Termites are the main dung removals in a degraded landscape in Brazil

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Termites are one of the most relevant groups for recycling nutrients and keeping the flow of energy in ecosystems. Although their role as lignocellulose decomposers is the focus of studies, they also act as dung recyclers, but their importance in this process is poorly understood. Here we performed manipulation experiments to determine dung removal by termites in forest remnants and cattle pastures in a fragmented Atlantic Forest landscape. We used wire bags of different mesh sizes placed along transects in three forest fragments and pastures for 10 days to compare the contribution of termites and other coprophagous macrodetritivores to dung removal. Our results indicated that termites removed more dung in pastures than in the forest fragments. In addition, dung beetle exclusion significantly reduced the percentage of dung removal within forest fragments, but not on pastures, indicating termites are important dung recyclers in pastures.

KEYWORDS

Isoptera, forest fragmentation, cattle dung, Atlantic forest, beetles, ecological roles

Introduction

Most natural environments have been currently modified by human population growth causing different degrees of habitat loss (Fahrig, 2019). This loss in turn impacts biodiversity and causes the disruption of several ecological processes (Veldkamp et al., 2020). Due to a growing human population, cattle production has increased significantly over the years, which contributed about 12–18% of total greenhouse gas emissions, mainly through gut fermentation and excreta. In addition, livestock dung is also involved in eutrophication and acidification of natural ecosystems (Cai et al., 2021).

Termites (Blattodea) are ecosystem engineers, modulating the balance of carbon between the soil and the atmosphere through lignocellulose decomposition mediated by symbiotic microorganisms (Brune, 2014). The construction of tunnel networks and nests by these insects alters the physical and chemical properties of the soil through bioturbation and deposition of organic material, promoting growth and modifying the

community structure of plants in the surrounding soils (Jouquet et al., 2011; Ashton et al., 2019; Griffiths et al., 2021; Myer et al., 2021). Basal groups of termites (called *lower termites*) are primarily xylophagous and rely primarily on flagellate protozoans for lignocellulose digestion (Brune, 2014). However, the evolutionary success of the Termitidae (the most diverse and numerous family of termites, called *higher termites*) is attributed to the loss of protozoans and the acquisition of specialized lignocellulolytic bacterial lineages that allowed diet diversification, including wood, grass, soil, litter, lichen, and fungi (Bourguignon et al., 2011; Brune and Dietrich, 2015). In tropical environments, termites are the main macrodetritivores, decomposing half of deadwood in rainforests and more than 30% of the litter in savannas (Veldhuis et al., 2017; Griffiths et al., 2019; Sundsdal et al., 2020).

Dung removal is an important ecological function provided by some macrodetritivores that benefits to the environment through the mobilization of carbon and nitrogen into the soil, reduction of greenhouse gasses and ammonia (Cai et al., 2021), and fly pest suppression (Nichols et al., 2008; Sitters et al., 2014). Dung removal have been usually attributed to dung beetles (Scarabeinae) (Nichols et al., 2008); however, several termite species are also known to feed on a wide range of herbivore mammal dung; the majority of these termites belong to the grass and litter feeding guilds (Freymann et al., 2008) and are likely attracted to the fibrous plant material, nitrogen, and water content of feces (Anderson and Coe, 1974; Freymann et al., 2008).

Brazil is one of the largest producers of livestock in the world (OECD and FAO, 2021). Expanding cattle production requires additional land and water, in addition to increasing excrement output. The destruction of forests through the expansion of grazing land for livestock is one of the main drivers of decreased biodiversity (Sano et al., 2008; Freitas et al., 2010). The loss of coprophagous organisms, particularly termites and dung beetles (Braga et al., 2012; Cancello et al., 2014), may bring further issues to the environment due to their key role in removing dung and the other indirect ecosystem services they exert that were listed above (Nichols et al., 2008; Cai et al., 2021). However, there is no information on how habitat degradation simultaneously affects these organisms and their ecological role in dung removal. In this study, we established a manipulative experiment to quantify and compare the relative contribution of dung removal by termites and other coprophagous macrodetritivores to pastures and forest fragments in an Atlantic Forest landscape.

Materials and methods

Study site

We conducted this study in the rural areas of Alfenas (21°25′45″ S; 45°56′50″ W), a municipality in the southern part of the Brazilian state of Minas Gerais (**Supplementary Table 1**). This region was originally covered by Atlantic Forest but agricultural development resulted in a largely fragmented landscape (**Figure 1**). The Atlantic Forest is considered a biodiversity hotspot due to its high diversity and endemism (Myers et al., 2000). However, it is a domain severely fragmented and threatened with less than 28% of the original areas remaining (Rezende et al., 2018). Experiments were conducted during January–March 2014 in three forest fragments and three deforested areas converted in cattle pastures. These sites were selected using digital image processing of the satellite Sino-Brazilian CBERS-2B with a resolution of 20 m following two criteria: (i) Similarity of spectral attributes such as color and texture and (ii) the presence of natural cover forest in a circular buffer of 1 km radius from the center of selected sites. Forest fragments contains semi decidual vegetation (Carneiro et al., 2014) while the pastures, dominated by *Brachiaria* grasses were not exposed to cattle grazing to avoid interference with dung removal experiments. Sampling did not involve any endangered species and the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), a Brazilian Ministry of the Environment's enforcement agency, provided authorization for termite sampling (SISBIO n° 33269). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Termites associated with cattle dung

Fresh dairy (115 samples) and dry-cow dung pats (183 samples) were collected at cattle grazing pastures 1 km apart from the experimental areas. Termites were carefully removed using forceps and brought to the lab where they were identified to the lowest possible taxon.

Dung removal

We set up this experiment using circular arenas of 60 cm in diameter limited by a fence of nylon with 20 cm in height to avoid dung transportation outside the arenas. In the study site, we found that, apart from termites, the most abundant coprophagous macrodetritivores were dung beetles (Alves, 2015). To assess dung removal by termites, we used 3 mm wire mesh to produce "only termite accessible dung bags" because termite species found in cattle dung have a body width of 1.52 ± 0.39 mm (mean ± SD) (Araujo, 1970; Coles De Negret and Redford, 1982; Redford, 1984; Krishna et al., 2013). Because the smallest dung beetle species found in this study have body width of 3.47 ± 0.34 mm (*N* = 24) (**Supplementary Table 2**), 3 mm dung bags allow termites to feed on the dung, effectively excluding dung beetles (Howison et al., 2016). Each bag was filled with 200 g of a mixture of
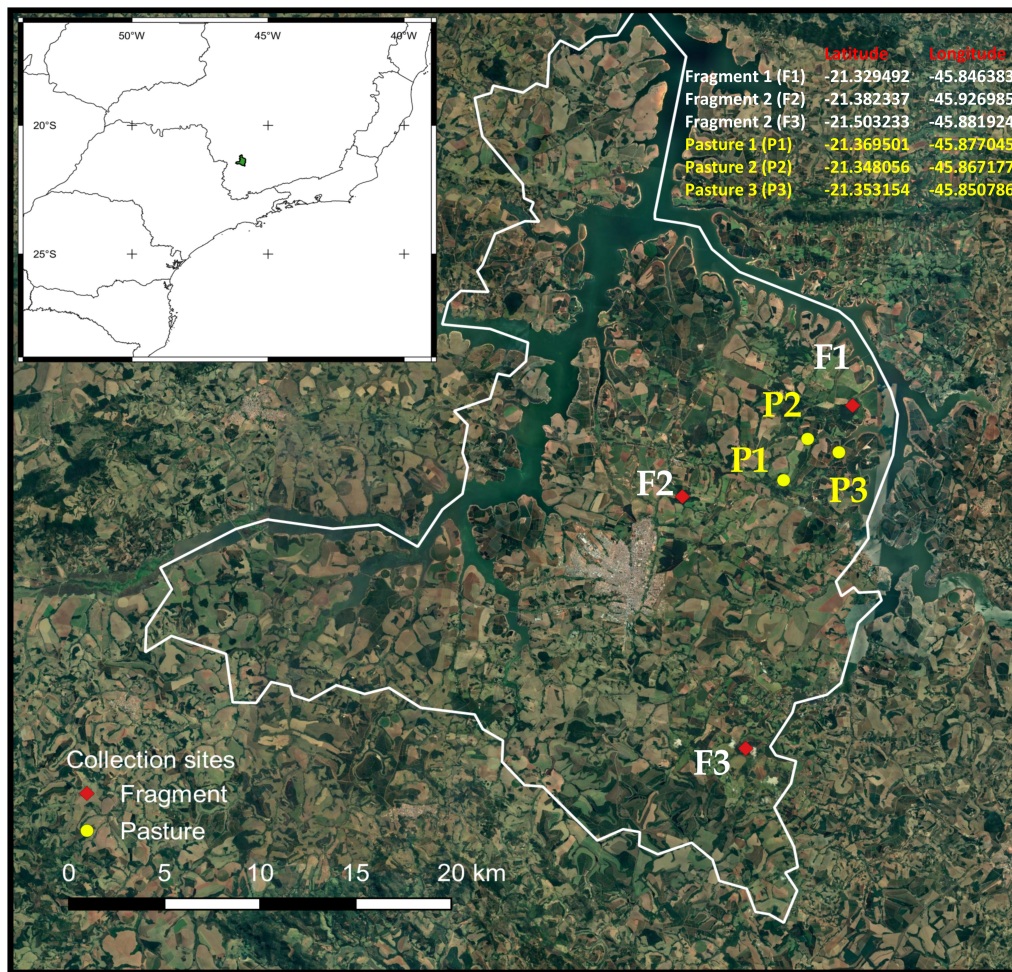
FIGURE 1
Map of study site and experimental design. Dung removal was evaluated in the Alfenas region of the southeastern Brazil, in the state of Minas Gerais.

herbivore (cow) and omnivore (pig) dung, obtained from local farmers and placed at the center of the arenas. Both cow and pig dung are effective attractants to a wide range of coprophagous organisms dependent on the dung of different mammal feeding guilds (Nichols et al., 2008). Two additional experiments with "dung bags" of 1 mm (macrodetritivores inaccessible) and 20 mm (macrodetritivores accessible) wire mesh were used in combination with "only termite accessible dung bags" to evaluate the contribution of all coprophagous macrodetritivores to dung removal (Table 1).

Each sample was protected from rain by covering it with a 30 cm diameter plastic plate placed 15 cm above it, as a roof. The arenas were placed along three 120 m transects at each habitat type. Transects were placed at the center of the site and perpendicular to one of the borders. In each transect, we randomly deployed 12 arenas (four for each treatment) separated by 10 m. We had a total of 216 arenas (forest $n = 108$, pastures $n = 108$) in 18 transects across two habitat types in

six sites (Figure 1). Dung removal was measured after 10 days. Only samples with termite or dung beetle activity (presence of these insects, termite galleries, dung beetle tunnels) were considered in the analyses. At the start of the experiment, we estimated the moisture content of twenty dung subsamples by determining their fresh and dry weight and used this value to calculate the initial dry biomass and the relative weight loss of each sample, following to Sitters et al. (2014). Dry weights were obtained oven drying fresh dung samples at 60°C for 24 h. Dung removal was calculated as a percentage of dry weight loss after 10 days for each experimental treatment. Termites and dung beetles were carefully removed from dung samples in the bags and identified to the lowest possible taxon using taxonomic keys (Vaz-De-Mello et al., 2011; Rocha et al., 2017) and comparison with a reference collection from the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the Invertebrate Ecology and Conservation Laboratory, at the Universidade Federal de Lavras (UFLA), Brazil, respectively.

TABLE 1 Richness and overall abundance of dung beetles and termites for the different treatments and habitat types.

Accessibility treatments	Dung bag mesh size	Symbol	Habitat	Richness (abundance)	
				Dung beetles	Termites
Macrodetritivore inaccessible	1 mm		Forest	0	0
			Pasture	0	0
Only termite accessible	3 mm		Forest	0	6 (213)
			Pasture	0	4 (36)
Macrodetritivore accessible	20 mm		Forest	26 (291)	1 (10)
			Pasture	32 (664)	2 (7)

Statistical analyses

All the analysis and graphics were generated using R version 3.4.4 (R Core Team, 2019). We examined differences in richness between pastures and forest fragments through individual-based accumulation curves (Chao et al., 2014) using de iNEXT package (Hsieh et al., 2016). A permutational multivariate analysis of variance (PERMANOVA) was used to evaluate differences of termites and dung beetle community composition between habitats (Anderson, 2001). Singletons and doubletons were excluded from the analyses. We fitted beta regressions models with a logit link function using the *betareg* function (Cribari-Neto and Zeileis, 2010) to test for differences of the percentage of dung removal between habitat types and the experimental treatments. Explanatory variables to affect the outcome were the type of habitat and macrodetritivore accessibility. We carried out least square mean analyses for multiple comparisons to evaluated the effect of model predictors using the *emmeans* function of the lsmeans package (Lenth, 2016). The significant threshold was $P < 0.05$.
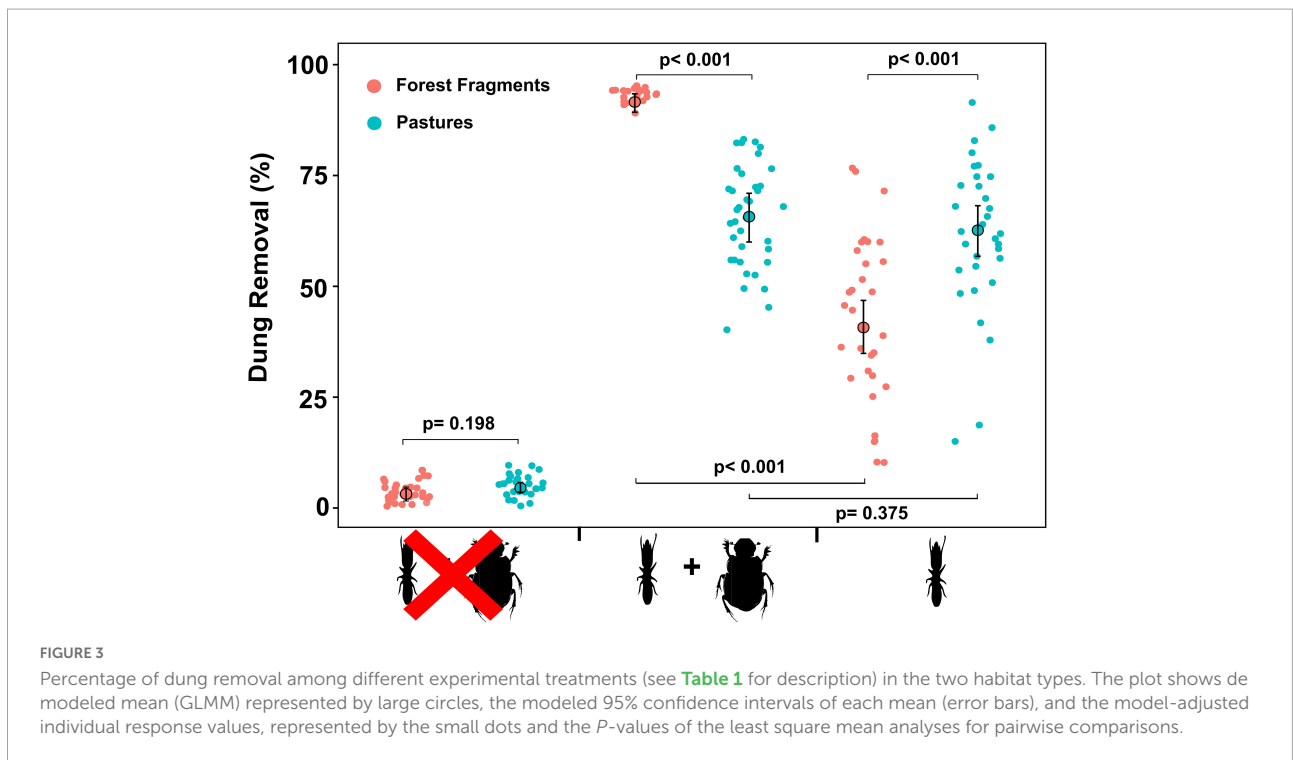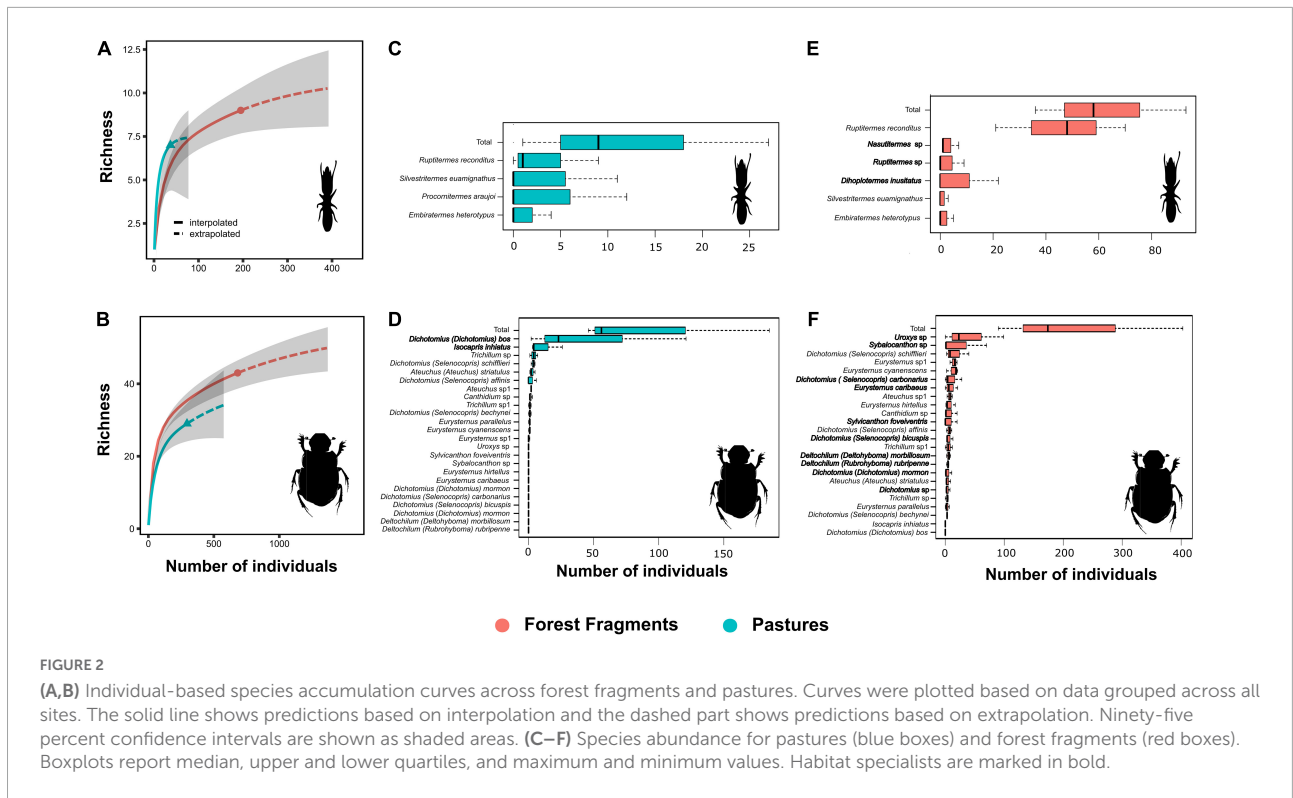
Results

Dung samples in the 3 mm mesh bags were colonized by termites and micro arthropods (mites and springtails), while samples in the 20 mm bags also attracted dung beetles. Dung samples in the 1 mm bags were colonized only by micro-arthropods. Simultaneous colonization by termites and dung beetles was observed in only 12 bags. We collected eight species of termites from the dung bags. *Ruptitermes reconditus* (Apicotermitinae) was found in both pastures and forest fragments; however, it was the most abundant species in forest fragments). Three species were found exclusively in forest fragments and one in the pastures. In the areas with cattle activity, we found seven species of termites in 36.6% of the dry dung pats, with a higher incidence of *R. reconditus* and *Procornitermes araujoi* (Syntermitinae) (Supplementary Table 3). Fresh wet dung pats were not colonized by termites. On the other hand, 40 dung beetle species were collected. *Uroxys*

sp. (Ateuchini) and *Dichotomius bos* (Coprini) were the most abundant species in forest fragments and pastures, respectively (Supplementary Table 2).

Our results indicated that richness (Figures 2A,B) and species composition of termite and dung beetles were not affected by habitat loss (Termites: $F = 0.43$; $P = 0.50$; Dung-beetles: $F = 4.63$; $P = 0.10$; PERMANOVA), but the abundance of these insects on pastures decreased (Figures 2C–F). Dung removal has also been impacted by reduction of forest cover and macrodetritivore suppression. For instance, exclusion of dung beetles significantly reduced the percentage of dung removal within forest fragments ($Z = -17.78$; $P < 0.001$) but not on pastures ($Z = -0.89$; $P = 0.375$). On the other hand, termites removed more dung from pastures than from forest fragments ($Z = 6.33$; $P < 0.001$). Finally, dung samples in the macrodetritivore-inaccessible bags showed a non-significant weight reduction ($Z = 1.29$; $P = 0.198$) (Supplementary Tables 4, 5 and Figure 3).

Discussion

In this study, we demonstrate that termites play an important role in dung removal, particularly in pasture areas, where these insects were the main dung removals. Savannah termites are more tolerant to habitat perturbation due to their cryptic lifestyle, their thermoregulated nests or by their habit of foraging at night when temperature and humidity are suitable for these insects (Coles De Negret and Redford, 1982; Korb, 2003). In this study, the absence of tree cover excluded forest-restricted dung beetle species as found in other ecosystems (Halffter and Arellano, 2002). Although the experimental setup did not allow us to quantify the dung removal by dung beetles alone, the exclusion of these insects significantly reduced dung removal within the forest fragments, but had no effect on pastures. It is possible that as dung beetle abundance decreases, termites assume a similar role in the ecosystem, thereby mitigating the effects of habitat loss on dung beetle abundance. These results support that the functional role of termites in removal of mammalian dung is widely

FIGURE 2

(A,B) Individual-based species accumulation curves across forest fragments and pastures. Curves were plotted based on data grouped across all sites. The solid line shows predictions based on interpolation and the dashed part shows predictions based on extrapolation. Ninety-five percent confidence intervals are shown as shaded areas. **(C–F)** Species abundance for pastures (blue boxes) and forest fragments (red boxes). Boxplots report median, upper and lower quartiles, and maximum and minimum values. Habitat specialists are marked in bold.

FIGURE 3

Percentage of dung removal among different experimental treatments (see **Table 1** for description) in the two habitat types. The plot shows de modeled mean (GLMM) represented by large circles, the modeled 95% confidence intervals of each mean (error bars), and the model-adjusted individual response values, represented by the small dots and the *P*-values of the least square mean analyses for pairwise comparisons.

underestimated (Freymann et al., 2008), especially in disturbed habitats.

Savannas and pastures in Brazil are populated by a wide variety of termite feeding guilds (Carrijo et al., 2009) and

our results showed that termite dung removal was higher on the pastures than in forest fragments, despite the decreasing abundance of these insects in the dung bags in this habitat in comparison with forest fragments. Due to the high temperatures

and low humidity, termites from savannas and pastures forage mainly at night to avoid dehydration. Dung bags were collected during daylight hours, which may explain the lower abundance of termite foragers observed in the pastures. Termites within forest fragments, on the other hand, are naturally protected against desiccation. Finally, in the absence of dung beetles and termites, physical weathering, the activity of micro arthropods and microbes account for only 5% of dung removal.

In the pastures with cattle activity, termites were only found in dry dung pats. This can be explained by the following factors. First, most adult dung beetles feed on fresh dung (Holter and Scholtz, 2007) and termite behavior may change in response to competition from dung beetles. The second possible explanation is the tolerance of termites to climatic conditions in the pastures, which could also allow these insects to use dry dung pats for a longer period. In addition, dung beetles, due to their narrow thermal tolerances, cannot cope with the drastic temperature and humidity changes characteristic of deforested habitats (Barragán et al., 2014; Gómez-Cifuentes et al., 2017); a third possible explanation is fiber, the main component of dry cattle dung (Holter, 2016) that could act as an extra source of grass and litter and thus attract termites; and finally, dung may provide termites with nitrogen to supplement their low-nitrogen diet (Higashi et al., 1992). Although there is no information on the interaction between dung beetle and termites, the small number of samples colonized by both insects suggests that they may be mutually exclusive (Gould et al., 2001).

Although this work is constrained by a relatively short duration and low number of sites, this is the first study to show the relative contribution of termites to dung removal under the influence of habitat degradation. A better understanding of termites' role in dung removal could be achieved by collecting samples at night when termites forage, and more species and individuals could be registered. To further disentangle climatic effects of season, additional experiments of dung removal with a longer duration could be established. Our results support the utility of termites as focal taxa in cattle pastures. The expansion of livestock in Brazil is expected to continue growing over the next decade (OECD and FAO, 2021) leading to increased deforestation and cattle-dung accumulation. Although termites from pastures in Brazil are often considered pests and their nests are removed by local farmers, dung removal by termites in livestock areas could reduce harmful emissions of ammonia and greenhouse gasses. Termite benefits are also linked to nutrient cycling and pedoturbation that help preserve soils (Herrick and Lal, 1996) and conservation of these insects should be a priority.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**,

further inquiries can be directed to the corresponding author.

Author contributions

AA designed the study. AA and FA performed the experiments. AA, FA, and DA-O analyzed the data. AA, MR, and DA-O wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.982602/full#supplementary-material

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