



Habitat type and seasonal variation in dung beetles (Coleoptera: Scarabaeidae) community structure in the Brazilian Atlantic Forest

Tipo de habitat e variação sazonal na estrutura da comunidade de escaravelhos (Coleoptera: Scarabaeidae) na Mata Atlântica Brasileira

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Dung beetles (Coleoptera: Scarabaeidae) feed on decomposing animal carcasses and mainly on dung that are also used for building their nests. This study aims to estimate the dung beetles ecosystems services in relation to dung removal and to secondary seed dispersal, as well as to characterize the beetles community based on richness, abundance, species composition and functional guilds, and verify how these ecological indicators are influenced by the habitat type and by the seasonal variation (dry and rainy season). The dung removal rate was only affected by the seasonal variation and was higher during the dry season. The seed dispersal presented a positive relation with the proportion of the dung removal. The richness and abundance of dung beetles were greater during the dry season; however, these indicators were not influenced by habitat types. The forest patch and pasture area only differed in relation to composition of species but the number of represented species of each functional guild did not vary significantly between the habitats. This study emphasizes the functional importance of dung beetles in ecosystems through their efficient development of primary (dung removal) and secondary (seed dispersal) ecosystem functions.

Key-words: dung removal, seed dispersal, seasonality.

Os escaravelhos (Coleoptera: Scarabaeidae) se alimentam de carcaças de animais em decomposição e, principalmente, de esterco que também é usado na construção de seus ninhos. Esse estudo objetiva estimar os serviços ecossistêmicos desempenhados pelos escarabeídeos no que tange à remoção de esterco e à dispersão de sementes, assim como, caracterizar a comunidade de besouros em função das variáveis de riqueza, abundância, composição de espécies e guildas funcionais, e verificar como que esses indicadores ecológicos são influenciados pelo tipo de habitat e pela variação das estações (seca e chuvosa). A taxa de remoção de esterco foi afetada apenas pela variação sazonal e foi maior durante a estação seca. A dispersão de sementes apresentou relação positiva com a proporção de remoção de esterco. A riqueza e abundância de escaravelhos foram maiores durante a estação seca; porém, esses indicadores não foram influenciados pelos tipos de habitat. A mancha florestal e a pastagem diferiram apenas em relação à composição de espécies, mas o número de espécies representadas de cada guilda funcional não variou significativamente entre os habitats. Este estudo enfatiza a importância funcional dos besouros rola-bosta nos ecossistemas através do desenvolvimento eficiente das funções ecossistêmicas primária (remoção de esterco) e secundárias (dispersão de sementes).

Palavras-chave: remoção de esterco, dispersão de sementes, sazonalidade.

1. INTRODUCTION

Ecosystem services are benefits provided by nature to people [1]. The complex interactions between organisms that transfer energy and materials through ecosystems and underpin ecosystem services are vital for the human well-being and to economic activities [2]. For example, Soil formation, seed dispersal and nutrient cycling are important ecosystems functions conducted by many of the organisms directly or indirectly [3-5]. Interactions between animals' dung, seeds and dung beetles drive secondary seed dispersal function that underpins food, medicine and culture as ecosystem services [2]. In this context, dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae) develop ecosystem services due to their detritivore behavior, which promotes removal of carcasses and dung of animals once they use the soil for allocation of resources, sheltering and nesting [4]. Studies assessing ecosystem services are vital for understanding how the decline of these services unfolds in the face of ecosystem degradation [6].

Among many ecological functions developed by dung beetles at natural areas, the relocation of dung material into the soil is crucial for the nutrient cycling, increasing soil aeration and fertilization [4, 7]. It also contributes to the control of parasites of cattle worms, protozoa and flies that use to grow up in the dung [8]. Dung removal rate by dung beetles could vary amongst seasonal periods due to soil moisture and to soil harshness variations [9] and it could also diverge between natural and anthropic habitats due to the availability of resources [10].

In Addition, the dung removal allows the secondary dispersal of seeds [11]. It is likely that beetles bury involuntarily seeds while remove more waste to their built tunnels under the soil or disperse the seeds inside the dung balls some horizontal distance away from the original deposition site [4]. This secondary function reduces seed mortality caused by predators and pathogenies, consequently helping with the recruitment of plants [12].

Most of the Scarabaeinae beetles species are divided in three categories based on their nesting and dung removal strategies: (1) paracoprid species, also called as tunnelers, which bury brood balls in vertical chambers in close proximity to original deposition site; (2) telecoprid species, called rollers, which transport dung balls some horizontal distance away before burial beneath the soil surface; and (3) endocoprid species, called as dwellers or residents, which brood their pups inside the dung mass itself [4].

Therefore, considering that dung beetles play a crucial role in the development of important functions of the ecosystem, it is imperative to understand how these insects respond to habitats type and seasonal variations. The abundance of these species, structure and composition of assemblages differ amongst habitats [13, 14], through changes in the availability of resources and microclimatic conditions (ecological niche) [15, 16]. Seasonal variations also promote fluctuations on the diversity of measures [17], once they alter the resources availability and the breeding season of dung beetle species [7]. At the onset of rainy season, dung beetles could be more abundant and as the season advances, higher resource scarcity limits population size, which likely results in a smaller foraging range, increasing β -diversity [17, 18]. In addition, the duration and intensity of a dry season can alter the diversity of the community decreasing ecological services [17]. Drought-tolerant species can increase in abundance and, in some cases, inhabit forest patches due to the low competition for resources during severe drought periods [19].

Considering that pastures are used to raise cattle and that the amount of dung in these ecosystems is much greater than in the forest, it is expected that the dung removal rate and secondary dispersal of seeds are greater at the pasture, and that the mimetic seeds dispersal would be positively related to the dung removal rate by dung beetles. Taking into consideration that different habitats present distinct degrees of heterogeneity that affect the resources availability [20, 21] and also that distinct microclimate conditions determine the occurrence of species based on their physiological tolerance [22, 23]. One possible hypothesis could be that the species composition would be different between both studied habitats, despite the high heterogeneity and the canopy cover of the forest fragment that buffers extreme temperatures [22, 24]; thus, it is expected a greater dung beetle diversity in the forest fragment than in the pasture. In relation to seasonal variations, it is expected that dung removal and beetle richness and abundance could be greater during the rainy season, once their breeding period is on this season [25] and due to the fact that most dung beetle species are drought-intolerant [17].

Therefore, this study aims to estimate the dung beetles ecosystems services in relation to dung removal and to secondary seed dispersal, as well as to characterize the beetles community and how these ecological indicators are influenced by the habitat type (forest and pasture) and by the seasonal variation (dry and rainy season).

2. MATERIAL AND METHODS

2.1 Study site

This study was conducted in a remnant of the Atlantic Forest with different stages of succession (400 ha), belonging to the Federal Institute of Education (IFS), Science and Technology (IFS), Municipality of São Cristóvão, State of Sergipe (11°01' latitude S; 37°12' longitude W), with an altitude of 20m. The area is located in a climate region, according to the Köppen classification, type As, tropical rainy with dry summer, with an average temperature of 25.5°C, with a rainy season between March and August, with average precipitation of 1,500 mm/year [26, 27].

2.2 Sampling

The fieldwork was conducted in 2018 at both two areas (the forest and the pasture), with one collection of beetles per season (dry season, January to March; rainy season, April to July) (Permanent license SISBIO, n° 76193-1). The study was carried out in two steps: (1) the first to evaluate some aspects of the community structure in function of forest and pasture habitats and to seasonal variations (dry and rainy season); and in the second to evaluate some ecosystems functions developed by dung beetles (dung removal; secondary seed dispersal).

For both steps, six transects of 150m, were marked arbitrarily per habitat (equidistance 100m), totaling 12 transects (Figure 1). Each transect had four sampling units, totaling 48 units. Following recommendations of Larsen and Forsyth (2005) [28], the distances amongst the units were of 50 m, minimum distance to ensure sampling independence amongst samples of dung beetles. A Preliminary a raffle of three transects for each habitat was done for fixing the traps. This care supported the sampling randomization, increasing the statistics accuracy and thus, avoided the spatial-temporal pseudo replicas.

For verifying the effect of seasonal variation on the structure of dung beetles community, six transects were sampled during the dry season and other six transects during the rainy season (3transects at forest, 3 transects at pasture per season) (Figure 1).

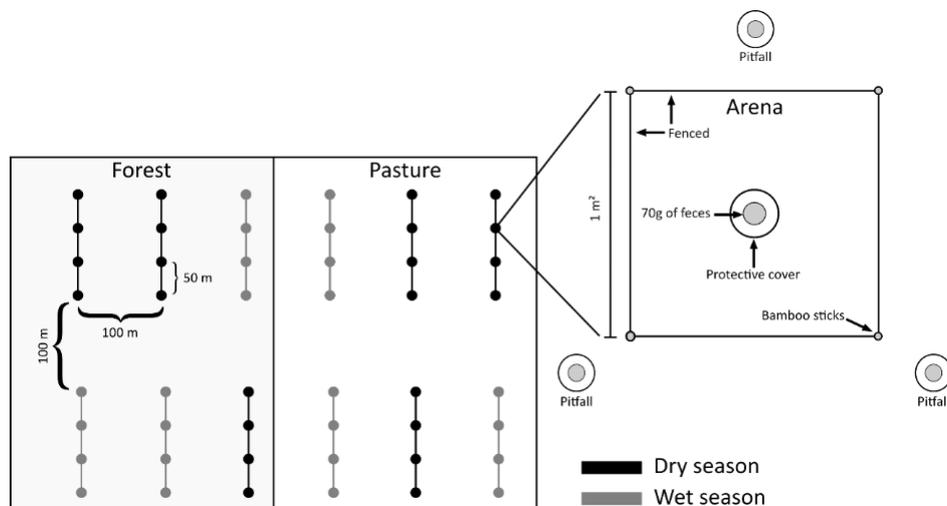


Figure 1: Schematic representation of sampling design of dung beetles catches at Federal Institute of Sergipe, Municipality of São Cristóvão, Brazil. The vertical lines show the transects with the sampled units, distributed at the two selected habitats (forest and pasture) during the dry and rainy seasons. Here the Arena built for the experiment of functional ecology is emphasized.

2.3 Community Structure

At each of the 48 sampling units, three soil traps (pitfalls) were placed to capture beetles, forming a triangle (total of 144 pitfalls). The traps were plastic recipients of 20cm of diameter and 15cm deep and they were buried up to the level of the soil edge [29]. Each container was filled with a solution consisting of the following proportions: water (200 mL), salt (50 g) and neutral detergent (5 mL) [30]. Pork dung was used as bait, distributed suspended at a small recipient in the center of a big recipient using wooden toothpick, in order to make beetles fall down in the trap before arriving at the bait. After three days, the beetles were collected and conserved at a 70 % alcohol solution. Then, the insects were taken to the Animal Biology Laboratory at IFS, Municipality of São Cristóvão. After the insects were dried and identified according to genus/species criteria by an expert dung beetle taxonomist (Dr. Fernando Vaz de Melo, Federal University of Mato Grosso), with extensive collection experience in the dung beetle fauna of the Atlantic Forest. The beetles community were identified considering their nesting strategies to then placed them in their correspondent functional guild, which represents implications for the ecological functions of ecosystem [4]. The present Scarabaeidae collection is deposited at the Collection of the Laboratory of Animal's Biology, Instituto Federal de Sergipe, Municipality of São Cristóvão, Brazil.

2.4 Estimating functions of ecosystem

In each habitat, arenas were distributed at the sampling units ($n_{total}=48$; forest=24 and pasture habitats=24). The litter was removed as well as the vegetation from the interior of each arena. The area of each arena was of 1 m², with edges delimited by a fence with bamboo-framed screen and stretched-out piece of voile fabric (approximately 15cm high) (Figure 2). The fence allowed to limit the horizontal movement of dung removal by the beetles, promoting a better accuracy of the quantitative data of buried/transported dung. In the center of each arena a pile of 70g of fresh dung of pork was placed, considered an efficient amount for sampling richness and abundance of dung beetles [31]. Inside each portion of dung, 80 plastic beads with different sizes (50 units of 3.5 mm; 20 of 8.6 mm and 10 of 15.5 mm) were placed (Figure 2), expecting they could work as mimetic seeds [32, 33]. The dung samples with these mimetic seeds were weighed and placed in the center of the arena and they were also protected from the rainfall by a plastic roof (Figure 2). The dung beetles had 48h to transport or bury the dungs with beads, time long enough to attract beetles to the pork dung bait traps [34]; this can allow to occur the activity of diurnal and nocturnal fauna. After 48h, the exposed dung and mimetic seeds which remained within the arena were considered as not buried/transported. The exposed dung were weighed and the plastic beads counted; to then subtract their weight from the original amount (per sampling unit: 70g of dung; 80 beads). In this study, as primary ecological function it was considered the dung removal and as secondary ecological function, the seed dispersal.



Figure 2. On the left, the area of each arena is 1 m², enclosed by a bamboo-framed screen and a stretched-out piece of voile fabric, approximately 15 cm high. On the right, the orange plastic beads of different sizes are visible inside a portion of pork dung.

2.5 Data analysis

Firstly, we described the dung beetle communities by examining species abundance distribution (SAD) and constructing individual-based interpolation and extrapolation curves (doubling to reference sizes) for each distinct sampling period (dry and wet seasons) and area (forest and pasture) [35]. Confidence intervals were determined using 999 bootstraps for all rarefaction and extrapolation curves.

Next, we used transects as independent sampling units and performed generalized linear models (GLMs) to assess whether abundance and richness patterns of dung beetles differed significantly based on habitat type (forest patch or pasture) and seasonal period (dry or rainy season). In these models, the response variables were the number of individuals (abundance) and the number of species (richness), while the explanatory variables were habitat type, seasonal period, and their interaction. The models followed a Poisson distribution since the response variables were count data. We assessed heteroscedasticity, under/overdispersion, and residual correlation through residual analysis and dispersion parameters (dispersion parameter ~ 1). When necessary, models were adjusted to a more appropriate distribution (Negative Binomial) [36]. All models were subjected to an Analysis of Deviance (ANODEV) using the Chi-square test [37].

We then evaluated differences in dung beetle species composition between habitats and seasons using permutational multivariate analysis of variance (PERMANOVA [38]). The analysis was performed using an abundance matrix (12 rows [transects], 31 columns [dung beetle species]) and was based on the Bray-Curtis index with 999 permutations. The results were visualized using a principal coordinates analysis (PCoA). Additionally, to identify dung beetle species more strongly associated with a particular habitat or seasonal period, we applied a multinomial species classification method (CLAM) [39]. The CLAM approach classified species as specialists of a given habitat or season, generalists with no preference between categories, or rare species with insufficient occurrences to confidently assign a classification. For CLAM, we used a significance threshold of $p < 0.05$ and a specialization threshold of 0.67, as recommended by Chazdon et al. (2011) [39] for a conservative classification.

Finally, we used Linear Mixed Models (LMMs) to estimate the effects of habitat type (forest vs. pasture) and seasonal variation (dry vs. wet) on dung beetle-mediated ecosystem functions (dung removal and seed dispersal). Since dung arenas were treated as non-independent observations, we included transects as a random effect in the models (random effect: ~ 1 |transect; #observations: 48, #transects: 12). Two models were constructed: (i) proportion of dung removed as a function of habitat type and season, and (ii) proportion of seed dispersal as a function of dung removal proportion. All models followed a Gaussian distribution.

All statistical analyses were conducted in R v.4.4 [40]. We used the iNEXT package [41] for computing individual-based extrapolation curves, vegan [42] for PERMANOVA, PCoA, and CLAM analyses, and lme4 [43] for implementing mixed linear models. Significance testing in LMMs was performed using the Anova function with Kenward-Roger's method.

3. RESULTS AND DISCUSSION

In this study, 373 specimens representing 32 species of dung beetles were collected at IFS (Table 1). The three most abundant species were *Dichotomius valoisae* ($n = 69$ individuals), *Eurysternus nigrovirens* ($n = 54$), and *Canthon lituratus* ($n = 47$), collectively accounting for 45.7% of the total dung beetle abundance sampled (Figure 3). Among the collected species, 13 were found exclusively in the forest area, while 16 were recorded only during the dry season. In contrast, only six species were sampled exclusively in the pasture area, and four species were found only during the wet season. Additionally, 12 species were present in both habitats, and 11 species were recorded in both seasons (Figure 3). The individual-based extrapolation curves indicated that species richness was higher in the pasture area and during the dry season compared to the forest area and wet season. However, none of the curves appeared to reach an asymptote (Figure 3).

Table 1: Species and number of specimens of dung beetles species (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae, Rutelinae) collected at Federal Institute of Sergipe, Municipality of São Cristóvão, Brazil. Functional guilds and abundance amongst habitats and seasonal periods.

| Subfamily | Species | Functional guild | Habitat | | | |
|--|--|------------------|---------------|-----------|----------------|-----------|
| | | | Forest Season | | Pasture Season | |
| | | | Dry | Rainy | Dry | Rainy |
| Aphodiinae | <i>Ataenius</i> sp. | Dweller | 0 | 0 | 20 | 0 |
| Scarabaeinae | <i>Eurysternus aeneus</i> Génier, 2009 | Dweller | 43 | 5 | 4 | 2 |
| | <i>Canthon chalybaeus</i> Blanchard, 1843 | Roller | 2 | 0 | 4 | 0 |
| | <i>Pseudocanthon xanthurus</i> (Blanchard, 1845) | Roller | 1 | 1 | 6 | 1 |
| | <i>Canthon lituratus</i> (Germar, 1813) | Roller | 1 | 1 | 40 | 5 |
| | <i>Canthon cinctellus</i> (Germar, 1824) | Roller | 0 | 2 | 3 | 12 |
| | <i>Canthon histrio</i> Serville, 1825 | Roller | 0 | 0 | 1 | 0 |
| | <i>Canthon</i> sp. 1 | Roller | 1 | 0 | 0 | 0 |
| | <i>Canthon</i> sp. 2 | Roller | 0 | 0 | 0 | 1 |
| | <i>Canthon</i> sp. 3 | Roller | 13 | 5 | 1 | 1 |
| | <i>Canthon nigripennis</i> Lansberge, 1874 | Roller | 0 | 0 | 1 | 0 |
| | <i>Pseudocanthon perplexus</i> (LeConte, 1847) | Roller | 0 | 0 | 0 | 1 |
| | <i>Sylvicanthon bridarollii</i> (Martinez, 1949) | Roller | 1 | 0 | 0 | 1 |
| | <i>Ateuchus lecontei</i> (Harold, 1868) | Tunneler | 0 | 0 | 2 | 0 |
| | <i>Ateuchus</i> sp. 1 | Tunneler | 3 | 0 | 2 | 0 |
| | <i>Ateuchus</i> sp. 2 | Tunneler | 0 | 0 | 2 | 0 |
| | <i>Ateuchus semicribratus</i> (Harold, 1868) | Tunneler | 1 | 0 | 0 | 0 |
| | <i>Dichotomius boreus</i> (Olivier, 1789) | Tunneler | 1 | 0 | 0 | 0 |
| | <i>Canthidium</i> sp. 1 | Tunneler | 2 | 1 | 0 | 0 |
| | <i>Canthidium</i> sp. 2 | Tunneler | 0 | 0 | 1 | 0 |
| | <i>Canthidium</i> sp. 3 | Tunneler | 0 | 0 | 1 | 0 |
| | <i>Diabroctis mimas</i> (Linnaeus, 1758) | Tunneler | 12 | 0 | 5 | 1 |
| | <i>Dichotomius</i> sp. 1 | Tunneler | 0 | 0 | 3 | 0 |
| | <i>Dichotomius bos</i> | Tunneler | 0 | 0 | 12 | 0 |
| | <i>Dichotomius</i> sp. 2 | Tunneler | 1 | 0 | 0 | 0 |
| | <i>Dichotomius</i> sp. 3 | Tunneler | 5 | 0 | 0 | 0 |
| | <i>Dichotomius nisus</i> (Olivier, 1789) | Tunneler | 0 | 0 | 13 | 0 |
| <i>Dichotomius valoisae</i> (de Moura, 2020) | Tunneler | 48 | 19 | 1 | 1 | |
| <i>Dichotomius</i> sp. 4 | Tunneler | 21 | 7 | 1 | 0 | |
| Aphodiinae | <i>Trichaphodiellus brasiliensis</i> (Castelnau, 1840) | Tunneler | 0 | 7 | 0 | 0 |
| | <i>Onthophagus ranunculus</i> Arrow, 1913 | Tunneler | 1 | 0 | 14 | 4 |
| Rutelinae | <i>Leucothyreus</i> sp. | Dweller | 0 | 0 | 0 | 1 |
| Total by category | | | 157 | 48 | 137 | 31 |
| TOTAL | | | 373 | | | |

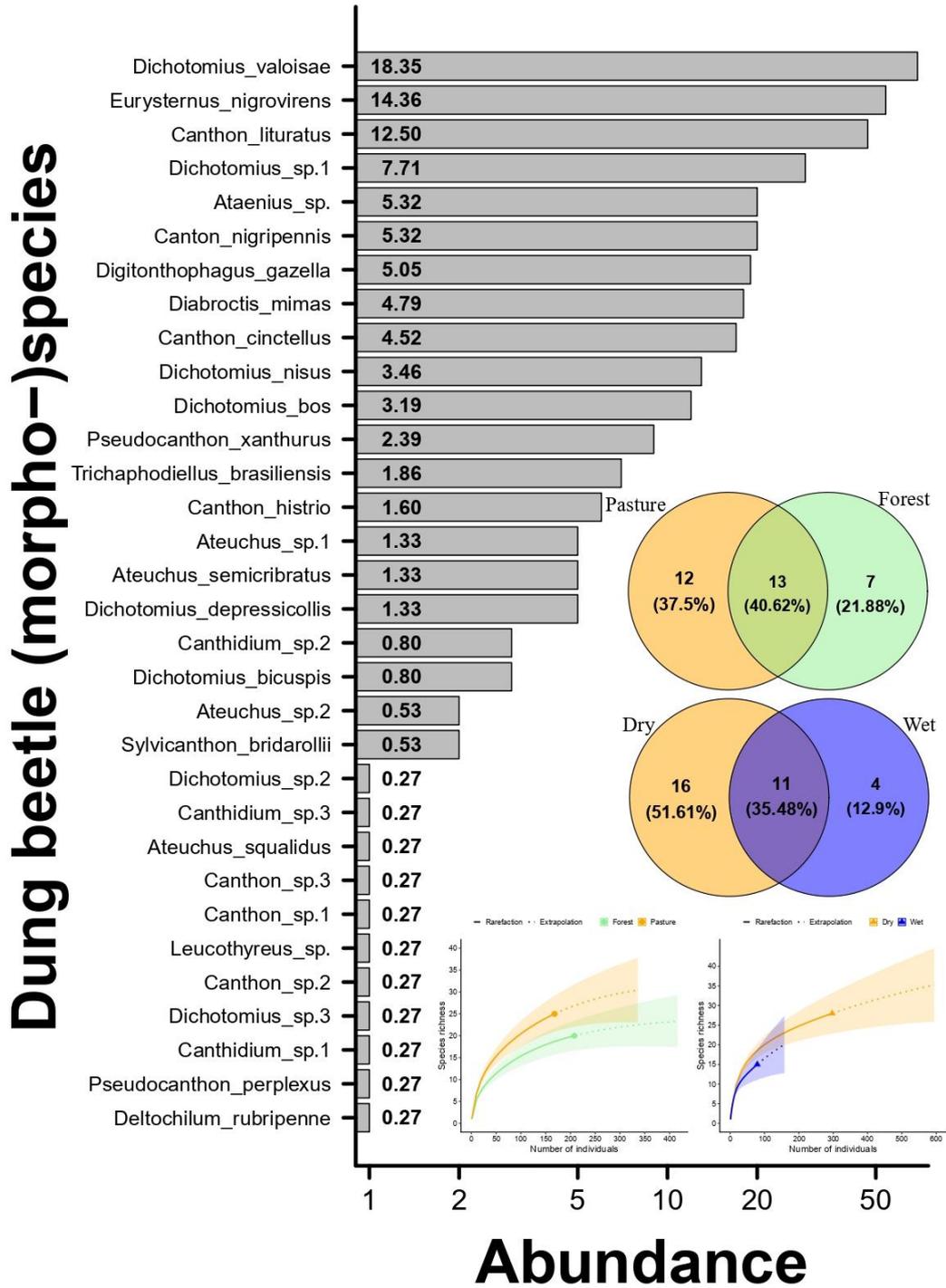


Figure 3. Barplot of distribution of abundances of the 32 species of dung beetle collected at Federal Institute of Sergipe, Municipality of São Cristóvão, Brazil. In the detail of barplot are two Venn diagram that show the exclusive and share species for each area and season. Also were insert in plot the interpolation and extrapolation curves individuals-based to both area and season.

We found that the seasonal period was the only significant predictor of dung beetle abundance and species richness in the study area (Table 2, Figure 4). Specifically, the dry season exhibited an average number of individuals per transect that was 3.5 times higher than that of the rainy season (*Dry season*: 48.83 ± 5.14 ; *Rainy season*: 12.16 ± 2.62). Additionally, the average number of species per transect was twice as high during the dry season compared to the rainy season (*Dry season*: 11.83 ± 1.22 ; *Rainy season*: 5.33 ± 0.88).

Table 2. Analysis of deviance of generalized linear models to abundance of individuals and species richness of dung beetle at Federal Institute of Sergipe, Municipality of São Cristóvão, Brazil. D.F.: treatment degrees of freedom, Resid. Dev.: residual deviance. *** for significant p value less than 0.001.

| Response | Predictors | D.F. | Deviance | Resid. Dev. | Pr(>Chi) |
|----------------------------------|--------------|-------|----------|-------------|-------------|
| Abundance (Negative binomial) | Sites (SIT) | 1, 10 | 1.747 | 72.352 | 0.186 |
| | Season (SEA) | 1, 9 | 58.885 | 13.446 | < 0.0001*** |
| | SIT:SEA | 1, 8 | 0.623 | 12.844 | 0.430 |
| Richness (Poisson) | Sites (SIT) | 1, 10 | 0.772 | 24.87 | 0.379 |
| | Season (SEA) | 1, 9 | 16.443 | 8.432 | < 0.0001*** |
| | SIT:SEA | 1, 8 | 0.340 | 8.092 | 0.559 |

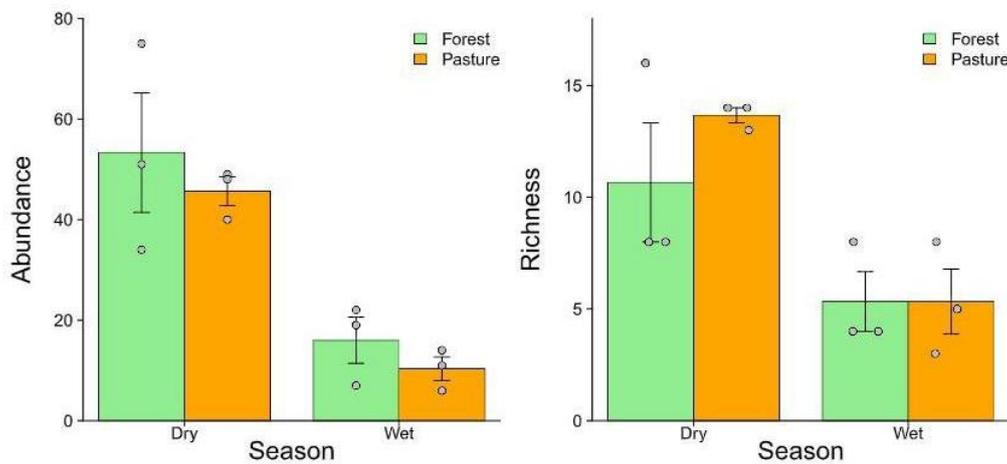


Figure 4. Mean (\pm SE) abundance (number of specimens) and species richness of dung beetles according to area and seasonal period collected at the Instituto Federal de Sergipe, São Cristóvão, Brazil. The results of this graph can be seen in Table 2.

However, both the seasonal period and the habitat type, as well as the interaction between these two factors, were significant predictors of species compositional abundance (Table 3).

Table 3. Results of the permutational multivariate analysis of variance (PERMANOVA) to assess as area and season, and your interaction, modulate the dung beetle community composition at Federal Institute of Sergipe, Municipality of São Cristóvão, Brazil. ** for significant p value less than 0.005.

| Predictors | Df | Sum Of Sqs | R2 | F | Pr(>F) |
|--------------|----|------------|-------|--------|---------|
| Sites (SIT) | 1 | 1.398 | 0.386 | 11.444 | |
| Season (SEA) | 1 | 0.714 | 0.204 | 6.059 | 0.002** |
| SIT:SEA | 1 | 0.481 | 0.137 | 4.080 | 0.002** |
| Residual | 8 | 0.943 | 0.270 | | |
| Total | 11 | 3.489 | 1.000 | | |

The PCoA plot shows a clear separation between the groups, highlighting the strong spatial and temporal complementarity of the dung beetle community in the study area (Figure 5). According to the Multinomial Species Classification Method, three species are identified as forest specialists (*Dichotomius valoisae*, *Dichotomius* sp. 1, *Eurysternus nigrovirens*), while three others are classified as pasture specialists (*Canthon lituratus*, *Digitonthophagus gazella*, *Ataenius* sp.). Among the remaining species, three showed no preference between forest and pasture, whereas 22 occurred at such low frequencies that their habitat preferences could not be determined (Figure 5). In both seasonal periods, *Canthon cinctellus*, a generalist species in both habitat sites, is

classified as a specialist during the rainy season. No species is classified as specialist in the dry season. Five species are considered generalists across seasonal periods, while 25 species are classified as rare (Figure 5).

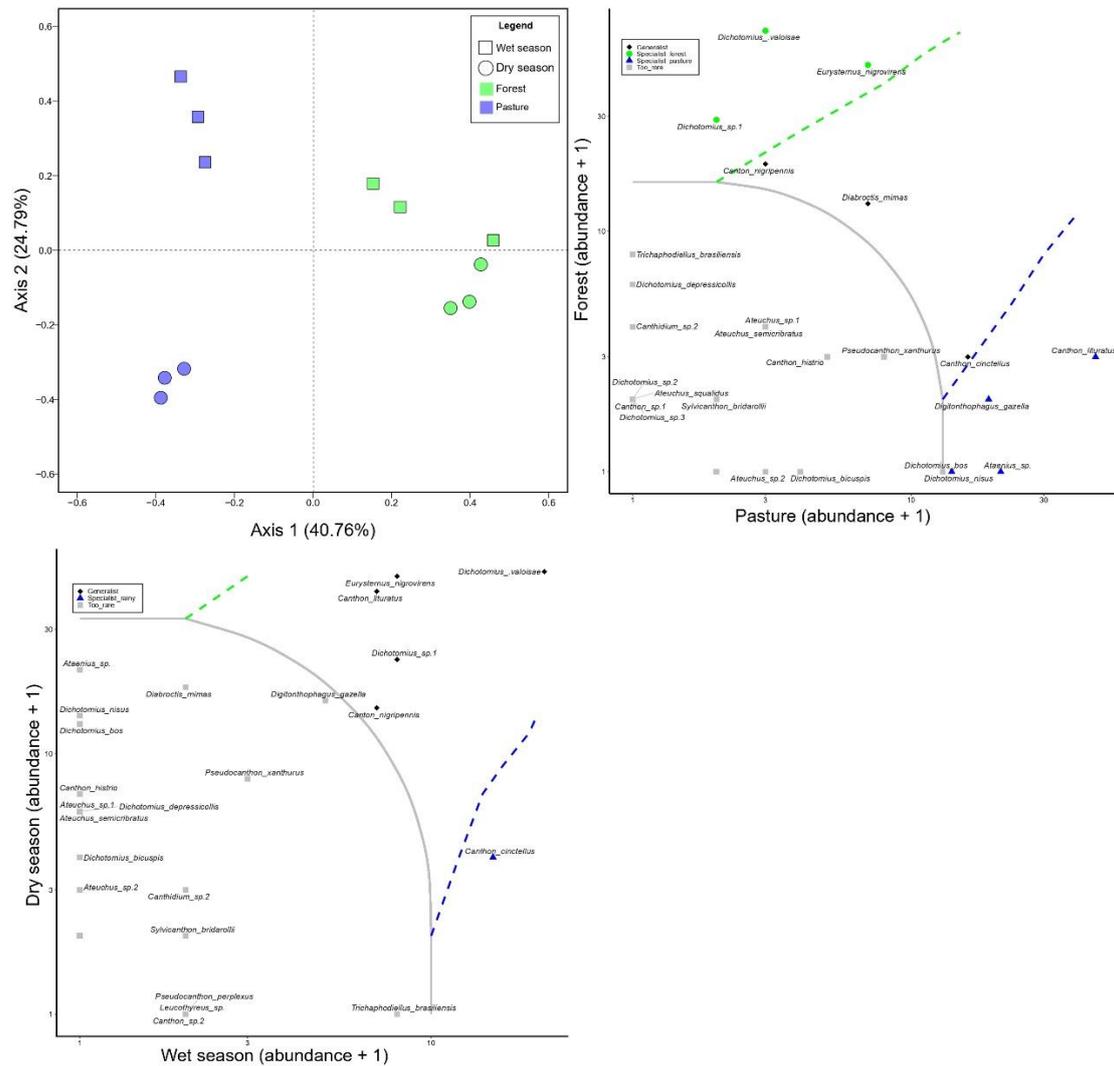


Figure 5. Principal Coordinates Analysis (PCoA) ordination diagrams of dung beetles collected at the Instituto Federal de Sergipe, São Cristóvão, Brazil. The PCoA was performed based on an abundance matrix using the Bray-Curtis distance index. The plots on the right and below represent the CLAM analysis, which classifies the 32 collected dung beetle species into four categories based on their frequency of occurrence across habitats and seasons: generalists (black diamonds), too rare to be assigned a preference (gray triangles), associated with the dry season or forest specialists (green circles), and associated with the wet season or pasture specialists (blue triangles).

Lastly, the rate of dung removal by beetles did not differ between forest and pasture habitats; however, this primary ecological function varied between seasonal periods (Table 4), being greater during the dry season (Figure 6). Our results indicate that the secondary function of seed dispersal was efficient and proportional to dung removal (Table 4, Figure 6). In summary, a positive relationship is observed: the greater the dung removal, the greater the seed dispersal (Figure 6).

Table 4. Results of the Analysis of Variance of Linear Mixed Model with Kenward-Roger's method, having as intercept of random effect the transects of study ($\sim 1/\text{transect}$). SumSq: Sums of squares; MeanSq: Mean squares. *** for significant p value less than 0.001.

| Response | Predictors | SumSq | MeanSq | F-value | Pr(>F) |
|---------------------|------------------|-------|--------|---------|-------------|
| Removed dung (%) | Sites (SIT) | 0.038 | 0.038 | 2.169 | 0.149 |
| | Season (SEA) | 1.309 | 1.309 | 75.132 | < 0.0001*** |
| | SIT:SEA | 0.003 | 0.003 | 0.200 | 0.667 |
| Dispersed seeds (%) | Removed dung (%) | 2.135 | 2.135 | 62.335 | < 0.0001*** |

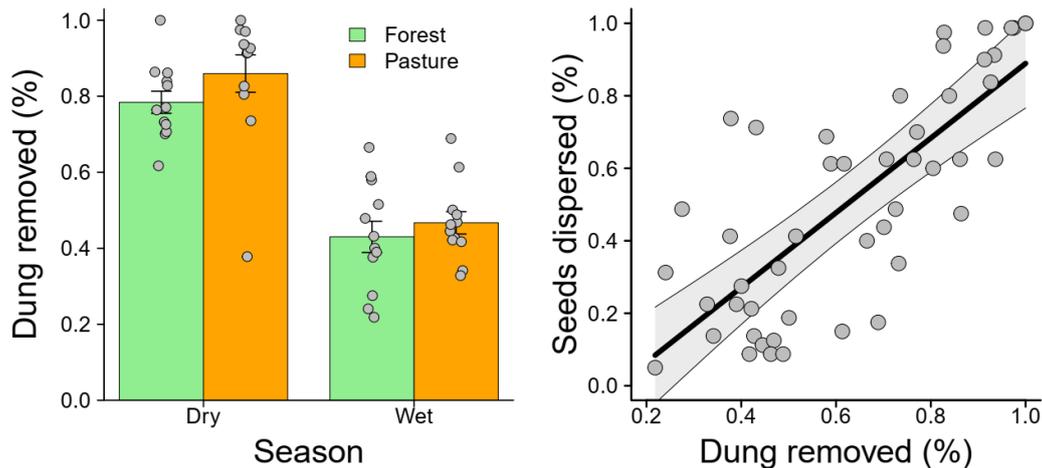


Figure 6. Panel plot of ecosystem services provided by dung beetles (*Coleoptera: Scarabaeidae*) at the Federal Institute of Sergipe, Municipality of São Cristóvão, Brazil. On the left, the proportion of dung removal by dung beetles is compared between dry and rainy seasons and between forest and pasture areas. On the right, the relationship between dung removal proportion and seed dispersal by dung beetles is shown.

The dung beetles abundance at IFS habitats (400 ha) was low (373 individuals) in comparison to studies realized at other tropical humid forest sites. However, proportionally the richness (32 species) was highly representative, once other studies on tropical humid forests presented similar or lower number of species than the richness presented in the study site. For instance, Amézquita and Favila (2010) [7] collected 658 individuals of 19 species in the Humid tropical Forest of Mexico at forest fragments that varied from 3 to 700 ha, while in the South of Brazilian Atlantic forest, 1.210 individuals of 11 species were sampled in two areas smaller than 2000 ha in total [14]. In the Argentine Humid Chaco were sampled 28.387 individuals of 57 species [44]. At Atlantic forest of São Paulo, Barreto et al. (2023) [29] recorded 50 species across 95 sampling units of forest cover, ranging from 10.1% to 48.8%. Their sampling effort was nearly twice the effort of this study ($n=48$ sampling units). This scenario highlights the effectiveness of the sampling effort of this study in accurately characterizing the dung beetle community of IFS.

In contrast to what was expected, the richness and abundance of dung beetles did not differ between the habitat types (forest patch and pasture) at IFS. Studies show that the climatic and environmental conditions such as high temperatures and the floristic simplicity at pasture are limiting factors that could reduce the richness and affect the species composition at these areas [44, 45]. On the other hand, other studies show that the dung type available at certain habitats could result in strong differences on the abundance and richness of the species [10]. So, it is possible that the lack of difference in dung beetle diversity between habitat types could be related to the bait type used (pork dung) or could be the result of a defaunation process in the forest patch. The use of dung from exotic species in natural habitats, where this resource is not naturally available could influence on the capture rate of beetles, once the typically forest beetles prefer the dung of wildlife mammals, specially the omnivorous ones [7, 46]. In addition, there is a clear

relation between the diversity of forest mammals and the diversity of dung beetles [7]. In this way, the reduced number of forest specialists beetles ($n=3$) at IFS could reflect the occurrence of a depleted mammal fauna, made up of low abundant omnivorous species due to the anthropic impacts in the area, such as hunting practices and deforestation [27]. Although no significant difference was found between richness, abundance and habitat types, the community composition differed between forest patch and pasture

Corroborating the previsions of the hypothesis, the composition of beetles assemblages differed between the habitat types. Many dung beetles presented specific characteristics on the habitat use, where forest species present low tolerance to extreme microclimate conditions at open areas while other species are adapted to environmental conditions of pastures [19, 44, 47]. Despite the dung is abundant at pastures, many species typically from the forest could not occupy the pasture due to climate and environment variations such as soil compaction and high temperatures [45, 48, 49]. Therefore, the structural and climate differences between the forest and pasture alter the species composition [4], as verified at IFS. Despite have being observed a dissimilarity on the beta diversity in relation to habitat types, in this study it did not find significant differences on the species number for functional guilds between forest and pasture. It was important for the ecosystem functionality that tunnelers beetles were abundant in both habitats, once tunnelers are the most efficient beetles to bury seeds in the soil [50], and this condition was observed in the present study.

The rate of dung removal in the present study is only affected by the seasonal period. Contrary to the expectations (hypothesis), the proportion of dung removal is greater during the dry period. The ecological mechanisms related to this result are still unclear once it is known that beetles activity increases during the rainy season due to the greater availability of resources [7]. It is possible that the lack of available resources during the dry season attracted more beetles to the baits used in this study, leading to an overestimation of the data that show higher dung removal in the dry season. Finally, in relation to the secondary function of seed dispersal, the proportion of mimetic seeds dispersed is positively related to the dung removal rate by dung beetles. This shows that dung beetles in the study area contribute to the process of plant recruitment. The dispersal/burial of seeds could offer protection against predators and thus represent an essential ecological attribute for the tropical forests regeneration [33].

4. CONCLUSION

In general, the results were partially in line with the hypothesis. The dung beetles responded only to seasonal variation, considering the estimated indicators of the primary ecological function (dung removal) and of richness and abundance. The habitat types presented significant influence only at the species composition, showing that many beetles had specific adaptations to the habitat they use. The similarity on the species abundance and richness between the two phytophysiognomies provoked two important questions, one related to the bait type used in the experiment and the other related to the low diversity of mammal at the forest fragment.

In general, forest species are specialists on native resources and the use of exotic dung could not have attracted a larger number of beetles in the forest patch of IFS, being necessary further studies testing native and exotic dung to solve this question. Alternatively, a poor-wild mammal community and the anthropic impacts in this environment could indicate the species loss of forest dung beetles. This highlights the importance of the dung beetles as environment indicators of forest conservation.

This study brings new information related to greater abundance and richness of dung beetles species during dry season. New studies at the Northeastern Atlantic Forest are necessary to test and confirm this information in order to identify mechanisms behind the response of dung beetles community to the dry season.

In relation to the secondary ecological function (seed dispersal) this result is especially important for altered Atlantic forest environments, such as IFS forest patch, once it could contribute to a successful reproduction of seedlings, favoring the forest regeneration. The results emphasize the importance of ecosystems services realized by the dung beetles with focus on the secondary dispersal of seeds.

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