

# Linking dung beetle-mediated functions to interactions in the Atlantic Forest: Sampling design matters



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## Abstract

Interactions between dung beetles and vertebrate dung are intimately linked to a suite of ecosystem functions in tropical forests. We show that the trapping method and the type of dung used affect the suite of beetles captured, with the potential to influence the outcome of experiments linking functions to interactions.

## KEYWORDS

Brazil, diet choice, dung beetle interactions, ecosystem functions, mammal, mammal dung, tropical forest

Not all species interactions are equal in terms of their contribution to the functioning of an ecosystem. A common assumption is that observational data on frequencies of interactions, measured using standard methods, can provide an accurate and meaningful estimate of functioning (Balvanera *et al.*, 2006); however, studies of ecosystem functioning need to distinguish functionally important species interactions and quantify their strength. For example, in plant-pollinator networks this can be done by distinguishing pollination from visitation (King, Ballantyne, & Willmer, 2013) and measuring the frequency of these interactions (Chacoff, Resasco, & Vázquez, 2018).

Understanding the functional consequences of interactions is particularly relevant in high-diversity tropical systems, where anthropogenic pressure is causing changes in the structure and function of many ecosystems (Morris, 2010). Dung beetles are widely used as biological indicators, and for the study of ecosystem functions in tropical forests (Nichols & Gardner, 2011; Santos-Heredia, Andresen, & Zárate, 2010). The majority of dung beetles use dung for feeding both as adults, and as the resource for larval development, with the formation and burial of brood balls contributing to ecosystem functions such as nutrient cycling, bioturbation, and seed

dispersal (Nichols *et al.*, 2008). In the tropics, most dung beetles relocate dung by rolling brood balls and burying them (rollers) or by burying them directly beneath the dung pad (tunnellers) (Hanski & Cambefort, 1991). In addition to dung beetle body size (Nervo, Tocco, Caprio, Palestini, & Rolando, 2014), the nesting strategy of dung beetles can influence the rate of dung removal (Slade, Mann, Villanueva, & Lewis, 2007). Dung beetle species assemblages therefore have an impact on the ecosystem functions they provide, but the magnitude of interactions between dung beetles and mammal dung have rarely been quantified at all, especially in tropical systems (but see Slade, Riutta, Roslin, & Tuomisto, 2016).

Although dung beetles are commonly assumed to be generalist feeders (Frank *et al.*, 2018; Hanski & Cambefort, 1991), species can show preference toward dung of certain mammal species or trophic guilds (Bogoni & Hernández, 2014; Santos-Heredia *et al.*, 2010). However, few studies have specifically tested the attractiveness of dung from mammal species native to the area of study (but see Enari, Koike, & Sakamaki, 2013; Frank, Hülsmann, Assmann, Schmitt, & Blüthgen, 2017). In addition, standardized bait sizes are often used irrespective of the mammal species (e.g., Bogoni & Hernández, 2014;

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Marsh, Louzada, Beiroz, & Ewers, 2013). Several factors influence dung choice by dung beetles. Dung volume affects the body size of dung beetles attracted, as well as their abundance (Finn & Giller, 2000; Peck & Howden, 1984). Dung beetles also vary in their method of feeding on dung between the larval and adult stage and may show life-stage specific preferences (Holter & Scholtz, 2007). Dung quality can also influence the size of brood balls and the resulting adult body size (Gittings & Giller, 1998; Arellano, Castillo-Guevara, Huerta, Germán-García, & Lara, 2015; but see Frank, Brückner, et al. 2017); it may also influence whether an individual chooses to feed on or breed in the dung.

We explored whether the type of mammal dung and the volume of it used in a trap influences the assemblage of dung beetles attracted to it. We assessed dung beetle species and functional groups captured in burial interception traps, which are thought to give a more realistic picture of the dung beetle assemblages actually using (rather than just attracted to) the dung, especially for nesting (see Arellano, 2016; Goh & Hashim, 2018). These were compared with data from pitfall traps, which attract dung beetles seeking to use dung for both feeding and nesting, and which are frequently used as a proxy for dung exploitation (Larsen & Forsyth, 2005). We asked (a) Does the type of dung and volume used affect the assemblage of beetles attracted to a trap? and (b) Are different assemblages of dung beetles attracted to pitfall and burial intercept traps? We compared each dung and trap type in terms of two assemblage-level metrics (total dung beetle abundance and biomass) and two functional categorisations (nesting strategy and per-beetle biomass).

Traps were baited with dung of native Atlantic Forest mammal species, sourced from a local zoo, using a realistic range of sizes for each mammal species. Lesser grison (*Galictis cuja* (Molina, 1782)), jaguar (*Panthera onca* (Linnaeus, 1758)), ocelot (*Leopardus pardalis* (Linnaeus, 1758)), crab-eating raccoon (*Procyon cancrivorus* (Cuvier, 1798)), and black capuchin (*Sapajus nigritus* (Goldfuss, 1809)) as well as human and pig dung were individually collected, weighed, and frozen until use (see Table S1 for the range of dung volumes used for each mammal). These dung types were deployed where available in both trap types (burial interception and pitfall) once per month from December 2015 to February 2016 and only in pitfall traps in March 2016. We also conducted additional sampling using human dung baited pitfall traps once per month throughout the sampling period.

Fieldwork took place at three sites of lowland tropical forest separated by 0.5–1 km within a continuous area of Atlantic Forest in Paraná, Brazil (25°27'11"S, 48°52'57"W; Figure S1). Two transects 200 m apart were established in each site. One transect consisted of burial intercept traps and the other of pitfall traps. Both transects had eight traps set 200 m apart. Pitfall traps followed a design consistent with previous studies (e.g., Marsh *et al.*, 2013; Slade, Mann, & Lewis, 2011), comprising 1-L circular plastic cups buried flush with the ground, half-filled with water, detergent and salt. Dung baits wrapped in muslin were suspended above the centre of the cups, and the traps were protected with rain covers. Traps were left for 48 hr before collection, a standard time for dung beetle pitfall trapping (Larsen & Forsyth, 2005). Burial intercept traps (Goh & Hashim,

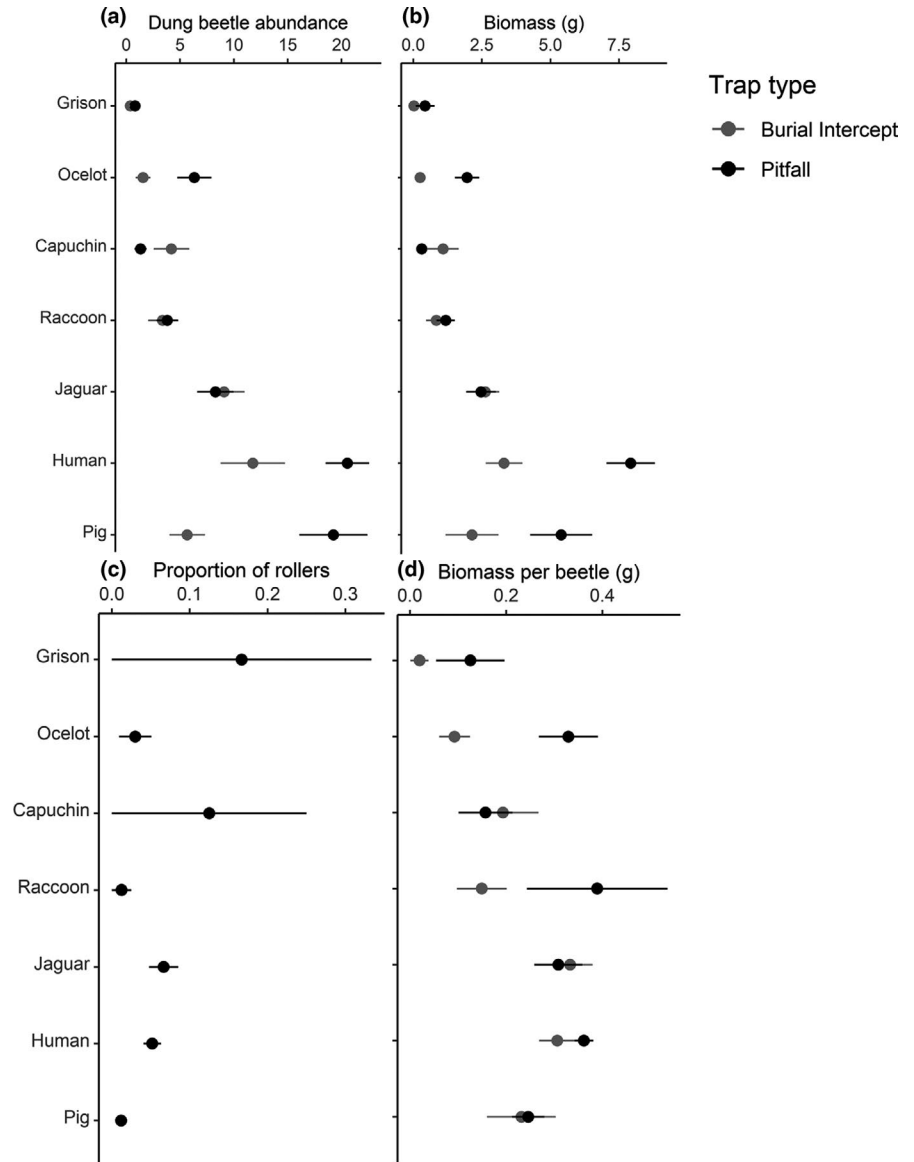
2018) were very simple in design: An agricultural bag 35 cm in diameter and approximately 78 cm deep was filled with soil and buried 75 cm deep, thus leaving only a 3 cm lip protruding above the soil surface. Dung was placed on the soil surface within the bag, allowing dung beetles attracted to the dung to form dung balls and bury them beneath the soil surface. Dung is often removed by dung beetles within the first 12–24 hr (personal observation; see also França, Louzada, & Barlow, 2018; Slade *et al.*, 2011); burial intercept traps were left for 24 hr before the soil was sieved exhaustively by hand and dung beetles collected to ensure as many beetles as possible were captured before they emerged from the soil. Dung beetles from both trap types were stored in 70% alcohol and frozen until identification at Universidade Federal de Mato Grosso (UFMT) by an expert taxonomist (F. Vaz-de-Mello). Dry biomass of each species was calculated by weighing 1–30 individuals, depending on availability, using a balance accurate to 0.001 g.

Statistical analyses were carried out in R 3.4.3 (R Core Team, 2017). We first calculated sampling completeness of the total dung beetle species attracted to each mammal dung and trap type using the package *iNEXT* (Hsieh, Ma, & Chao, 2016). We then ran linear models using *lme4* (Bates, Maechler, Bolker, & Walker, 2013), with the per-beetle biomass and (log-transformed) total dung beetle biomass per trap as response variables, and trap type, dung type and dung volume as explanatory variables. A generalized linear model was fitted with dung beetle abundance per trap as the response, and a quasipoisson error structure to account for over-dispersion. To assess variation in the ratio of rolling to tunneling dung beetles in different dung types, we specified the number of rolling and tunneling beetles in each trap as a binomial response variable, with dung type and dung volume as explanatory variables and fitted a generalized linear model. This analysis was only carried out for the pitfall traps, as rolling dung beetles are not reliably captured in burial intercept traps (Arellano, 2016). We also tested data for a subset of traps where the bait weighed less than 150 g to investigate whether the size of the dung bait was driving differences between dung types.

We tested the significance of the terms included in each of the models compared to a model with the term removed using chi-squared tests for generalized linear models and *F* tests for linear models, reporting *p*-values. We used a permutational analysis of variance (PERMANOVA) with *vegan* (Oksanen *et al.*, 2017), to compare dung beetle assemblages between trap and dung types, and non-metric multidimensional scaling (NMDS) to produce ordination plots of the dung beetle assemblages.

From a total of 203 traps using the seven dung types, we collected 2,295 beetles of 26 species (Table S2). Sampling completeness was >80% for each dung type in each trap type, apart from two instances where very few dung beetle individuals were collected (Table S2). Dung beetle abundance, total biomass, and per-beetle biomass all differed significantly among trap types and dung types (all  $p < .05$ , Figure 1, see Table S3 for test statistics), and in all cases were higher in pitfall traps than burial intercept traps. Only two burial intercept traps caught rolling dung beetles, and within the pitfall traps, there was a tendency for the proportion of rolling dung beetles collected

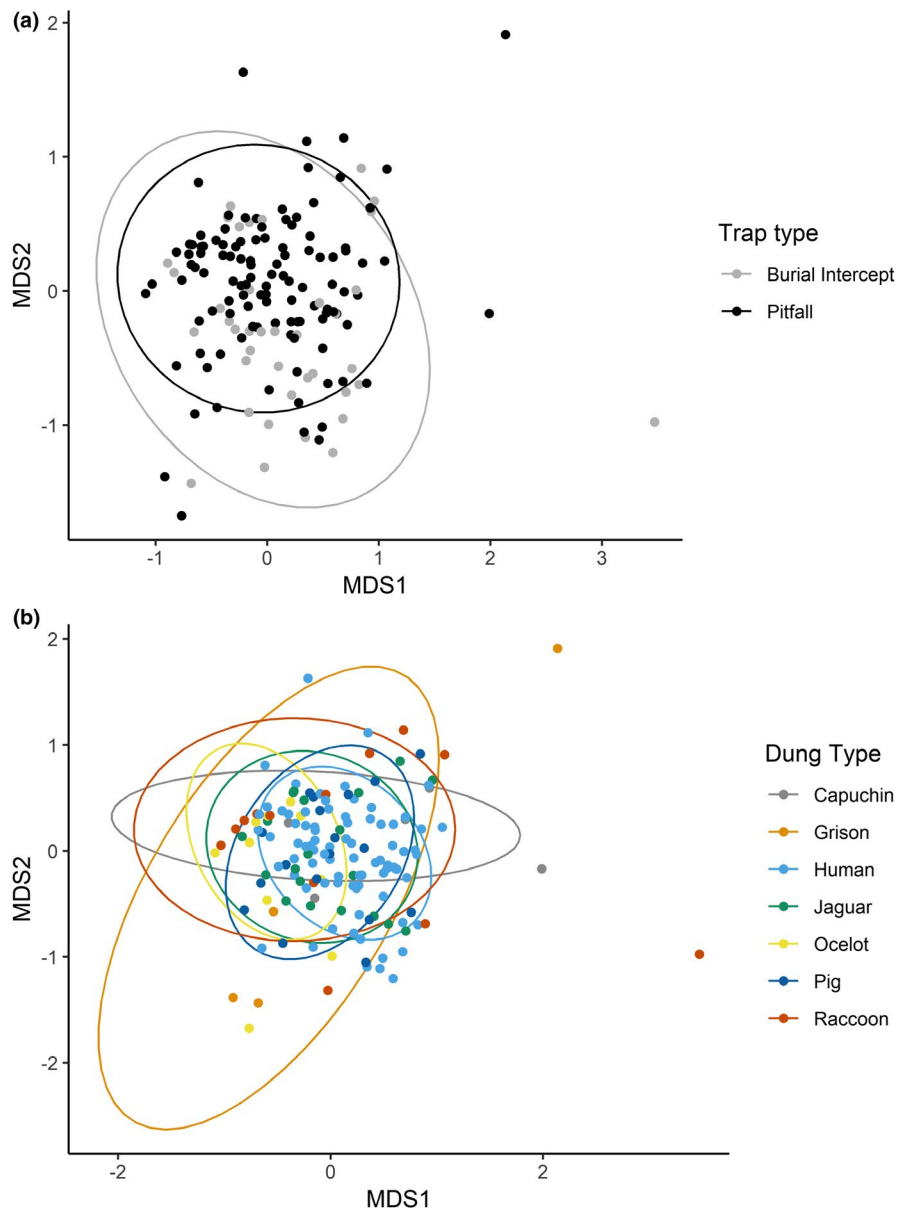
**FIGURE 1** Mean  $\pm$  SE for trap and dung types for (a) total dung beetle abundance, (b) total dung beetle biomass (g), (c) the proportion of rolling beetles (pitfall traps only), and (d) biomass per beetle (g). Dung types are ordered by volume from smallest (grison) to largest (pig)



to vary with dung type ( $p = .055$ , Table S3). For both dung beetle abundance and biomass, human and pig dung were the most attractive, and grison dung the least attractive; this also corresponds to increasing attractiveness with dung size (Figure 1a,b, Figure S2). For the measures of dung beetle functional composition, pig dung attracted a low proportion of rolling dung beetles compared to other dung types. Ocelot, raccoon, jaguar, and human dung attracted dung beetles with the largest average body sizes (Figure 1c,d). Analysis of the traps with <150 g dung involved 148 of the traps, and results were consistent for all analyses, confirming that dung type and volume were important for the abundance, species richness and biomass of dung beetles attracted. Bait type was found not to be significant in the subset analysis of the proportion of rolling dung beetles, indicating that dung volume drove differences in the functional group composition for pitfall traps (Table S4).

Dung beetle species assemblages differed significantly between trap types ( $F_{1,150} = 7.14$ ,  $p = .002$ ) and among dung types ( $F_{6,150} = 2.6152$ ,  $p = .002$ ), yet these factors explained only 5.1%

and 12% of the variation in community composition, respectively (NMDS stress = 0.15 with three dimensions; Figure 2a). Assemblages attracted to the dung of Atlantic Forest mammals overlapped with those collected in human dung, with only grison dung attracting a distinctive dung beetle assemblage (Figure 2b). The difference between dung beetle assemblage composition between the two trap types could indicate there is a difference in the dung beetle assemblage attracted to pitfall traps versus the composition of dung beetles attracted to burial intercept traps. This could be explained by a difference in choice of dung by dung beetles depending on their use of the dung (Holter, 2016), or alternatively be driven by differences in the attractiveness of dung based on the trap type used. As the dung remains exposed, pitfall traps continue to be attractive throughout the sampling period, whereas burial intercept traps, which mimic the natural temporal distribution of dung, are attractive for shorter periods as dung becomes buried. The difference in the total abundance and biomass of dung beetles collected between the two trap types suggests that pitfall



**FIGURE 2** Non-metric multidimensional scaling representing the dung beetle species assemblage (a) attracted to each dung type (across both trap types) and (b) attracted to the two trap types (across all dung types). Ellipses represent 95% confidence intervals

traps may give an overestimate if used to approximate the extent of ecosystem functions provided by dung beetles. However, burial intercept traps do not reliably capture rolling dung beetles (Arellano, 2016; Goh & Hashim, 2018), so alternative methods are needed to estimate how dung removal varies among dung beetle guilds in systems where rolling beetles make up a larger proportion of the dung beetle community.

We also found differentiation in the attractiveness of the seven dung types. This could be attributed to dung quality (Bogoni & Hernández, 2014) but also consistency, water content, and volume, which are known to vary among dung types (Frank, Brückner, Hilpert, Heethoff, & Blüthgen, 2017). Human and pig dung are often used as a convenient proxy for other mammal dung when surveying dung beetle communities in tropical forests (e.g., Larsen & Forsyth, 2005; Marsh *et al.*, 2013), and we found these were the most attractive in terms of the number of dung beetles collected. The lower dung beetle abundance and biomass collected in many of the native

dung types indicates that human dung baits may overestimate the magnitude of dung beetle–dung interactions. This highlights the importance of using the dung of naturally occurring mammal species in realistic dung sizes to quantify functional interactions between dung beetles and mammals (Frank *et al.*, 2018).

Dung beetle body size (Horgan, 2001; Nervo *et al.*, 2014) and functional group richness (Manning, Slade, Beynon, & Lewis, 2016; Slade *et al.*, 2007) affect the amount of dung removed. Here, we found that dung beetles captured in burial intercept traps were smaller-bodied than those in pitfall traps and that body size differed significantly among dung types. Within the pitfall traps, there was also variation in the attractiveness of dung types to rolling and tunneling dung beetles. This suggests that the common practice of using a single dung type (e.g., Nervo *et al.*, 2017; Slade *et al.*, 2011), deployed only within pitfall traps, to explore functioning-species traits associations may result in an unrealistic composition of dung beetles of each functional group.

Our results suggest that dung beetle–dung interactions for native mammal species may be substantially different. This is particularly important in ecosystem functioning studies where community data are being linked to the function of the ecosystem, and where realistic scenarios are needed to inform management plans. In these situations, a more informative estimate of the extent and magnitude of dung beetle–dung interactions with native mammal species is often needed. However, identifying the mammal community of an ecosystem and sourcing this dung is often logistically challenging and the low numbers of beetles captured using realistic dung volumes also means that higher trapping effort is required to estimate interactions reliably. If the purpose of a study is to document the coprophagic dung beetle fauna of a site, or to compare across multiple sites with different mammal faunas then standardized human dung baited pitfall traps will give a good estimate of overall dung beetle community composition. If standardized measures of beetle-mediated functions are also needed, then we recommend using the same dung type (e.g., Milić et al., 2019) and same (realistic) volumes in both the pitfall traps and for the dung removal work so that these can be linked more informatively.

Moving from documenting biodiversity to recording associated ecosystem functions and services will require methods to infer functioning that are robust, representative, and meaningful. Trapping method and dung type used as bait should be considered when designing experiments to identify mammal–dung beetle interactions, and when conducting experiments that link dung beetle species to ecosystem functioning.

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## DATA AVAILABILITY STATEMENT

The data will be made available at a later date.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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