-1})	0.51	t = 0.751, DF = 7, p = 0.477	t = -0.839, DF = 8, p = 0.425	t = 2.171, DF = 5, p = 0.082	t = 0.375, DF = 4, p = 0.726	t = -0.046, DF = 3, p = 0.966
MBC (μg g^{-1})	33.98	t = 2.066, DF = 7, p = 0.078	t = 1.905, DF = 8, p = 0.093	t = 2.469, DF = 5, p = 0.056	t = 2.470, DF = 4, p = 0.069	t = 6.684, DF = 3, p = 0.007*

WMD: weighted mean diameter, GMD: geometric mean diameter, SB: sum of bases, CEC: cation exchange capacity, TN: total nitrogen, OM: organic matter, POC: particulate organic carbon, PON: particulate organic nitrogen, MOM-C: mineral organic matter carbon, MOM-N: mineral organic matter nitrogen, BSR: basal soil respiration, MBC: microbial biomass carbon, DF: degrees of freedom.

Table S2

Description of the activities conducted during the mesocosm experiment to analyze the effect of dung beetles on the physical, chemical, and microbiological characteristics of the soil and on the physiology and productivity of forage grasses.

Date	Activity
22/12/2020	Sowing of 20 *Urochloa brizantha* seeds/pot
25/01/2021	Sowing 15 g of *Urochloa brizantha* seeds/pot
16/02/2021	Application of 100 ml of Hoagland and Arnon solution/pot
24/02/2021	Transplanting seedlings to match the number of plants/pot
05/03/2021	Adding dung beetles to treatments T1, T2 and T3
12/03/2021	Application of 1.1 g of KCl + 1.53 g of STP + 0.24 g of urea
09/04/2021	Application of 0.24 g of urea
07/05/2021	Application of 0.24 g of urea
01/06/2021	Leaf sample removal for photosynthetic pigment analysis
04/06/2021	Soil samples for physical, chemical and microbiological analysis

Table S3

Results of soil's physical, chemical, and microbiological analyses in mesocosm experiment with dung beetles. T1 (t): treatment with telecoprids, T2 (p): treatment with paracoprids, T3 (t+p): mixed treatment, with both functional groups, T4 (NPK): treatment with mineral fertilizer. Different letters indicate significant differences according to Tukey's test with a significance level of 0.05. * indicates a significant difference between the treatments, with $p < 0.05$.

Soil variables	Mean and standard deviation per treatment					LR	DF	P
	Control	T1 (t)	T2 (p)	T3 (t+p)	T4 (NPK)			
Soil bulk density (g cm^{-3})	1.24 ± 0.06 ^{ab}	1.28 ± 0.08 ^{a}	1.15 ± 0.05 ^{b}	1.23 ± 0.09 ^{ab}	1.24 ± 0.07 ^{ab}	12.950	4	0.011*
WMD (mm)	1.64 ± 1.42 ^{ab}	1.49 ± 0.14 ^{ab}	1.68 ± 0.07 ^{a}	1.59 ± 0.20 ^{ab}	1.38 ± 0.24 ^{b}	12.803	4	0.012*
GMD (mm)	0.57 ± 0.08	0.56 ± 0.05	0.54 ± 0.09	0.53 ± 0.06	0.52 ± 0.08	1.669	4	0.796
Macroaggregates (g)	5.07 ± 0.79 ^{ab}	4.32 ± 0.70 ^{ab}	5.40 ± 0.41 ^{a}	4.97 ± 1.16 ^{ab}	3.68 ± 1.18 ^{b}	14.136	4	0.007*
Mesoaggregates (g)	11.09 ± 1.48	11.93 ± 1.53	9.61 ± 2.02	10.45 ± 2.58	12.51 ± 0.94	8.953	4	0.062
Microaggregates (g)	6.70 ± 1.31	6.14 ± 0.86	7.02 ± 1.70	6.84 ± 1.46	6.60 ± 0.55	2.287	4	0.683
pH	4.49 ± 0.24 ^{b}	4.26 ± 0.11 ^{b}	4.62 ± 0.22 ^{ab}	4.41 ± 0.19 ^{b}	5.07 ± 0.59 ^{a}	28.830	4	< 0.001*
H + Al (cmol$_c$ dm^{-3})	9.08 ± 1.76 ^{a}	4.94 ± 1.79 ^{b}	5.36 ± 0.53 ^{b}	6.93 ± 1.28 ^{ab}	6.20 ± 0.91 ^{ab}	32.135	4	< 0.001*
K (mg dm^{-3})	18.83 ± 1.19 ^{c}	36.89 ± 8.52 ^{b}	53.67 ± 9.78 ^{a}	60.53 ± 5.49 ^{a}	53.58 ± 12.37 ^{a}	184.320	4	< 0.001*
P (mg dm^{-3})	2.21 ± 0.56 ^{d}	5.80 ± 1.35 ^{c}	9.93 ± 0.92 ^{b}	9.81 ± 3.54 ^{b}	39.06 ± 16.69 ^{a}	354.790	4	< 0.001*
Ca (cmol$_c$ dm^{-3})	1.78 ± 0.28	2.06 ± 0.56	2.34 ± 0.52	2.44 ± 0.85	1.71 ± 0.38	8.003	4	0.091
Mg (cmol$_c$ dm^{-3})	0.40 ± 0.12 ^{b}	0.68 ± 0.37 ^{ab}	0.85 ± 0.27 ^{a}	1.35 ± 0.66 ^{a}	0.37 ± 0.11 ^{b}	35.377	4	< 0.001*
Al (cmol$_c$ dm^{-3})	2.09 ± 0.32 ^{a}	1.57 ± 0.51 ^{ab}	0.94 ± 0.36 ^{c}	1.01 ± 0.33 ^{bc}	1.92 ± 0.32 ^{a}	41.482	4	< 0.001*
SB (cmol$_c$ dm^{-3})	2.23 ± 0.31 ^{b}	2.83 ± 0.87 ^{ab}	3.32 ± 0.63 ^{ab}	3.95 ± 1.31 ^{a}	2.22 ± 0.49 ^{b}	20.087	4	< 0.001*
CEC$_{pH\ 7.0}$ (cmol$_c$ dm^{-3})	11.31 ± 1.72 ^{a}	7.77 ± 1.54 ^{c}	8.68 ± 0.40 ^{bc}	10.87 ± 0.77 ^{ab}	8.42 ± 0.75 ^{bc}	39.990	4	< 0.001*
Effective CEC (cmol$_c$ dm^{-3})	4.32 ± 0.31	4.40 ± 0.52	4.26 ± 0.36	4.97 ± 1.05	4.14 ± 0.30	6.725	4	0.151
Aluminum saturation (%)	48.32 ± 6.40 ^{a}	36.58 ± 13.11 ^{ab}	22.56 ± 9.97 ^{b}	22.27 ± 12.58 ^{b}	46.72 ± 9.32 ^{ab}	24.393	4	< 0.001*
Base saturation (%)	20.18 ± 4.45 ^{b}	37.52 ± 11.78 ^{a}	38.16 ± 6.52 ^{a}	36.23 ± 11.64 ^{a}	26.51 ± 6.15 ^{ab}	30.863	4	< 0.001*
TN (g kg^{-1})	0.41 ± 0.04 ^{c}	0.53 ± 0.06 ^{b}	0.73 ± 0.12 ^{a}	0.94 ± 0.26 ^{a}	0.45 ± 0.03 ^{bc}	121.680	4	< 0.001*
OM (g kg^{-1})	6.93 ± 0.48 ^{c}	11.24 ± 1.46 ^{b}	23.52 ± 3.99 ^{a}	22.96 ± 7.42 ^{a}	6.99 ± 0.63 ^{c}	303.800	4	< 0.001*
POC (g kg^{-1})	0.64 ± 0.09 ^{c}	3.15 ± 1.15 ^{b}	9.37 ± 2.28 ^{a}	8.54 ± 3.02 ^{a}	0.64 ± 0.09 ^{c}	434.810	4	< 0.001*
MOM-C (g kg^{-1})	3.37 ± 0.22	3.37 ± 0.56	4.27 ± 2.00	4.77 ± 3.72	3.42 ± 0.41	4.554	4	0.336
PON (g kg^{-1})	0.07 ± 0.01 ^{c}	0.18 ± 0.05 ^{b}	0.48 ± 0.10 ^{a}	0.68 ± 0.33 ^{a}	0.07 ± 0.00 ^{c}	344.320	4	< 0001*

MOM-N (g kg^{-1})	0.34 ± 0.04 ^{ab}	0.35 ± 0.03 ^{ab}	0.25 ± 0.12 ^{b}	0.26 ± 0.11 ^{ab}	0.38 ± 0.01 ^{a}	14.128	4	0.007*
BSR (μg C-CO_2 g dry $soil^{-1}$ h^{-1})	0.64 ± 0.49	0.41 ± 0.37	0.90 ± 0.43	0.57 ± 0.37	0.51 ± 0.20	5.607	4	0.230
MBC (μg g^{-1})	51.69 ± 24.25	55.02 ± 33.15	81.91 ± 47.54	76.82 ± 38.77	88.76 ± 16.39	5.688	4	0.224

WMD: weighted mean diameter, GMD: geometric mean diameter, SB: sum of bases, CEC: cation exchange capacity, TN: total nitrogen, OM: organic matter, POC: particulate organic carbon, PON: particulate organic nitrogen, MOM-C: mineral organic matter carbon, MOM-N: mineral organic matter nitrogen, BSR: basal soil respiration, MBC: microbial biomass carbon, LR: likelihood ratio test, DF: degrees of freedom.

Table S4

Physiological and nutritional analyses of *Urochloa* (*Brachiaria*) *brizantha* grass in a mesocosm experiment with dung beetles. T1 (t): treatment with telecoprids, T2 (p): treatment with paracoprids, T3 (t+p): mixed treatment, with both functional groups, T4 (NPK): treatment with mineral fertilizer. Different letters indicate significant differences according to Tukey's test with a significance level of 0.05. * indicates a significant difference between the treatments, with $p < 0.05$.

Plant variables	Mean and standard deviation per treatment					LR	DF	P
	Control	T1 (t)	T2 (p)	T3 (t+p)	T4 (NPK)			
DMS/plant (g)	0.05 ±0.05	0.06 ± 0.02	0.04 ± 0.02	0.03 ± 0.02	0.05 ± 0.03	3.406	4	0.492
DMR/plant (g)	0.04 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.04 ± 0.01	2.885	4	0.577
TDM/plant (g)	0.09 ± 0.05	0.09 ± 0.02	0.07 ± 0.01	0.06 ± 0.02	0.09 ± 0.04	3.936	4	0.415
Chlorophyll *a* (μg g^{-1})	33.06 ± 9.92	30.06 ± 9.36	32.99 ± 9.02	26.72 ± 5.91	39.72 ± 21.55	3.773	4	0.438
Chlorophyll *b* (μg g^{-1})	18.92 ± 4.01	17.08 ± 4.27	21.24 ± 6.13	16.99 ± 2.75	22.35 ± 11.25	4.403	4	0.354
Carotenoids (μg g^{-1})	5.06 ± 1.28	4.71 ± 1.17	4.39 ± 0,99	4.26 ± 0.10	5.10 ± 0.67	2.603	4	0.626
Total chlorophyll (μg g^{-1})	51.99 ± 13.60	47.15 ± 13.45	54.23 ± 14.80	43.72 ± 8.38	62.08 ± 32.79	3.847	4	0.427
Foliar K (g kg^{-1})	11.39 ± 3.24 ^{a}	11.06 ± 0.95 ^{a}	11.56 ± 1.33 ^{a}	10.69 ± 1.57 ^{ab}	7.91 ± 0.81 ^{b}	13.544	4	0.008*
Root K (g kg^{-1})	1.51 ± 0.33 ^{ab}	1.40 ± 0.62 ^{ab}	1.95 ± 0.66 ^{a}	1.08 ± 0.27 ^{b}	1.19 ± 0.25 ^{ab}	10.916	4	0.027*
Foliar N (g kg^{-1})	19.84 ± 2.00	22.17 ± 1.47	20.26 ± 1.65	20.94 ± 1.76	20.96 ± 1.38	8.799	4	0.066
Root N (g kg^{-1})	7.53 ± 1.16	7.73 ± 0.99	7.85 ± 1.40	7.30 ± 1.07	7.90 ± 0.79	1.027	4	0.906
Foliar P (g kg^{-1})	0.58 ± 0.25 ^{b}	1.42 ± 0.26 ^{a}	1.36 ± 0.24 ^{a}	1.25 ± 0.23 ^{a}	1.08 ± 0.15 ^{a}	62.710	4	< 0.001*
Root P (g kg^{-1})	1.76 ± 0.65	1.81 ± 0.69	2.29 ± 0.36	2.05 ± 0.64	2.24 ± 0.58	4.017	4	0.404

DMS: dry mass of the shoot, DMR: dry mass of the root, TDM: total dry mass, LR: likelihood ratio test, DF: degrees of freedom.

Table S5

Relationship between the amount of cattle dung removed and physical, chemical, and microbiological variables of the experimental soil in mesocosm with dung beetles.

Soil variables	**t**	**DF error**	**P**
Soil bulk density	-1.806	18	0.088
WMD	1.833	18	0.083
GMD	-1.684	18	0.109
Macroaggregates	2.519	18	0.021*
Mesoaggregates	-3.599	18	0.002*
Microaggregates	1.556	18	0.137
pH	1.922	18	0.070
H + Al	2.748	18	0.013*
K	1.482	18	0.155
P	2.422	18	0.026*
Ca	-0.084	18	0.934
Mg	0.861	18	0.400
Al	-0.846	18	0.409
SB	0.712	18	0.485
CECph7.0	2.410	18	0.026*
Effective CEC	0.408	18	0.688
Aluminum saturation	-1.081	18	0.294
Base saturation	-0.802	18	0.433
TN	3.669	18	0.001*
OM	3.013	18	0.007*
POC	2.558	18	0.019*
MOM-C	1.296	18	0.211
PON	3.834	18	0.001*
MOM-N	-1.889	18	0.075
BSR	1.430	18	0.170
MBC	0.829	18	0.418

WMD: weighted mean diameter, GMD: geometric mean diameter, SB: sum of bases, CEC: cation exchange capacity, TN: total nitrogen, OM: organic matter, POC: particulate organic carbon, PON: particulate organic nitrogen, MOM-C: mineral organic matter carbon, MOM-N: mineral organic matter nitrogen, BSR: basal soil respiration, MBC: microbial biomass carbon, DF: degrees of freedom.

Table S6

Relationship between the amount of cattle dung removed and variables of biomass, photosynthetic pigments, and macronutrients from leaves and roots of grasses in a mesocosm experiment with dung beetles.

Plant variables	t	DF error	P
DMS/plant	-1.528	18	0.144
DMR/plant	0.759	18	0.457
TDM/plant	-1.641	18	0.118
Chlorophyll *a*	-0.209	18	0.837
Chlorophyll *b*	0.426	18	0.675
Carotenoids	-0.277	18	0.785
Total chlorophyll	0.003	18	0.998
Foliar K	-0.913	18	0.373
Root K	-0.224	18	0.825
Foliar N	-2.225	18	0.039*
Root N	0.413	18	0.684
Foliar P	-0.576	18	0.572
Root P	1.859	18	0.079

DMS: dry mass of the shoot, DMR: dry mass of the root, TDM: total dry mass, DF: degrees of freedom.

3 CONCLUSÃO

A remoção de fezes efetuada por besouros coprófagos é uma função ecossistêmica precursora de várias modificações positivas em ambientes pecuários, que repercutem em serviços ecossistêmicos de aumento de produtividade e qualidade ambiental. Neste estudo, por meio de experimento em mesocosmos, pôde-se observar a diferença na eficiência dos grupos funcionais de rola-bostas em realizar a remoção de fezes bovinas, sendo os paracoprídeos mais eficientes. Corroborando as hipóteses iniciais, os resultados das análises de solo e das plantas também mostram diferenças entre as espécies na modificação das características físicas e químicas do solo e nutricionais das plantas, muitas delas superando a aplicação de fertilizante mineral. Porém, diferentemente da predição inicial, não houve sinergia entre os grupos na realização da maioria das funções ecossistêmicas analisadas. Paracoprídeos da espécie *Dichotomius sericeus* se destacaram na melhoria das condições físicas e químicas do solo, e, de forma geral, os besouros aumentaram o teor de matéria orgânica e as frações particuladas de C e N do solo, tendo efeito corretivo ao diminuir as concentrações de alumínio. Nas plantas, a ação dos besouros foi mais discreta, mas também influenciou positivamente os conteúdos de P e K. A remoção de fezes bovinas foi positivamente relacionada a vários atributos físicos e químicos do solo. Desta forma, ressalta-se a importância desse grupo de organismos em sistemas pecuários, onde podem ser usados como uma forma sustentável de fertilização.

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