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Centro Bimédico
Instituto de Biologia Roberto Alcântara Gomes


Fabiana Cassar de Barros Couto

**The dung beetle assemblage and their relationship with the mammals
and the phytophysiognomies at Reserva Natural Vale, ES, Brazil**

Rio de Janeiro
2018

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Dissertação apresentada, como requisito parcial
para obtenção do título de Mestre, ao Programa de
Pós-Graduação em Ecologia e Evolução da
Universidade do Estado do Rio de Janeiro.

Orientadora: Prof.^a Dra. Helena de Godoy Bergallo

Rio de Janeiro

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RESUMO

COUTO, Fabiana Cassar de Barros. *A assembleia de rola bostas e sua relação com os mamíferos e as fitofisionomias na Reserva Natural Vale, ES, Brasil*. 2018. 62f. Dissertação (Mestrado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2018.

Os besouros rola-bostas (Scarabaeidae) são um grupo de insetos distribuídos globalmente com sua maior diversidade nos Trópicos e Savanas, onde estão presentes as maiores das espécies de mamíferos dos quais se alimentam das fezes, embora também consumam carcaças, frutas podres e fungos. Possuem diversos papéis no ecossistema como a ciclagem de nutrientes, a bioturbação, entre outros. Por essas funções, os rola-bostas são uma ótima fonte biondicadora da qualidade do ambiente, são suscetíveis direta e indiretamente a distúrbios no ambiente e aos mamíferos. Em locais onde a pressão de caça é forte e os mamíferos começam a se extinguir, os besouros podem ser afetados em sua abundância, riqueza e na composição da sua comunidade através de um efeito cascata. As assembleias de rola-bostas nas florestas tropicais também dependem de fatores característicos dos habitats, como a estrutura da vegetação, podendo divergir entre florestas tropicais primárias, secundárias e plantações. A Reserva Natural Vale, junto com a Reserva Biológica de Sooretama, é um bloco contínuo de vegetação nativa de baixada, onde encontra-se um mosaico de fitofisionomias, com uma rica fauna de médios e grandes mamíferos, alguns ameaçados de extinção e outros endêmicos. A pressão antrópica nessas áreas é forte sobre os mamíferos devido à caça ilegal e a presença de estradas e rodovias. Este estudo visou conhecer a assembleia de rola-bostas na Reserva Natural Vale (RNV) e sua relação com a assembleia de médios e grandes mamíferos e com as diferentes fitofisionomias. O estudo foi desenvolvido de abril a setembro de 2016 em 21 parcelas de 250 m de extensão. Em cada parcela foram usadas seis armadilhas de queda para os rola-bostas e uma armadilha fotográfica. Medidas sobre a estrutura da vegetação foram tomadas em 25 pontos na parcela. Reduzimos a composição e a abundância dos rola-bostas através do NMDS e relacionamos através de regressão múltipla com a estrutura da vegetação e a biomassa dos mamíferos. Coletamos 13708 indivíduos de rola bosta pertencentes a 32 espécies, sendo quatro espécies nunca haviam sido registradas na área anteriormente e uma espécie é exótica invasora (*Digitontophagus gazela*). Registramos 23 espécies de médios e grandes mamíferos na área, a biomassa total em cada parcela foi de 2341 a 10723 kg. Os resultados das regressões múltiplas mostraram que a assembleia dos rola-bostas se relaciona fortemente com a estrutura da vegetação quando comparamos parcelas em fitofisionomias abertas e fechadas. Porém, a assembleia de rola-bostas responde à biomassa de mamíferos quando analisamos apenas as parcelas localizadas em fitofisionomias florestais. Os resultados corroboraram a hipótese que a assembleia de rola-bostas é estruturada pela biomassa dos mamíferos e pela estrutura da vegetação. Análises futuras são necessárias para melhor entendimento de especificidade entre as fezes de certos mamíferos e algumas espécies de rola-bostas.

Palavras-chave: Rola-bosta. Mamíferos. Biomassa. Mata Atlântica. Biodiversidade. Caça.

ABSTRACT

COUTO, Fabiana Cassar de Barros. *The dung beetle assemblage and their relationship with the mammals and the phytophysionomies at Reserva Natural Vale, ES, Brazil*. 2018. 62f. Dissertação (Mestrado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2018.

Dung Beetles (Scarabaeidae) are a group of insects, globally distributed with greatest diversity at the Tropics and Savannas, probably because of their habit of feeding on mammalian dung, although they also feed on carcasses, decaying fruits and fungi. They play several roles in the ecosystem, which include nutrient cycling, bioturbation, plant growth enhancement, secondary seed dispersal, parasite suppression, enteric parasite reduction, fly control, trophic regulation and pollination. Due to these functions they have become an excellent source of environmental quality and are susceptible directly and indirectly to disturbances on the environment and on the mammals assemblages. In places where hunting pressure is strong and mammals begin to die out, beetles can be affected in their abundance, richness and community composition through a cascading effect. Dung beetles assemblages in tropical forests also depend habitat characteristics such as vegetation structure, diverging between primary tropical forests, secondary forests and plantations. Vale Natural Reserve(RNV) along with Sooretama Biological Reserve, form a continuous block of vegetation native to the lowland, where there is a mosaic of phytophysionomies, sheltering a rich fauna of medium and large mammals, some of them threatened of extinction and other endemic. Anthropogenic pressure in these areas is very strong on mammals due to illegal hunting and the presence of roads and highways. In this context, the purpose of this study was to get to know the dung beetles assembly in the Vale Natural Reserve(RNV) and its relationship with the assembly of medium and large mammals and the different phytophysionomies. The study was developed from April to September 2016 in 21 plots of 250m of extension. In each plot six pitfall traps for dung beetles and a camera trap were established. Vegetation structure measurements were taken at 25 points in the plot. We reduced the composition and abundance of dung beetles through NMDS and related through multiple regression with vegetation structure and mammals biomass. We collected 13708 individuals of dung beetles belonging to 32 species, four of them had never been recorded at the area previously and one species is an exotic invasive. We recorded 23 species of medium and large mammals at the area, the total biomass in each plot ranged from 2341 to 10723kg. The results of the multiple regressions showed that the dung beetles assembly is strongly related to the vegetation structure when we compared plots in open and closed phytophysionomies. However, the dung beetles assembly responds to mammalian biomass when we analyze only the plots located in forest areas. Our results corroborate the hypothesis that the assemblage of dung beetles is structured by mammals biomass and vegetation structure. Future analyzes are needed to improve our understanding of whether there is any specificity certain mammalian species dung and dung beetles species.

Key words: Dung Beetles. Mammals. Biomass. Atlantic Forest. Biodiversity. Poaching.

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INTRODUCTION

Dung beetles are a globally distributed group of insects from the Coleoptera order and superfamily Scarabaeoidea. They are characterized by the lamellate antennae club and have a highly modified prothorax for burrowing. The Scarabaeidae family has 13 subfamilies of which eight are found in Brazil. The term dung beetle is used to group members of three subfamilies of Scarabaeidae: Scarabaeinae, Aphodiinae and Geotrupinae, because of their coprophagous feeding habits, even though some can also feed from carcasses or decaying fruits (Halffter & Matthews, 1966). Dung beetle's highest diversity is at the tropics and savannahs probably because of the presence of large mammals which they feed on their feces (Hanski & Cambefort, 1991).

Their morphology is intimately connected to the feeding and nesting habits. There are three main functional groups that are based on how they manage dung: endocoprids, paracoprids and telocoprid (Halffter & Edmonds, 1982). Endocoprids live and brood their young inside or immediately below dung. Paracoprids, also known as tunnelers can excavate complex tunnels and chambers under the dung resource where they can take and store dung. Telecoprids carry the dung away from the source in the shape of balls and bury them later. These behaviors can drive a series of ecological processes such as soil aeration, secondary seed dispersal, nutrient cycling and parasite suppression (Nichols et al., 2008). All these functions make this group a good ecological indicator of the quality of the environment and also make them susceptible directly and indirectly to the environmental changes that may affect mammals to which they are intimately connected (Nichols et al, 2007; 2009).

Human disturbances such as plantations and hunting can lead to a series of direct and indirect effects on the environment. Gardner et al (2008) showed that in secondary and plantation forests the dung beetles community is impoverished in comparison to primary forests and, combined with loss of biomass, the ecosystem services are impaired. Overhunting may be a cause to local extinction or severe declines of medium and large mammals which increases the concern for the outcomes of zoochory in plant communities and also for the secondary extinction of dependent groups and their ecosystem functions (Stoner, 2007; Feer & Boissier, 2015).

Brazil is the country with the greatest diversity of mammals in the Neotropics (Costa et al., 2005). There are 791 species of mammals in Brazil, distributed in 243 genera, 50 families and 12 orders (Paglia et al., 2012) with 298 of them occurring in Atlantic forest, with 90 endemic and 69 under threat according to International Union for Conservation of Nature red list (IUCN) of threatened species (Machado et al., 2008). Mammals are often under threat due to loss of habitat and environmental fragmentation in Brazil (Costa et al., 2005).

The Atlantic forest has been suffering from vegetation cover loss since the country discovery, even though is one of the 35 world's hotspots of biodiversity (<https://www.conservation.org/How/Pages/Hotspots.aspx>). There is only 11.7% of the original vegetation left and the remaining areas are most of small and scarce fragments (Ribeiro et al., 2009). The Atlantic Forest Biome is extremely heterogeneous in their vegetation composition (Tabarelli et al., 2005) and it's mainly composed by two major vegetation types: Atlantic Rain Forest and Atlantic Semi-deciduous forest (Morellato & Haddad, 2000) but some consider Araucaria mixed forests also as part of the biome (Oliveira-Filho & Fontes, 2000).

In the State of Espírito Santo, Reserva Natural Vale (RNV or Vale Natural Reserve) together with Reserva Biológica de Sooretama (Sooretama Biological Reserve) form a continuous block of lowland Atlantic forest, where can be found a mosaic of phytophysiognomies. This region is one of the last ones that house a rich fauna of 26 species of medium and large mammals, being 8 species endangered and 7, endemic. Anthropogenic pressure, as in most of the Atlantic forest areas, is severe with the presence of agriculture lands, roads and highways. Some species of medium and large mammals are negatively affected by hunting, showing low occupancy and detectability rates (Ferregueti et al., 2015; 2017).

Dung beetles are sensitive to forest disturbance and have been widely used as an indicator group related with ecological functions (Barragán et al., 2011; Braga et al., 2013; Edwards et al., 2013). But the specific effect of mammal abundance on dung beetles diversity remains poorly documented. Several studies showing the effects of tropical forest fragmentation partially attribute the decline in the dung beetle fauna to an impoverished mammal assemblage (Klein, 1989; Estrada et al., 1998; Vulinec, 2000; Andresen, 2003; Feer and Hingrat, 2005). Dung beetles can be considered a good indicator of environmental changes, with their abundances declining with disturbances (Larsen, Williams, Kremen, 2005). Dung

beetles also go through significant changes in undisturbed forest following mammal defaunation and the declining of dung resources affecting their reproduction and survival (Andresen & Laurence, 2007; Nichols et al., 2009).

Because dung beetles play a diverse role in the ecosystem, they are important environmental indicators exerting a strong influence on the analysis of threatened and conserved area. In this sense, the present study aims to characterize the assemblage of dung beetles at Reserva Natural Vale (RNV) and look at their direct and indirect relationship with the vegetation structure, medium and large mammals biomass and diversity and also hunting effect.

1 OBJECTIVES

1.1. Main objective

Our main objectives are to know the assemblage of dung beetles in Reserva Natural Vale (RNV) and evaluate which factors most affect dung beetles' assemblages, if the composition and abundance of mammals, the mammalian biomass or the vegetation structure.

1.2. Specific objectives

To achieve the main goal, we answer the following specific questions:

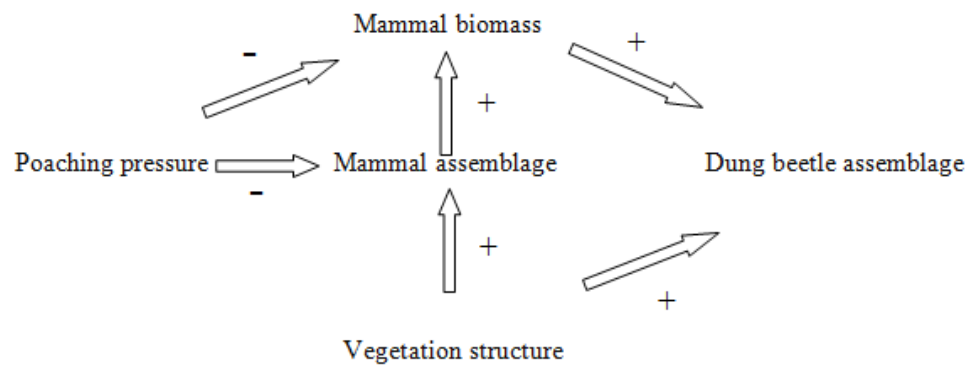
- 1) What are the species of dung beetles and its abundances in the study area?
- 2) Do the assemblage (composition and abundance) of dung beetles have a specific structure in the study area?
- 3) Does the assemblage of mammals and the structure of vegetation explain the structure of dung beetle assemblage?
- 4) Is there any indirect effect of poaching via mammalian biomass decrease or abundance on the assemblage of dung beetle?

1.3. Hypothesis

Our working hypothesis is that the dung beetle is structured both by the mammal assemblage biomass and by the structure of the vegetation. Hence, the abundance and richness of dung beetles will be higher in environments with greater habitat complexity once these species respond to habitat changes and consequently, a richer and abundant mammal community. However, the effects of mammal biomass will be greater than their records, since the amount of feces produced is related to the biomass of the species. On the other hand, poaching can have an indirect negative effect through mammal assemblage and biomass. Areas with higher poaching effects will have lower dung beetle species richness and abundance by

hunting effect onto medium and large mammals. On the image below (Figure 1) is the work flowchart showing our hypothesis, where each signal represents the expected effect.

Figure 1- Work hypothesis flowchart of the direct and indirect effects of poaching, mammal assemblage and biomass and vegetation structure in dung beetle assemblage.



Source: The author, 2018

2. MATERIAL AND METHODS

2.1. Study site

This study was conducted in Reserva Natural Vale (RNV) (19°06' – 19°18' S e 39°45' – 40°19' W), situated between the municipalities of Linhares and São Mateus, North of Espírito Santo state, southeastern Brazil. The reserve area is 23,500 ha and, together with the Sooretama Biological Reserve, forms a forest block of about 50,000 ha, being one of the largest conservation areas located in the central corridor of the Atlantic Forest (MMA, 2000). This forest block represents almost 10% of forest cover of the entire Espírito Santo state (Fundação SOS Mata Atlântica & INPE, 2011).

RNV was created in gradative process of land acquisitions that started in 1955, when Vale do Rio Doce Company started buying lands in the region. The main objective was to create beam supply for the Vitória-Minas Gerais railroad (Jesus & Rolim, 2005). Fortunately, the initial results from the management of a small area in 1960 revealed that the project for wooden use would not be economically viable, so the forest was kept as a reserve by Vale. The current boundaries of the reserve were established in 1973, being made of a main block (98.1% of the total area) and a little adjacent area southwest of the main one. In 1978 actions to protect the area took place, like prevention against fire, wood extraction and hunting. These actions were named as Proteção Ecossistêmica and RNV officially became a biodiversity conservation area.

The climate is classified as Aw according to the Koppen system and it is characterized by seasonality, with one rainy season from October to March and a dry season from April till September (Garay & Rizzini, 2003). The mean annual rainfall and mean annual temperature for the past 41 years (1975 to 2016) were 1,202 mm and 23.3 °C, respectively (Kierulff et al. 2014).

2.1.1. Vegetation

Reserva Natural Vale is covered by dense forest and composed by four distinct vegetation types: Tabuleiro forest (Coastal Plain Forest), “Mussununga” forest, Riparian forest, and natural grassland (Jesus 1987; Peixoto & Gentry, 1990).

The evergreen Tabuleiro forest is the most representative formation at RNV and covers about 68% of the area. This vegetation type is distributed upon Podzolic soils and differs from other vegetations by the presence of large trees and thin and very shadowed undergrowth (Garay & Rizzini, 2004). The floor is covered by relatively thick leaf litter with trees whose canopy reaches up to 40 m in height, occurring in a dense form (Peixoto et al. 2008).

Mussununga forest covers about 8% of RNV area and is located in sand soils. The vegetation is more open than Tabuleiro forest and the trees reach lower heights varying between 7 and 10 m, with some emerging trees reaching 18 m in height (Kierulff et al. 2014; Peixoto et al. 2008).

The Riparian forest covers 4% of the reserve area and is a mixed type of vegetation associated with water bodies, represented by sparse trees and a prevalence of palms (Jesus 1987; Peixoto & Gentry, 1990).

The natural grasslands are open fields in the middle of the forest covering 6% of the RNV area. Vegetation consisting of bromeliads and herbaceous creates particular clumps similar to those found in the “restingas” (coastal sand dunes) on southeastern Brazil (Peixoto, 1982).

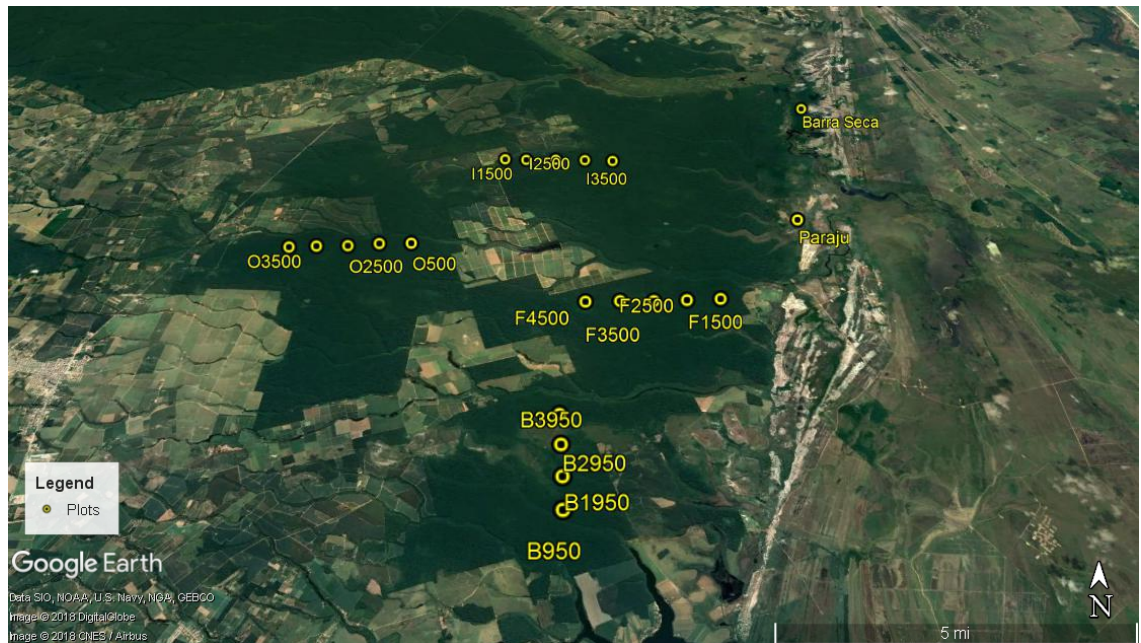
2.2. **Methods**

Field sampling

The study was carried out between April and September of 2016. The samples took place in 21 plots of 250 m long, all of them proportionately distributed in the vegetation types of RNV. The plots were established 1 km apart from each other in five lines transects of 5 km each (Figure 2). The transects were allocated in order to sample all phytophysiognomies proportionally. The 250 m plots follow the isoclines according to the RAPELD methodology

(Magnusson et al. 2005). Line transects and plots were established in the study area by the Biodiversity Research Program Network of the Atlantic Forest (PPBio MA).

Figure 2- Study plots placed 1km apart from each other at Reserva Natural Vale, Espirito Santo, Brazil.



Source: Google earth, 2018

At each plot, we used six pitfall traps with 20 cm of diameter and 10 cm of depth. Each pitfall trap was baited with approximately 20 g of human feces in a small coffee cup placed in the middle of the trap with its rim at ground level, according to Milhomem et al. (2003). Pitfalls were filled to one-third of its capacity with a solution of soap and water. At each site the traps were placed with 50m of intertrap space and leaved there for two nights (Larsen and Forsyth, 2005). The beetles caught in the traps were put in absolut alcohol (99.9%) in plastic containers (SISBIO license number 53696-4). Each container had the information about date, site of collection in the plot and the plot. In the laboratory using a stereoscopic microscope, I separated all specimens into morphotypes for further identification. The specimens were identified by Dr. Fernando Zagury Vaz de Mello from Universidade Federal do Mato Grosso and part of the

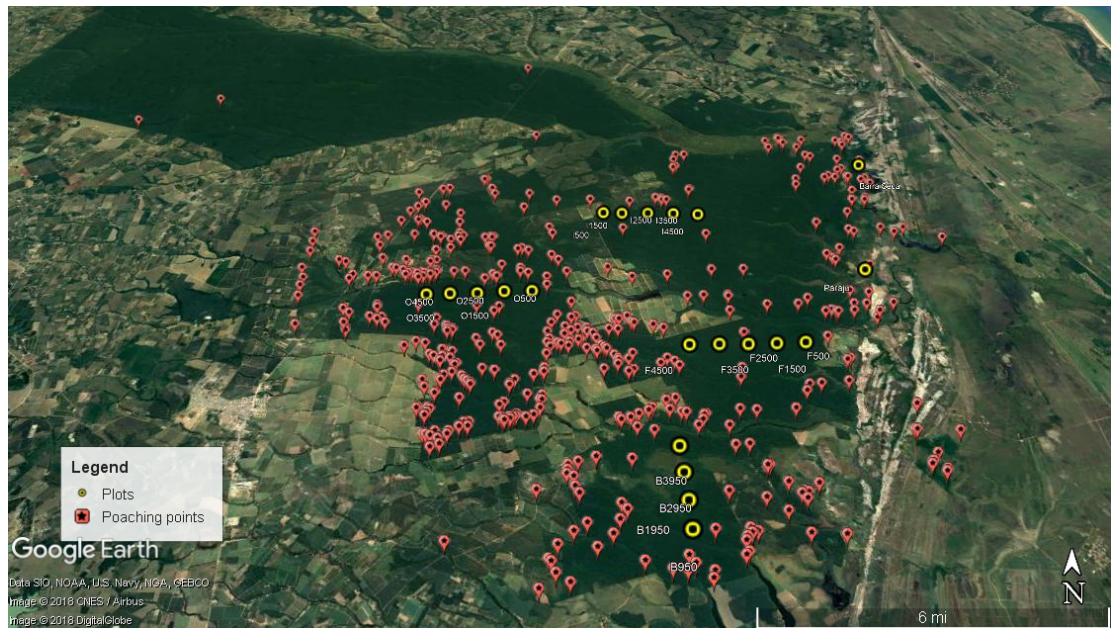
material was deposited in the Entomological Section of the Zoological Collection (CEMT) at Universidade Federal do Mato Grosso (UFMT), Brazil.

The medium and large mammals were sampled using camera traps. A Bushnell® camera trap with infrared sensor, photo and video shooting function was installed at each 21 sampling plot. Camera traps were checked in a period of 20-25 days when batteries and SD cards were replaced by new ones.

The environmental covariates were measured in 25 points 10 meters apart in the 250 meters length of the plot. At each point, we measured the covariates at 5m distance from the central point. The covariates are: tree hollows, lianas densities, palm trees, trees diameter at breast height greater than or equal to 50 cm ($DAP \geq 50\text{cm}$) and 20 to 49 cm ($DAP < 50\text{cm}$), tabular roots, dead trees, bromeliads, fallen logs and mammal dens. The covariates of foliage depth, canopy and sub-forest cover were measured in 5 points (50m, 100m, 150m, 200m, and 250m) and their average value were taken.

We used a georeferenced database of 14 years of poaching records collected by the reserve's surveillance guards. From these records, we took the point closest to each of the plots and used the distances to see if there was any relationship between the poaching activity and mammalian records (Figure 3).

Figure 3- Poaching points from 14 years database collected at Reserva Natural Vale, Espirito Santo, Brazil.



Source: Google Earth, 2018

Statistical analysis

To evaluate which factors most affect dung beetles' assemblages in Reserva Natural Vale (RNV), we had to reduce the dimensionality of the dung beetles and mammals' assemblages using ordination techniques. The reduction of dimensionality was also necessary for vegetation structure.

For the dung beetles, first we summed their abundances at each point in each plot to obtain a total number of each species per plot. Then, we transformed these numbers in natural logarithm (neperian logarithm) due to the extreme variation of its values (0-2089 individuals). We did a non-metric multidimensional scaling (NMDS) to order each plot by its similarity according to dung beetle species and abundances. In all plots there were absences of some species of dung beetles, so we used the Bray-Curtis dissimilarities index to ignore double absences when we compared the differences between plots (Legendre & Legendre, 1998).

We used four different ways to quantify the effect of mammals in dung beetles' assemblages: 1) using the number of each species of mammal recorded in the camera traps in

each plot (henceforth occurrence); 2) using mammal's transformed biomass for each species in each plot (henceforth transformed biomass); 3) using the mammal's biomass without transformation for each species in each plot (henceforth biomass); and 4) using the total biomass in the plots (henceforth total biomass). We obtained in the literature (Paglia *et al.*, 2012) the average mass of the species recorded in the camera traps and multiplied by the number of records of each species in each plot, in this way we obtained the biomass without transformation. We divided the biomass without transformation of each species by the total biomass of the plot to obtain the transformed biomass. We also used an NMDS with Bray-Curtis dissimilarity index to order each plot by its similarity according to the occurrence, transformed biomass and biomass of medium and large mammal assemblages.

For the vegetation structure that we measured in each plot we did a principal component analysis (PCA) using a correlation matrix.

The NMDS single axis of dung beetles and mammals were used in multiple regressions, as well as, the first two axes of PCA of the vegetation structure. We did four models to test, as can be seen below:

$$\text{NMDS_DungBeetle} = \text{constant} + \text{PCA1} + \text{PCA2} + \text{NMDS_Transformed Biomass}$$

$$\text{NMDS_DungBeetle} = \text{constant} + \text{PCA1} + \text{PCA2} + \text{NMDS_Biomass}$$

$$\text{NMDS_DungBeetle} = \text{constant} + \text{PCA1} + \text{PCA2} + \text{NMDS_Total Biomass}$$

$$\text{NMDS_DungBeetle} = \text{constant} + \text{PCA1} + \text{PCA2} + \text{NMDS_Occurrence}$$

These four models were used in three different scenarios, considering all plots, without plot B3950 and without plots B3950, Barra Seca and Paraju. We did it because plot B3950 had one record of one species of dung beetles that only occurred there. Being an outlier, this plot has pulled the structuring of the assembly of dung beetles. We also removed Barra Seca and Paraju plots because they are open phytophysionomies and the rest of the plots, forested areas.

We also analysed the dung beetles assemblages according to the three functional groups: endocoprids, paracoprids and telocoprids. We used the studies of Pacheco *et al.* (2016), Lima (2013), Koller *et al.* (1999) and Farias & Hernandez (2017), in order to separate the species in their functional groups. We grouped only those species that we knew the functional group. We did an NMDS to see how the plots were ordered. We conducted the same multiple regressions

combinations with the first axes of the NMDS, to see which variable explained the community structure based in the functional groups.

Path analysis

In order to evaluate indirect effects of poaching on the dung beetles assemblage we used the path analysis. This analysis is used to reduce the limitations that multiple regressions have to assess the real influence of factors and causal mechanisms on the assemblages (Crespi & Bookstein, 1989; Kingsolver & Douglas, 1991). We used the diagram proposed on the hypothesis (Figure 1) to calculate the effects via each path on the dung beetles assemblage. The path analyses were made with all plots, without B3950 plot and without B3950, Barra Seca e Paraju. For the mammals we used the assemblage at all models and used total biomass and biomass without transformation as different models.

The analyses were carried out in R environment (R Development Core Team, 2008) and Systat 13.

3. RESULTS

Dung beetles

We collected 13708 individuals of dung beetle from 36 different species (Table 1). The most abundant plot was F500 with 3283 individuals collected and it was also the one with the greatest diversity of species totalizing 20 (Table 2). The least abundant and less diverse plot was B3950 with only 1 individual from 1 species, *Digitonthophagus gazella*. The most abundant species was *Canthon staigi* totalizing 6469 individuals, occurring in 18 plots out of 21, followed by *Dichotomius irinus* with 5119 specimens and that occurred in all plots except B3950. Seven species appeared in only one plot (*Canthidium* sp3, *Canthon nigripennis*, *Coprophanaeus bellicosus*, *Dichotomius geminatus*, *Dichotomius nisus*, *Digitonthophagus gazella* and *Holocephalus sculptus*).

Table 1 – Dung Beetle species and number of individuals collected on the 21 plots uniformly distributed at Reserva Natural Vale, ES.

| Species | F300 | F1500 | F2500 | F3500 | F4500 | O500 | O1500 | O2500 | O3500 | O4500 | I500 | I1500 | I2500 | I3500 | I4500 | B950 | B1950 | B2950 | B3950 | Barranca | PARAJU |
|------------------------------------|------|-------|-------|-------|-------|------|-------|-------|-------|-------|------|-------|-------|-------|-------|------|-------|-------|-------|----------|--------|
| <i>Aphengium capreum</i> | 24 | 21 | 6 | 19 | 2 | 0 | 6 | 3 | 3 | 2 | 22 | 1 | 4 | 35 | 73 | 64 | 4 | 2 | 0 | 0 | 0 |
| <i>Atenichus vigilans</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 9 | 16 | 7 | 0 | 0 | 0 |
| <i>Atenichus pygmaeus</i> | 11 | 15 | 5 | 12 | 14 | 0 | 2 | 0 | 0 | 2 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Atenichus squalidus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Canthidium chapeale</i> | 29 | 8 | 0 | 4 | 0 | 0 | 2 | 2 | 0 | 1 | 1 | 2 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Canthidium</i> sp1 | 2 | 4 | 0 | 0 | 0 | 0 | 8 | 3 | 4 | 1 | 0 | 1 | 0 | 1 | 5 | 1 | 4 | 0 | 0 | 0 | 0 |
| <i>Canthidium</i> sp2 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Canthidium</i> sp3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Canthidium</i> sp4 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Canthon ibarrae</i> | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Canthon nigripennis</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Canthon prasinus</i> | 130 | 46 | 22 | 101 | 34 | 58 | 6 | 22 | 1 | 0 | 12 | 7 | 1 | 6 | 26 | 37 | 29 | 4 | 0 | 0 | 0 |
| <i>Canthon</i> sp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Canthon smaragdinus</i> | 28 | 29 | 9 | 29 | 6 | 8 | 1 | 2 | 1 | 7 | 35 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Canthon stagi</i> | 2089 | 709 | 233 | 954 | 390 | 76 | 15 | 11 | 33 | 30 | 560 | 235 | 33 | 149 | 260 | 275 | 311 | 106 | 0 | 0 | 0 |
| <i>Canthonella sulphurea</i> | 58 | 9 | 6 | 18 | 11 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 3 | 31 | 14 | 2 | 0 | 0 | 0 |
| <i>Chalcocoris hesperus</i> | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Coprophanaeus bellicosus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Deltotium</i> sp | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Dichotomius camptocentrus</i> | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dichotomius depressicollis</i> | 0 | 0 | 0 | 6 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Dichotomius irinus</i> | 812 | 474 | 223 | 689 | 545 | 59 | 61 | 47 | 42 | 100 | 281 | 62 | 100 | 141 | 295 | 454 | 368 | 362 | 0 | 2 | 2 |
| <i>Dichotomius geminatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Dichotomius nigrus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Dichotomius schifflii</i> | 2 | 2 | 2 | 81 | 87 | 0 | 40 | 1 | 47 | 0 | 9 | 1 | 0 | 9 | 2 | 15 | 28 | 27 | 0 | 4 | 17 |
| <i>Dichotomius semisquamatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 4 | 0 | 0 | 0 |
| <i>Digitonophagus gazela</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Eurysternus caribaeus</i> | 15 | 4 | 1 | 5 | 1 | 1 | 0 | 0 | 0 | 0 | 56 | 0 | 0 | 0 | 0 | 23 | 19 | 0 | 0 | 0 | 0 |
| <i>Eurysternus iridellus</i> | 10 | 4 | 0 | 7 | 0 | 1 | 1 | 0 | 0 | 0 | 5 | 3 | 0 | 0 | 0 | 2 | 8 | 2 | 0 | 0 | 0 |
| <i>Holocephalus sculptus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Onthophagus haematophus</i> | 44 | 12 | 2 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Phanaeus splendidulus</i> | 10 | 3 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 0 | 2 | 3 | 2 | 0 | 0 | 0 |
| <i>Streblospus apatroides</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Trichillum</i> sp | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 0 | 2 | 0 | 0 | 0 |
| <i>Trichillum externopunctatum</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Uroxys</i> sp | 12 | 6 | 4 | 5 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 2 | 0 | 0 | 0 |

Source: The author, 2018

Table 2 – Dung beetle and mammal species richness and abundances found at each of the 21 plots uniformly distributed along Reserva Natural Vale, ES.

| Plots | Dung beetle abundances | Dung beetle richness | Mammal richness | Mammal biomass |
|------------|------------------------|----------------------|-----------------|----------------|
| F500 | 3283 | 20 | 10 | 5432 |
| F1500 | 1350 | 18 | 14 | 7031 |
| F2500 | 513 | 11 | 14 | 8155 |
| F3500 | 1942 | 19 | 13 | 4800 |
| F4500 | 1095 | 14 | 12 | 7185 |
| O500 | 206 | 9 | 13 | 8206 |
| O1500 | 143 | 11 | 10 | 10723 |
| O2500 | 95 | 10 | 14 | 10015 |
| O3500 | 133 | 8 | 15 | 8942 |
| O4500 | 146 | 9 | 15 | 7779 |
| I500 | 1023 | 17 | 15 | 6544 |
| I1500 | 315 | 10 | 11 | 6069 |
| I2500 | 142 | 7 | 15 | 8180 |
| I3500 | 354 | 13 | 12 | 6398 |
| I4500 | 67 | 14 | 12 | 5752 |
| B950 | 925 | 18 | 14 | 6422 |
| B1950 | 806 | 13 | 13 | 7545 |
| B2950 | 524 | 14 | 14 | 7710 |
| B3950 | 1 | 1 | 5 | 2341 |
| Barra Seca | 13 | 7 | 16 | 4945 |
| Paraju | 22 | 5 | 6 | 5758 |

Source: The author, 2018

The relationships between richness of dung beetles with richness and biomass of mammals can be seen in table 2. Considering all plots, mammal richness explained positive and significantly part of the variance observed in dung beetle richness after withdrawing the effect of mammal biomass. Without the three plots, the mammal biomass explained significantly part of the variance observed in dung beetle richness after withdrawing the effect of mammal richness, although the effect has been negative (Table 3). Dung beetle abundances were explained negative and significantly by mammal biomass in two scenarios, without B3950 plot and without the three plots (Table 3).

Table 3 – Multiple regressions between dung beetle richness and mammal richness and biomass in Vale Natural Reserve, ES, Brazil.

| Scenarios | Dung beetles | Mammals | Coefficient | P | Model |
|--------------------------------------|--------------|-----------------|---------------|--------------|---|
| All plots | Richness | Richness | 0.797 | 0.033 | R ² =0.230; F=2.684; P=0.095 |
| | | Biomass | -0.001 | 0.294 | |
| Without B3950 | Richness | Richness | 0.386 | 0.322 | R ² =0.169; F=1.732; P=0.207 |
| | | Biomass | -0.001 | 0.096 | |
| Without B3950, Paraju and Barra Seca | Richness | Richness | -0.237 | 0.621 | R ² =0.464; F=6.480; P=0.009 |
| | | Biomass | -0.002 | 0.005 | |
| All plots | Abundance | Richness | 71.351 | 0.238 | R ² =0.141; F=1.481; P=0.254 |
| | | Biomass | -0.182 | 0.111 | |
| Without B3950 | Abundance | Richness | 17.507 | 0.797 | R ² =0.212; F=2.291; P=0.131 |
| | | Biomass | -0.235 | 0.049 | |
| Without B3950, Paraju and Barra Seca | Abundance | Richness | -82.989 | 0.400 | R ² =0.451; F=6.159; P=0.011 |
| | | Biomass | -0.318 | 0.008 | |

Source: The author, 2018

We reduced the dimensionality of the dung beetles' assemblage with NMDS and the first result considering all plots had a stress of 0.003, suggesting that there was a good fit between the distances among the objects and the original distances after reducing the dimensionality. However, in the two dimensions NMDS' graph, B3950 is completely isolated in the first axes, while Paraju and Barra Seca are close together and far from the other plots in the second axes (Fig 4A). The second NMDS without B3950 plot had a stress of 0.07 and separated Barra Seca and Paraju plots from the rest (Fig 4B). The third NMDS excluding

Vegetation Structure

The environmental covariates were reduced with the Principal Component Analysis (PCA). The two first axes of PCA explained 66.8% of the variation considering all plots, explained 67.0% without B3950 plot, and 59.6%, without B3950, Barra Seca and Paraju. In the first axis considering all plots and without B3950 (Table 4a; b) trees with DBH>50 (Arv_50), depth of leaf litter (prof_folhico) and canopy (dossel) had the highest values and plots with these characteristics are those in forested areas, while bromeliads (Bromelia) characterize plots in grassland areas (Table 4a, b; Fig 5a, b). In the third PCA (without B3950, Barra Seca and Paraju), the first axis was related with big trees (Arv_50), tabular roots (Raiz Tabular), hollows (Ocos) and burrows (Tocas) characteristic of Tabuleiro forest plots in one side, and sub-forest (Subbosque), canopy cover (Dossel) and lianas, characteristics from Mussununga in the opposite site (Table 4c; Figure 5c). The second axis of the PCA is related to palm trees common in ecotone plots.

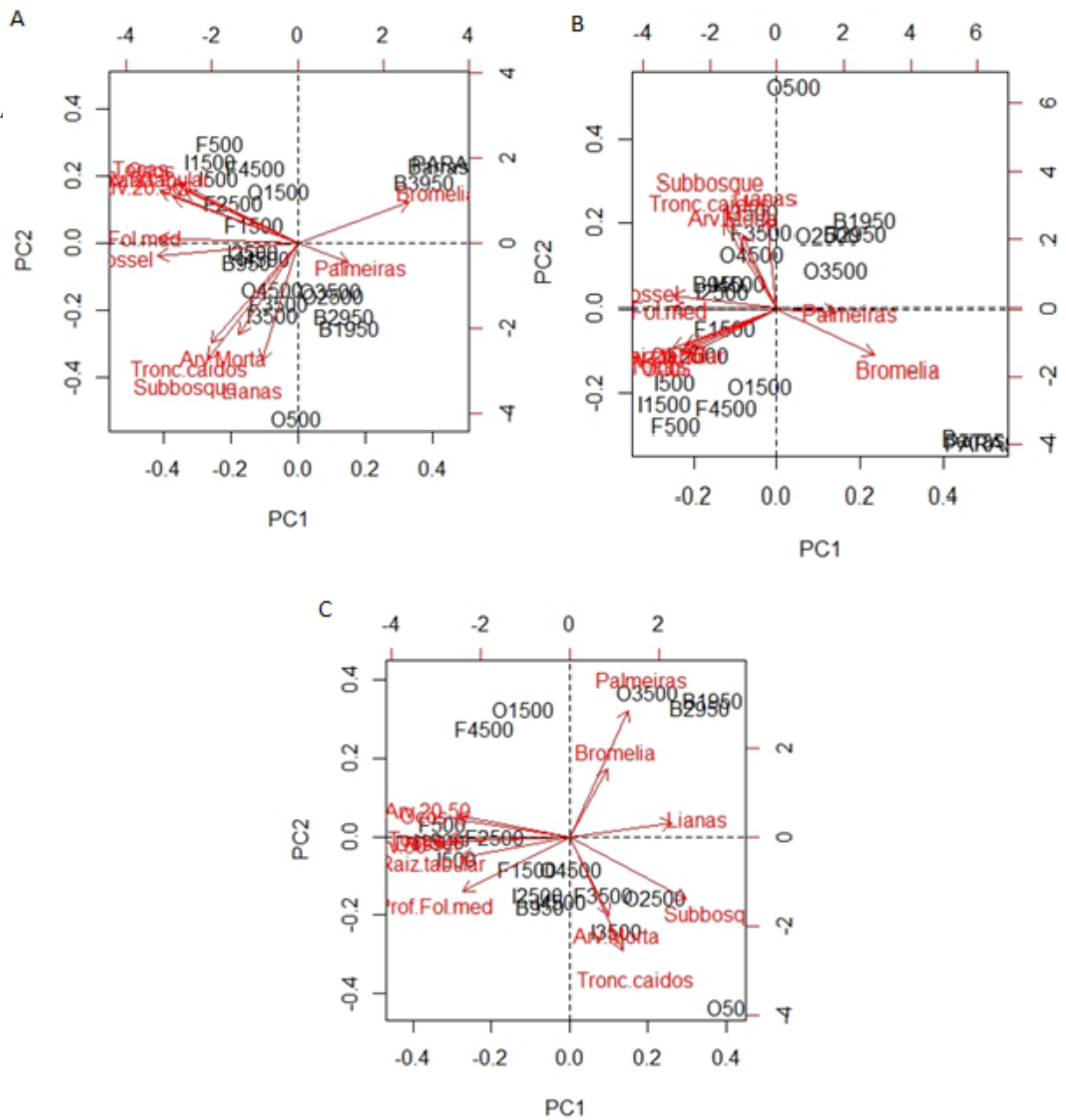
Table 4 - Loadings from the PCA in the three scenarios:.

| A Environmental Covariates | PC1 | PC2 | B Environmental Covariates | PC1 | PC2 | C Environmental Covariates | PC1 | PC2 |
|----------------------------|----------------|-----------------|----------------------------|----------------|----------------|----------------------------|----------------|----------------|
| Ocos | -0.3005 | 0.237912 | Ocos | -0.3002 | -0.225 | Ocos | -0.3213 | 0.07968 |
| Arv.50 | -0.3559 | 0.209908 | Arv.50 | -0.3604 | -0.1986 | Arv.50 | -0.3788 | -0.0275 |
| Arv.20.50 | -0.3202 | 0.184213 | Arv.20.50 | -0.3154 | -0.1842 | Arv.20.50 | -0.3143 | 0.09886 |
| Raiz.tabular | -0.2905 | 0.209025 | Raiz.tabular | -0.2936 | -0.1839 | Raiz.tabular | -0.3047 | -0.0933 |
| Arv.Morta | -0.1508 | -0.36548 | Arv.Morta | -0.1175 | 0.35635 | Arv.Morta | 0.10808 | 0.35812 |
| Bromelia | 0.28903 | 0.16337 | Bromelia | 0.33331 | -0.236 | Bromelia | 0.10414 | 0.31228 |
| Palmeiras | 0.13069 | -0.07509 | Palmeiras | 0.19963 | -0.0149 | Palmeiras | 0.16176 | 0.57725 |
| Tronc.caídos | -0.223 | -0.39876 | Tronc.caídos | -0.184 | 0.41943 | Tronc.caídos | 0.14649 | -0.5179 |
| Tocas | -0.3201 | 0.239437 | Tocas | -0.3228 | -0.2205 | Tocas | -0.3382 | -0.0037 |
| Lianas | -0.0915 | -0.47016 | Lianas | -0.0315 | 0.4379 | Lianas | 0.28559 | 0.06493 |
| Prof.Fol.med | -0.3587 | 0.020073 | Prof.Fol.med | -0.3594 | -0.006 | Prof.Fol.med | -0.298 | -0.2476 |
| Dossel | -0.3605 | -0.04948 | Dossel | -0.3579 | 0.05779 | Dossel | 0.31748 | -0.0181 |
| Subbosque | -0.2314 | -0.46429 | Subbosque | -0.1826 | 0.48951 | Subbosque | 0.32545 | -0.2851 |

Source: The author, 2018

Subtitle: A) considering all plots, B) without B3950 and C) without B3950, Paraju and Barra Seca, in Vale Natural Reserve, Brazil

Figure 5- Biplot of the vegetation structure (PCA) in three scenarios:



Source: The author, 2018.

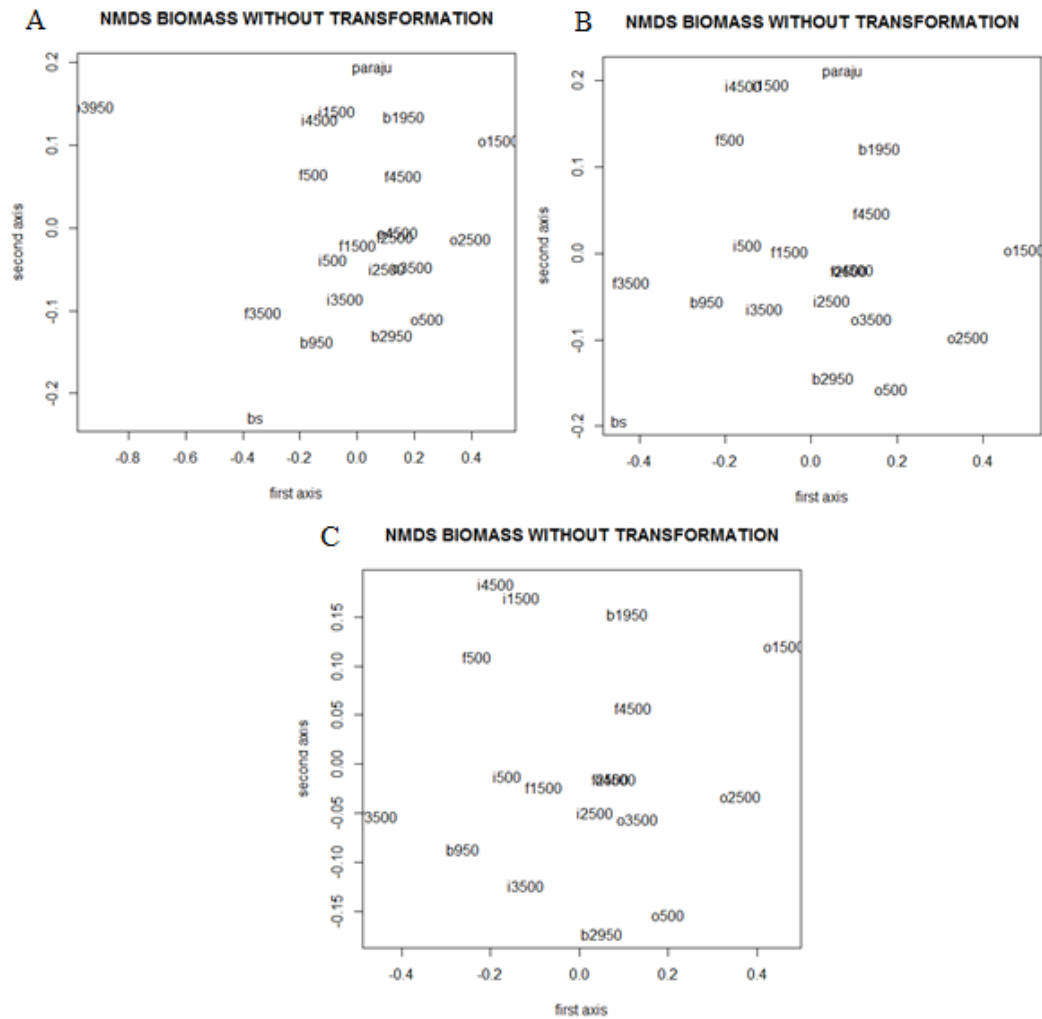
Subtitle: A) considering all plots, B) without B3950 and C) without B3950, Paraju and Barra Seca, in Vale Natural Reserve, Brazil

Table 5- Mammal species and occurrences at the 21 plots uniformly distributed at Reserva Natural Vale, ES.

| Species | f500 | f1500 | f2500 | f3500 | f4500 | o500 | o1500 | o2500 | o3500 | o4500 | i500 | i1500 | i2500 | i3500 | i4500 | b950 | b1950 | b2950 | b3950 | bs | paraju |
|----------------------------------|------|-------|-------|-------|-------|------|-------|-------|-------|-------|------|-------|-------|-------|-------|------|-------|-------|-------|----|--------|
| <i>Tapirus terrestris</i> | 16 | 19 | 23 | 12 | 23 | 26 | 34 | 31 | 25 | 23 | 17 | 18 | 22 | 18 | 17 | 15 | 22 | 22 | 8 | 12 | 20 |
| <i>Tajacu pecari</i> | 0 | 12 | 14 | 11 | 9 | 16 | 0 | 0 | 15 | 9 | 12 | 0 | 15 | 13 | 0 | 23 | 0 | 23 | 0 | 12 | 0 |
| <i>Pecari tajacu</i> | 11 | 15 | 11 | 8 | 0 | 12 | 0 | 18 | 13 | 8 | 12 | 14 | 15 | 19 | 11 | 12 | 0 | 18 | 0 | 9 | 0 |
| <i>Mazama americana</i> | 11 | 13 | 17 | 12 | 12 | 0 | 23 | 8 | 13 | 9 | 13 | 18 | 12 | 0 | 13 | 15 | 23 | 0 | 0 | 0 | 0 |
| <i>Mazama gouzoubira</i> | 15 | 23 | 19 | 14 | 0 | 16 | 34 | 25 | 23 | 23 | 27 | 0 | 23 | 21 | 0 | 22 | 18 | 13 | 11 | 19 | 15 |
| <i>Sylvilagus brasiliensis</i> | 3 | 6 | 10 | 7 | 12 | 11 | 0 | 0 | 5 | 6 | 8 | 0 | 7 | 0 | 0 | 6 | 0 | 8 | 0 | 9 | 0 |
| <i>Leopardus pardalis</i> | 0 | 8 | 8 | 9 | 11 | 0 | 6 | 12 | 11 | 9 | 12 | 9 | 7 | 9 | 12 | 13 | 8 | 9 | 0 | 17 | 0 |
| <i>Puma yagouaroundi</i> | 0 | 4 | 0 | 0 | 0 | 0 | 5 | 6 | 7 | 2 | 5 | 0 | 7 | 0 | 8 | 0 | 5 | 0 | 3 | 4 | 0 |
| <i>Tamandua tetradactyla</i> | 0 | 6 | 0 | 4 | 0 | 0 | 0 | 6 | 5 | 5 | 6 | 0 | 6 | 0 | 3 | 0 | 0 | 9 | 0 | 6 | 0 |
| <i>Hydrochoerus hydrochaeris</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 4 | 0 | 4 | 0 | 2 | 6 | 0 |
| <i>Dasypus novemcinctus</i> | 0 | 6 | 11 | 12 | 8 | 9 | 5 | 12 | 14 | 9 | 11 | 7 | 13 | 11 | 0 | 10 | 8 | 3 | 0 | 6 | 9 |
| <i>Euphractus sexcinctus</i> | 0 | 3 | 6 | 9 | 11 | 6 | 0 | 15 | 12 | 5 | 4 | 6 | 7 | 2 | 3 | 8 | 5 | 7 | 5 | 11 | 0 |
| <i>Cabassous tatouay</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 0 | 1 | 0 |
| <i>Procyon cancrivorus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Eira barbara</i> | 8 | 0 | 4 | 0 | 5 | 4 | 0 | 14 | 16 | 11 | 3 | 11 | 8 | 4 | 6 | 2 | 7 | 0 | 0 | 7 | 0 |
| <i>Dasypsecta leporina</i> | 11 | 9 | 13 | 8 | 9 | 7 | 11 | 11 | 8 | 11 | 3 | 12 | 3 | 5 | 6 | 12 | 11 | 9 | 0 | 0 | 0 |
| <i>Cerdocyon thous</i> | 3 | 0 | 4 | 0 | 5 | 3 | 5 | 6 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 4 | 0 | 3 | 0 | 3 | 5 |
| <i>Nasua nasua</i> | 12 | 16 | 9 | 5 | 6 | 6 | 13 | 15 | 13 | 8 | 12 | 3 | 0 | 4 | 11 | 6 | 19 | 12 | 0 | 4 | 11 |
| <i>Cuniculus paca</i> | 8 | 3 | 6 | 9 | 11 | 4 | 9 | 11 | 13 | 11 | 2 | 6 | 9 | 11 | 7 | 6 | 5 | 11 | 0 | 8 | 13 |

Source: The author, 2018

Figure 6- NMDS of mammal biomass without transformation in the three scenarios

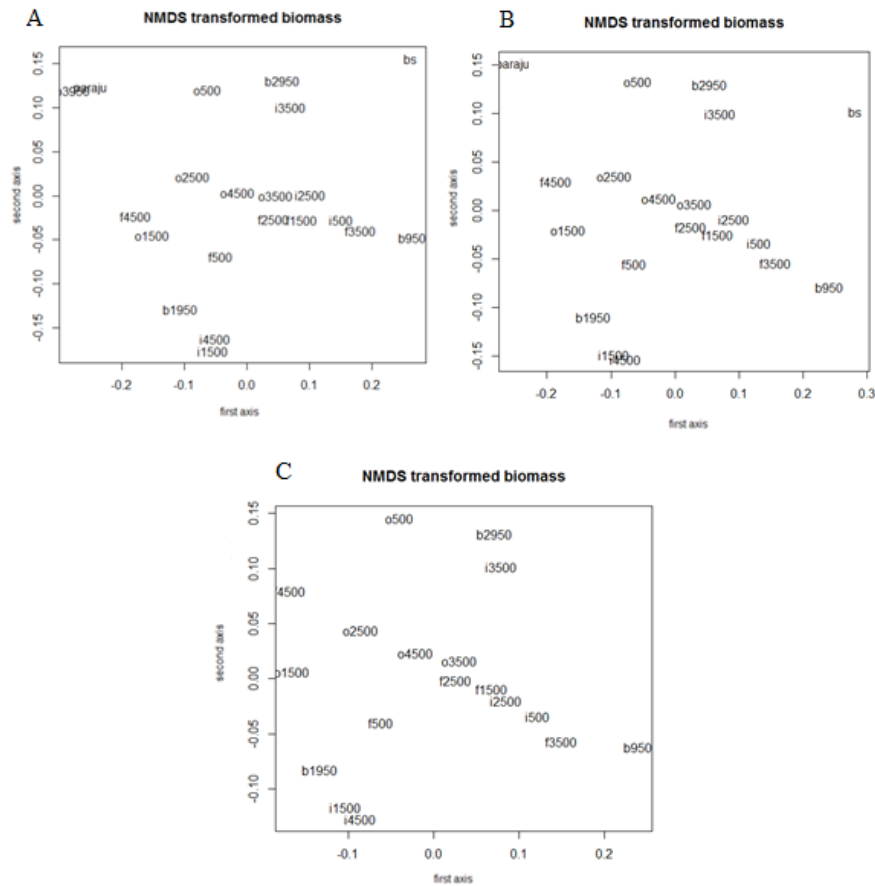


Source: The author, 2018

Subtitle: A) considering all plots, B) without B3950 and C) without B3950, Paraju and Barra Seca

When we transformed the biomass, the NMDS of medium and large mammals considering all plots had a stress of 0.086 grouping B3950 and Paraju plots, away from the other plots, as well as Barra Seca (Fig 7A). The second NMDS excluding B3950 plot, had a stress of 0.09 and repeated the same pattern with Barra Seca and Paraju apart from the other plots (Fig. 7B). Without the three plots the stress was 0.071 and there were no distinct groups formed among the plots (Fig. 7C).

Figure 7- NMDS of mammal transformed biomass in the three scenarios:



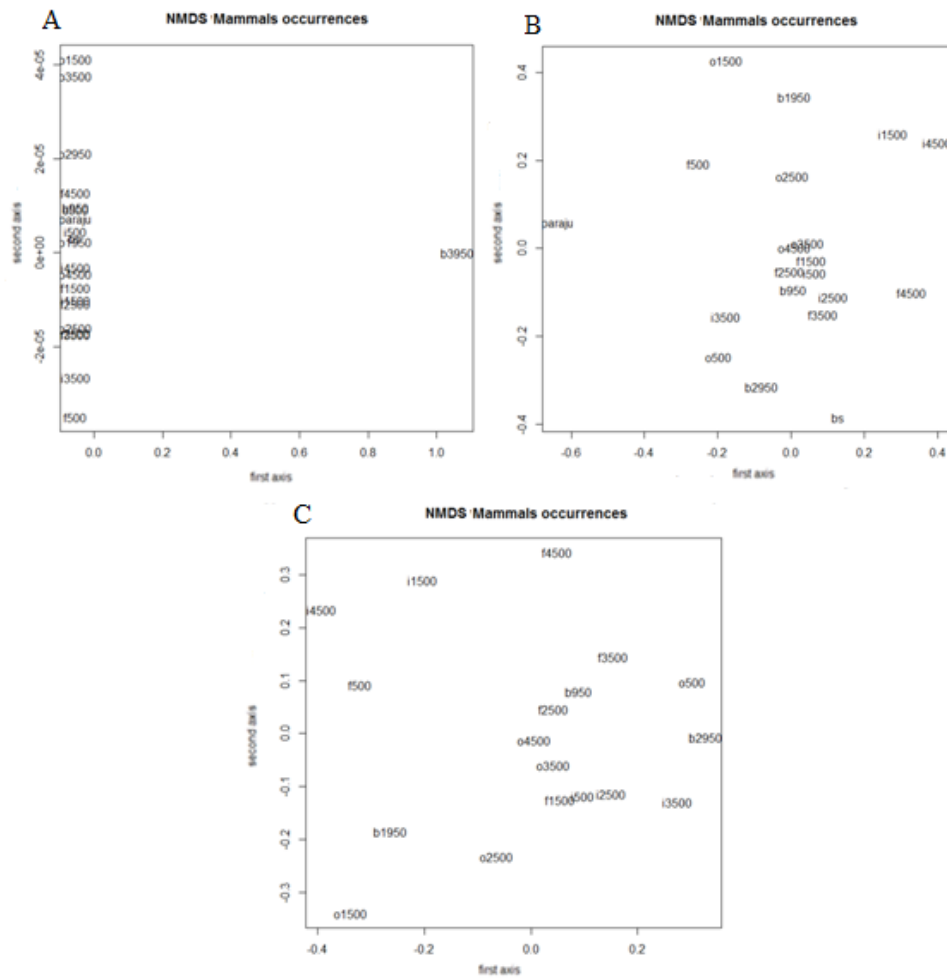
Source: The author, 2018

Subtitle: A) considering all plots, B) without B3950 and C) without B3950, Paraju and Barra Seca, in Vale Natural Reserve, Brazil

For the mammal occurrences, the NMDS had a stress of nearly zero ($8.696e-0.5$) considering all plots, with B3950 completely apart (Fig. 8A). When we did the NMDS for the occurrences without plot B3950, there was a stress of 0.198 and Paraju plot was apart from the other plots (Fig. 8B). The NMDS for the mammal occurrences in the third scenario (without the three plots) had a stress of 0.183 and no groups were formed among the plots (Fig. 8C).

Figure 8- NMDS of mammal occurrences in the three scenarios:

Source: The author, 2018



Subtitle: A) considering all plots, B) without B3950 and C) without B3950, Paraju and Barra Seca, in Vale Natural Reserve, Brazil

Explaining the dung beetle assemblages

The multiple regression models using the single axis of the dung beetles' NMDS with mammals (Total biomass, transformed biomass, biomass without transformation and occurrences) and vegetation structure (PCA1 and PCA2) in all three scenarios (all plots, without B3950 plot and without B3950, Barra seca and Paraju plots) showed very congruent results (Table 6).

Table 6- Multiple regression results of the dung beetles' NMDS with mammals (Transformed biomass, Biomass, Total biomass or Occurrence) and vegetation structure (PCA1 and PCA2), in Vale Natural Reserve, ES, Brazil.

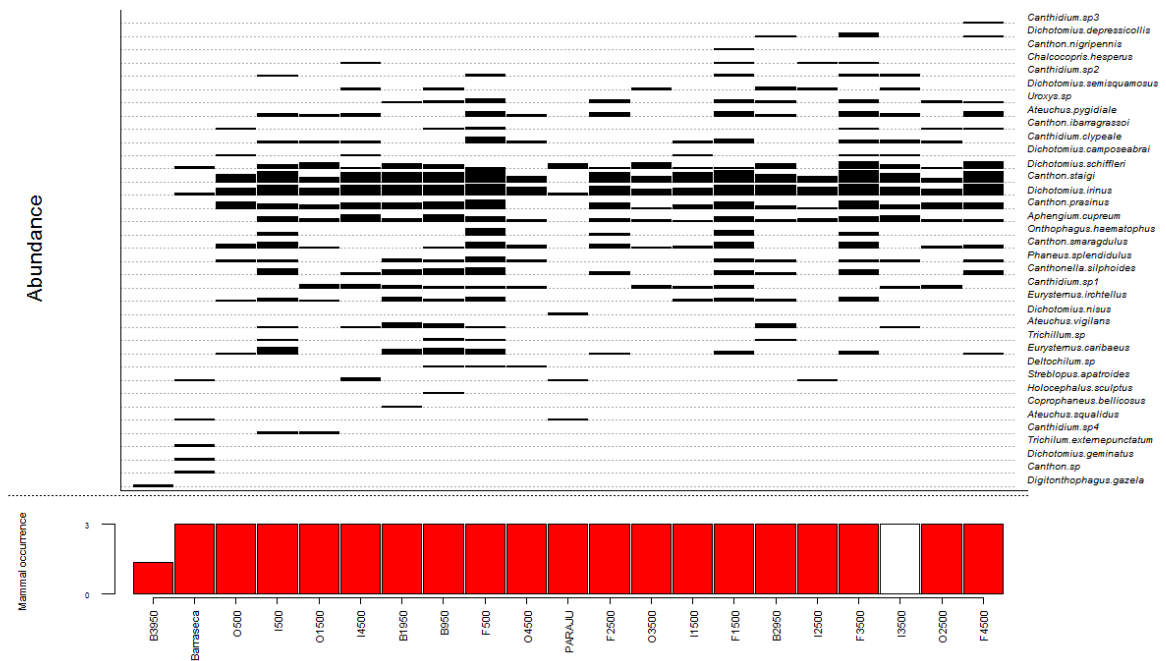
| Plots | Covariates | R ² | F | P |
|---|------------------------------|----------------|-------|------------------|
| All | Model | 0.305 | 2.491 | 0.095 |
| | Mammal's transformed biomass | | | 0.118 |
| | Vegetation structure PC1 | | | 0.159 |
| | Vegetation structure PC2 | | | 0.494 |
| Without B3950 | Model | 0.846 | 29.28 | <0.001 |
| | Mammal's transformed biomass | | | 0.303 |
| | Vegetation structure PC1 | | | <0.001 |
| | Vegetation structure PC2 | | | <0.001 |
| Without B3950, Paraju e Barra Seca | Model | 0.124 | 0.661 | 0.589 |
| | Mammal's transformed biomass | | | 0.329 |
| | Vegetation structure PC1 | | | 0.307 |
| | Vegetation structure PC2 | | | 0.653 |
| All | Model | 0.583 | 7.836 | 0.001 |
| | Mammal's biomass | | | 0.001 |
| | Vegetation structure PC1 | | | 0.306 |
| | Vegetation structure PC2 | | | 0.897 |
| Without B3950 | Model | 0.856 | 31.57 | <0.001 |
| | Mammal's biomass | | | 0.152 |
| | Vegetation structure PC1 | | | <0.001 |
| | Vegetation structure PC2 | | | <0.001 |
| Without B3950, Paraju e Barra Seca | Model | 0.357 | 2.591 | 0.094 |
| | Mammal's biomass | | | 0.023 |
| | Vegetation structure PC1 | | | 0.890 |
| | Vegetation structure PC2 | | | 0.323 |
| All | Model | 0.382 | 3.507 | 0.038 |
| | Mammal's total biomass | | | 0.036 |
| | Vegetation structure PC1 | | | 0.197 |
| | Vegetation structure PC2 | | | 0.9082 |
| Without B3950 | Model | 0.85 | 30.48 | <0.001 |
| | Mammal's total biomass | | | 0.207 |

| | | | | |
|---|--------------------------|--------|-----------|------------------|
| | Vegetation structure PC1 | | | <0.01 |
| | Vegetation structure PC2 | | | <0.01 |
| Without B3950, Paraju e Barra Seca | Model | 0.461 | 4.001 | 0.0293 |
| | Mammal's total biomass | | | 0.006 |
| | Vegetation structure PC1 | | | 0.918 |
| | Vegetation structure PC2 | | | 0.260 |
| All | Model | 1 | 3.601e+08 | <0.001 |
| | Mammal's occurrences | | | <0.001 |
| | Vegetation structure PC1 | | | <0.001 |
| | Vegetation structure PC2 | | | 0.002 |
| Without B3950 | Model | 0.8443 | 28.92 | <0.001 |
| | Mammal's occurrences | | | 0.343 |
| | Vegetation structure PC1 | | | <0.001 |
| | Vegetation structure PC2 | | | <0.001 |
| Without B3950, Paraju e Barra Seca | Model | 0.065 | 0.329 | 0.804 |
| | Mammal's occurrences | | | 0.771 |
| | Vegetation structure PC1 | | | 0.340 |
| | Vegetation structure PC2 | | | 0.855 |

Source: The author, 2018

All models considering all plots gave statistically significant results, except when we used mammal's transformed biomass ($R^2=0.305$; $F=2.491$; $p=0.095$). Mammals biomass without transformation ($p=0.001$), total biomass ($p=0.036$) and occurrences ($p<0.001$) explained a significantly part of the dung beetle variance after withdrew the effect of other variables. Vegetation structure (PC1, $p<0.001$ and PC2, $p<0.002$) was only statistically significant considering all plots when we used the mammal occurrences model. In this model, all the variance observed in dung beetle assemblage was explained by mammal occurrences and vegetation structure ($R^2=1$; $F=360100000$; $p<<0.001$) (Figure 9). This outcome does not have any biological meaning, but statistical, once it happened by the occurrence of one single individual at B3950 plot that bias the result. We can see the effect of *Digitonthophagus gazela* at the far end of the figure 9, occurring at only one plot (B3950).

Figure 9- Abundance of dung beetle species along mammal occurrences' gradient considering all plots in Vale Natural Reserve, Brazil.

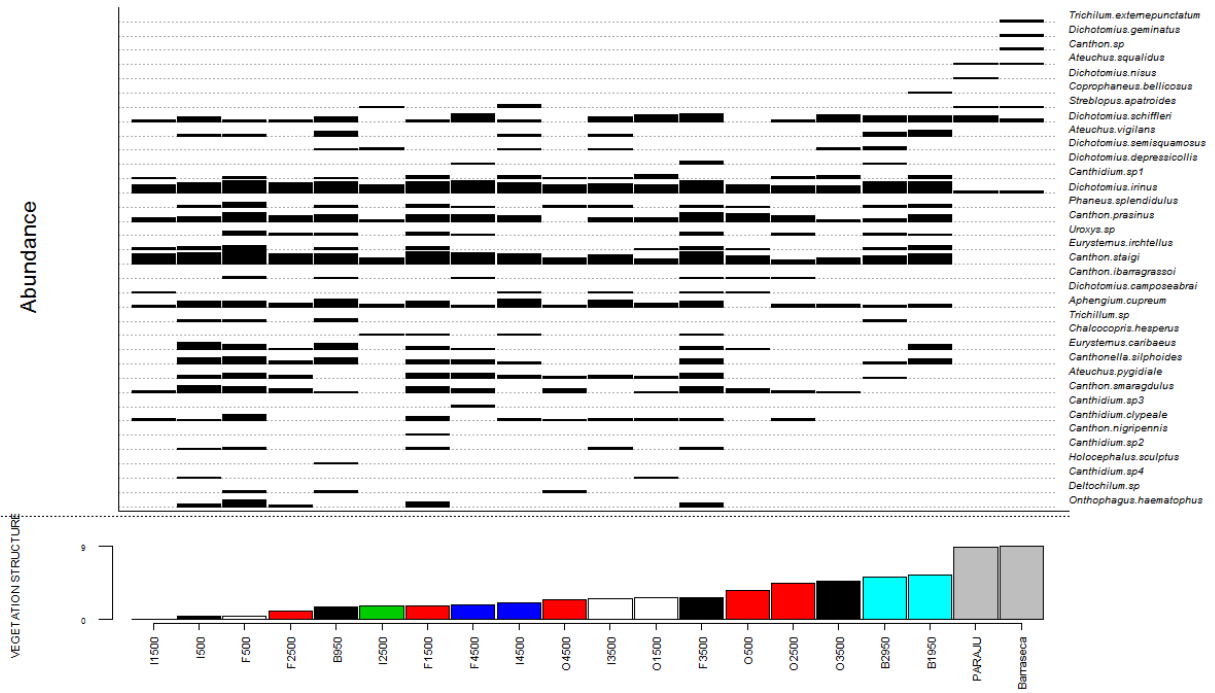


Source: The author, 2018

However, when plot B3950 with its only dung beetle collected was taken out of the analysis, all models were explained by the vegetation structure (Table 6), which separates open vegetation areas (Barra Seca and Paraju) from forested ones (Figure 4B). The model that had the higher determination coefficient ($R^2=0.856$) was the one with mammal biomass without transformation, although this variable did not explained the dung beetles assemblage ($p=0.152$) after the vegetation structure effect was taken out (PC1 – $p<0.001$, PC2 – $P<0.001$) (Table 6; Figure 10 and 11).

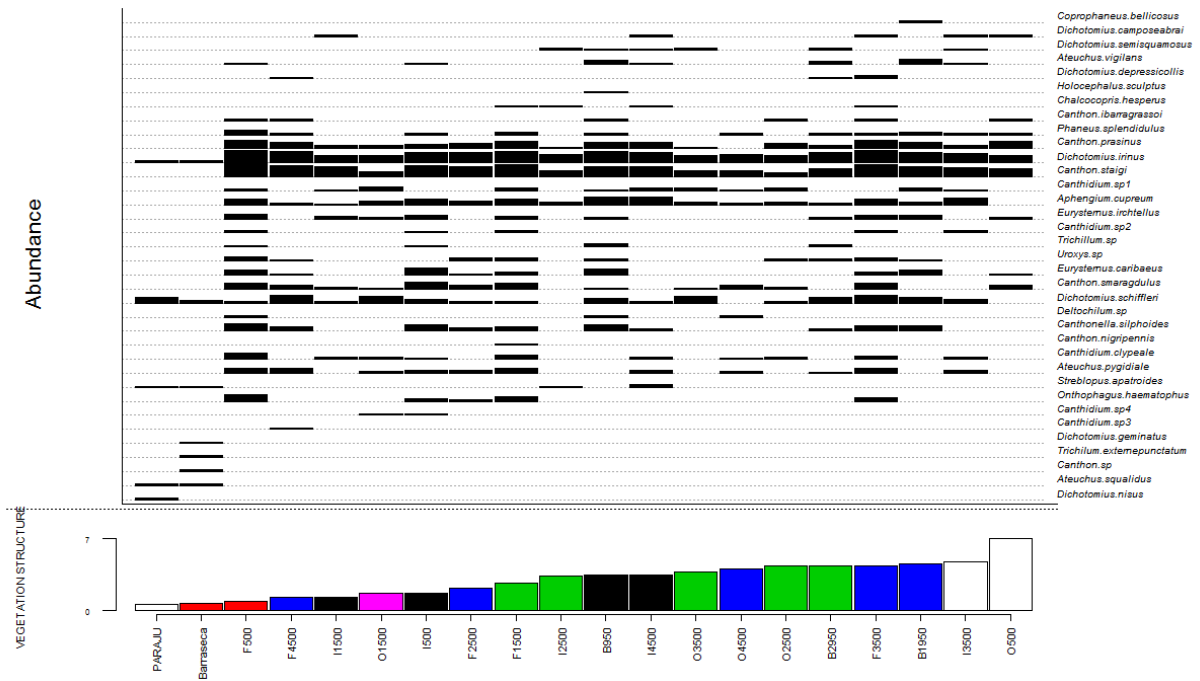
Ultimately, when all three plots were excluded, vegetation structure no longer explains the dung beetle assemblages, only biomass without transformation ($p=0.023$) and on the other model, total mammal biomass ($p=0.006$), after withdrawing the effect of the vegetation structure (PCA1 and PCA2) (Table 6). The best model ($R^2=0.461$; $F=4.001$, $p=0.0293$) was that with total biomass (Table 6; Figure 12 and Figure 13).

Figure 10- Abundance of dung beetle species along vegetation structure (PCA 1) gradient without B3950 in Vale Natural Reserve, Brazil.



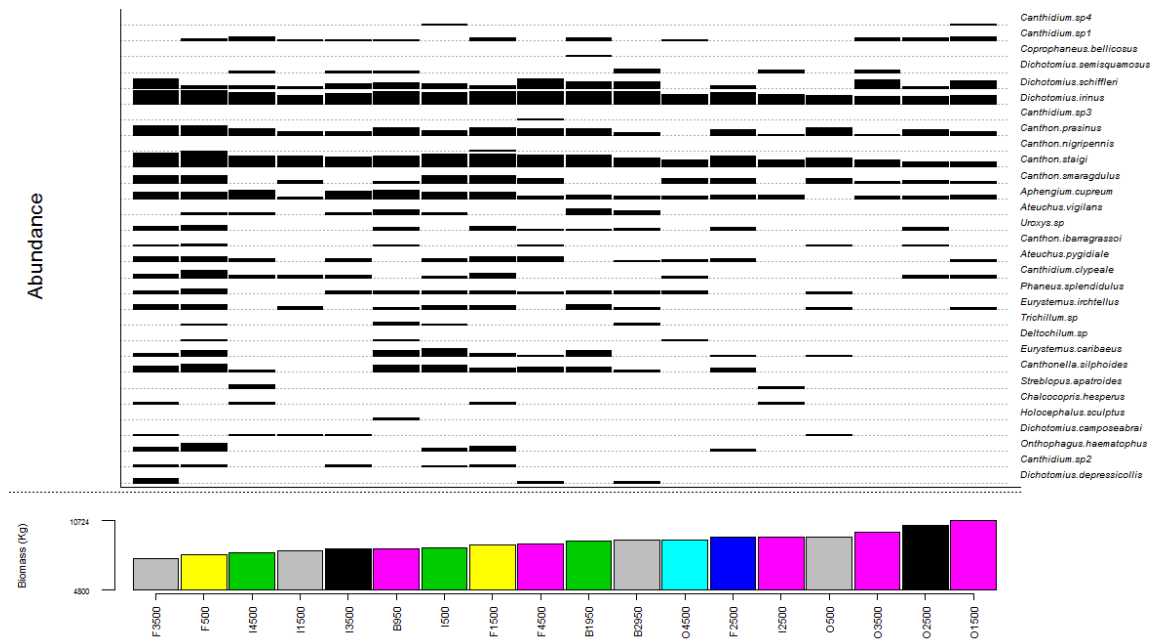
Source: The author, 2018

Figure 11- Abundance of dung beetle species along vegetation structure (PCA 2) gradient without B3950 in Vale Natural Reserve, Brazil.



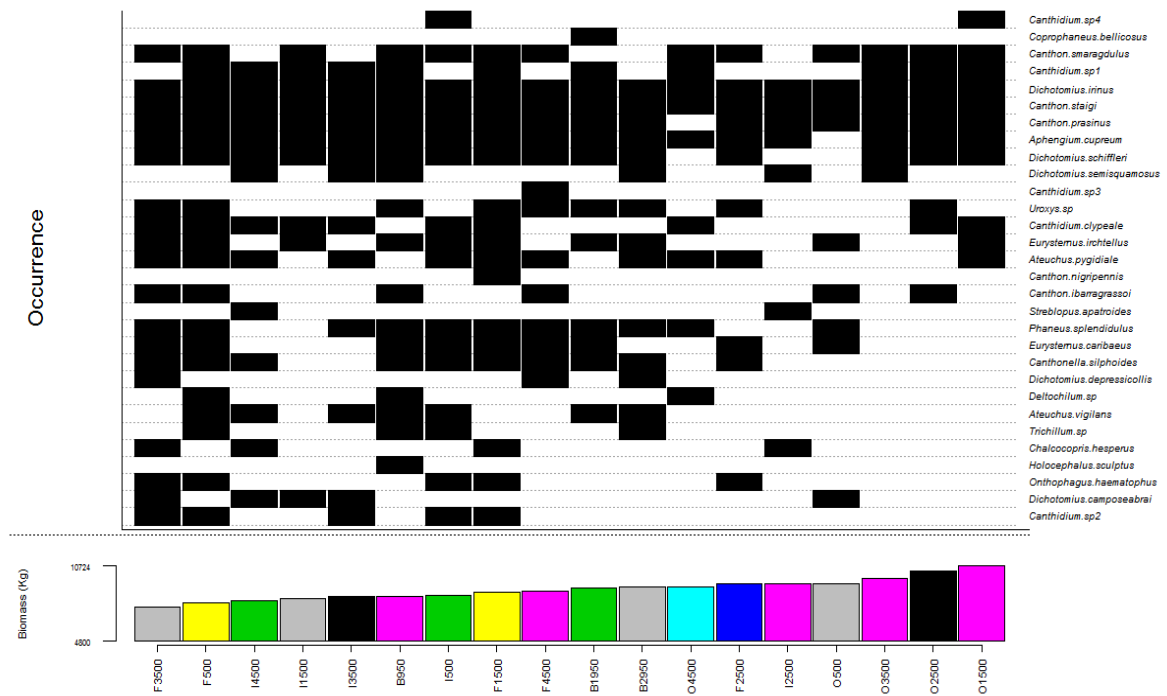
Source: The author, 2018

Figure 12- Abundance of dung beetle species along mammal's total biomass gradient without the three plots, in Vale Natural Reserve, Brazil.



Source: The author, 2018

Figure 13- Dung beetles' occurrence along mammal's total biomass gradient without the three plots, in Vale Natural Reserve, Brazil.



Source: The author, 2018

Dung beetles' functional groups

We collected 22 species of paracoprids, 7 of telecoprids and 3 of endocoprids, being the telecoprids the more abundant group (Table 7). The species *Aphengium cupreum*, *Canthonella silphoides*, *Holocephalus sculptus* and *Streboplus apatroides* were not classified as their functional groups and together correspond to only 3.5% of the records or 481 individuals.

Table 7 – Dung beetle functional groups at the 21 plots uniformly distributed at Reserva Natural Vale, ES

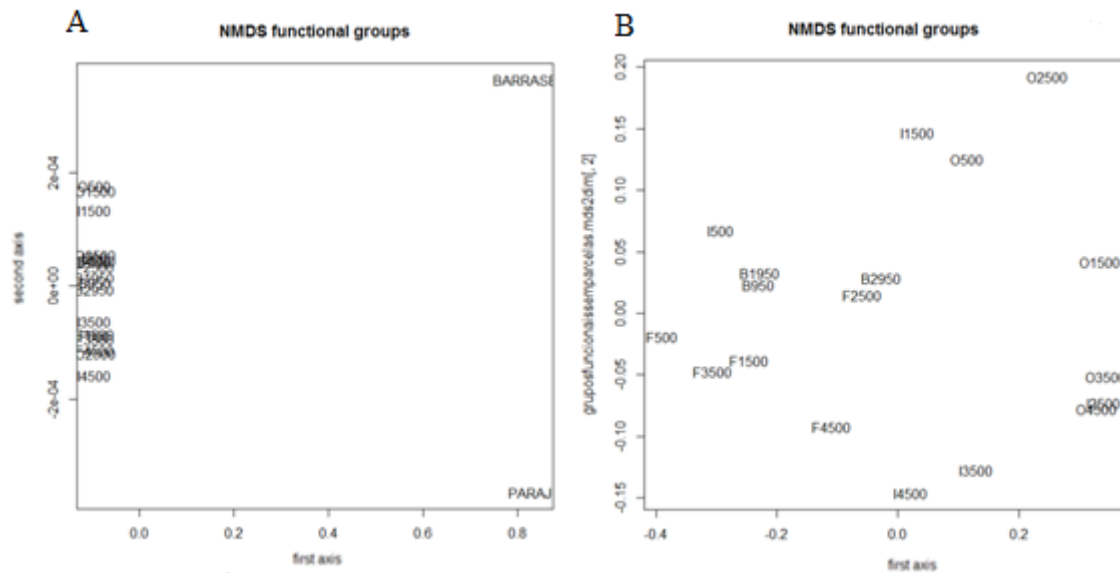
| Plots | Paracoprids | Telecoprids | Endocoprids |
|------------|--------------|--------------|-------------|
| F500 | 914 | 2250 | 37 |
| F1500 | 521 | 785 | 14 |
| F2500 | 232 | 264 | 5 |
| F3500 | 803 | 1085 | 17 |
| F4500 | 649 | 431 | 2 |
| O500 | 61 | 143 | 2 |
| O1500 | 114 | 22 | 1 |
| O2500 | 53 | 36 | 3 |
| O3500 | 95 | 35 | 0 |
| O4500 | 106 | 38 | 0 |
| I500 | 303 | 607 | 61 |
| I1500 | 67 | 244 | 3 |
| I2500 | 103 | 34 | 0 |
| I3500 | 164 | 155 | 0 |
| I4500 | 311 | 286 | 0 |
| B950 | 486 | 315 | 28 |
| B1950 | 420 | 340 | 28 |
| B2950 | 406 | 110 | 4 |
| B3950 | 1 | 0 | 0 |
| Barra Seca | 10 | 2 | 0 |
| Paraju | 21 | 0 | 0 |
| Total | 5840 (44.2%) | 7182 (54.3%) | 205 (1.5%) |
| Richness | 22 | 7 | 3 |

Source: The author, 2018

For the functional groups of dung beetles, we had to exclude plot B3950 because it only had one individual that it was known as an introduced species. The ordination with NMDS

without B3950 had a stress of 0.0037 and separated Barra Seca and Paraju plots from the other plots (Fig. 14A) The NMDS without Barra Seca and Paraju had a stress of 0.094 and did not showed any pattern (Fig 14B). On Figure 15 we can see the main group present at each plot marked.

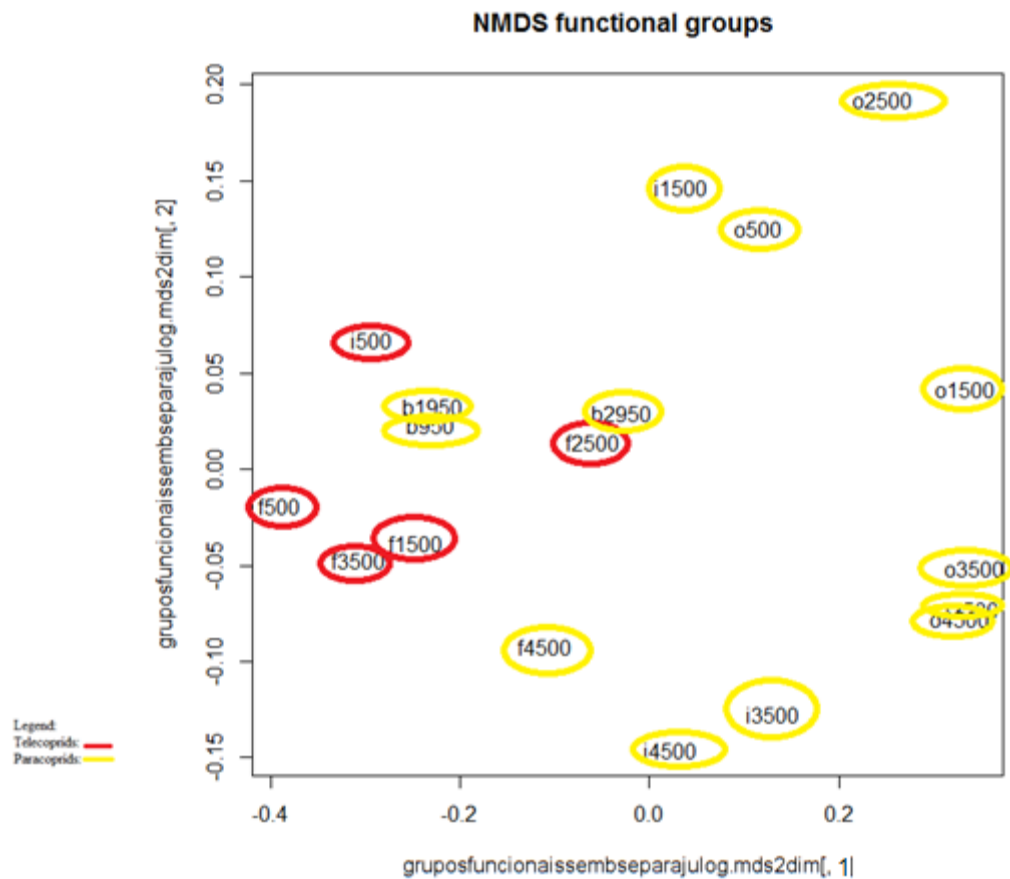
Figure 14- Dung beetle functional groups NMDS in two scenarios:



Source: The author, 2018

Subtitle: with all plots except B3950 (A), and without B3950, Barra Seca and Paraju (B)

Figure 15 - NMDS of dung beetle functional groups with the main groups present at each plot marked as red (Telecoprids) or yellow (Paracoprids).



Source: The author, 2018

All models of multiple regressions (Table 8) without plot B3950 had significant results, but the best result was found with mammals total biomass model ($r^2=0.894$; $F=44.96$; $p=5.08E-08$) and this variables explained the dung beetles assemblage ($p=0.0124$) as well as the vegetation structure ($PC1<0.001$; $PC2<0.001$). The multiple regressions model without the 3 plots was significant ($P=0.038$) and the variance observed in the functional groups of dung beetles was explained by mammal's biomass ($p=0.009$) after withdrawn the effect of the vegetation structure. The higher proportion of telecoprid dung beetles was observed in areas

with less mammal biomass, whereas paracoprids were more observed in areas with higher mammal biomass (Figure 15) and we can also see that in the NMDS first axis of dung-beetle functional groups related to the total biomass of mammals (Figure 16).

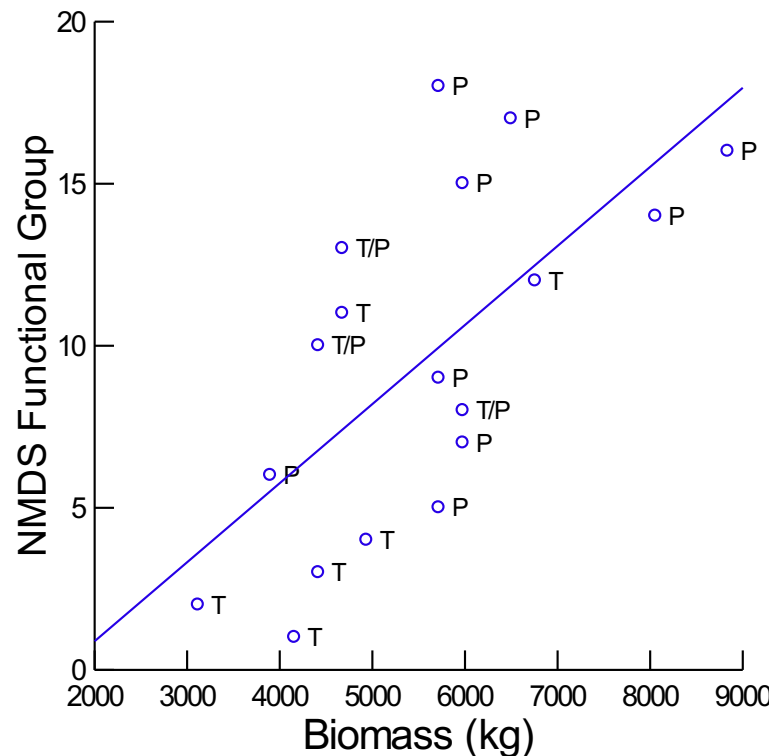
Table 8 - Multiple regression results of the dung beetles' functional groups NMDS with mammals (Transformed biomass, Biomass, Total biomass or Occurrence) and vegetation structure (PCA1 and PCA2), in Vale Natural Reserve, ES, Brazil.

| Plots | Covariates | R ² | F | P |
|---|------------------------------|----------------|--------|------------------|
| Without B3950 | Model | 0.8544 | 31.29 | 6.30E-07 |
| | Mammal's transformed biomass | | | 0.2512 |
| | Vegetation structure PC1 | | | <0.001 |
| | Vegetation structure PC2 | | | <0.001 |
| Without B3950, Paraju e Barra Seca | Model | 0.1519 | 0.8355 | 0.4965 |
| | Mammal's transformed biomass | | | 0.283 |
| | Vegetation structure PC1 | | | 0.245 |
| | Vegetation structure PC2 | | | 0.731 |
| Without B3950 | Model | 0.8894 | 42.87 | 7.12E-08 |
| | Mammal's biomass | | | 0.0181 |
| | Vegetation structure PC1 | | | <0.001 |
| | Vegetation structure PC2 | | | <0.001 |
| Without B3950, Paraju e Barra Seca | Model | 0.4411 | 3.683 | 0.0382 |
| | Mammal's biomass | | | 0.00912 |

| | | | | |
|---|--------------------------|-------|-------|------------------|
| | Vegetation structure PC1 | | | 0.851 |
| | Vegetation structure PC2 | | | 0.324 |
| Without B3950 | Model | | | 5.08E-08 |
| | Mammal's total biomass | | | 0.0124 |
| | Vegetation structure PC1 | | | <0.01 |
| | Vegetation structure PC2 | | | <0.01 |
| | | 0.894 | 44.96 | |
| Without B3950, Paraju e Barra Seca | Model | | | 0.0108 |
| | Mammal's total biomass | | | 0.002 |
| | Vegetation structure PC1 | | | 0.8511 |
| | Vegetation structure PC2 | | | 0.271 |
| | | 0.538 | 5.446 | |
| Without B3950 | Model | | | 8.71E-07 |
| | Mammal's occurrences | | | 0.4089 |
| | Vegetation structure PC1 | | | <0.001 |
| | Vegetation structure PC2 | | | <0.001 |
| | | 0.848 | 29.83 | |
| Without B3950, Paraju e Barra Seca | Model | | | 0.726 |
| | Mammal's occurrences | | | 0.398 |
| | Vegetation structure PC1 | | | 1.149 |
| | Vegetation structure PC2 | | | -0.081 |
| | | 0.086 | 0.442 | |

Source: The author, 2018

Figure 16 – NMDS first axis of dung-beetle functional groups related to the total biomass of mammals in Vale Natural Reserve, Brazil.



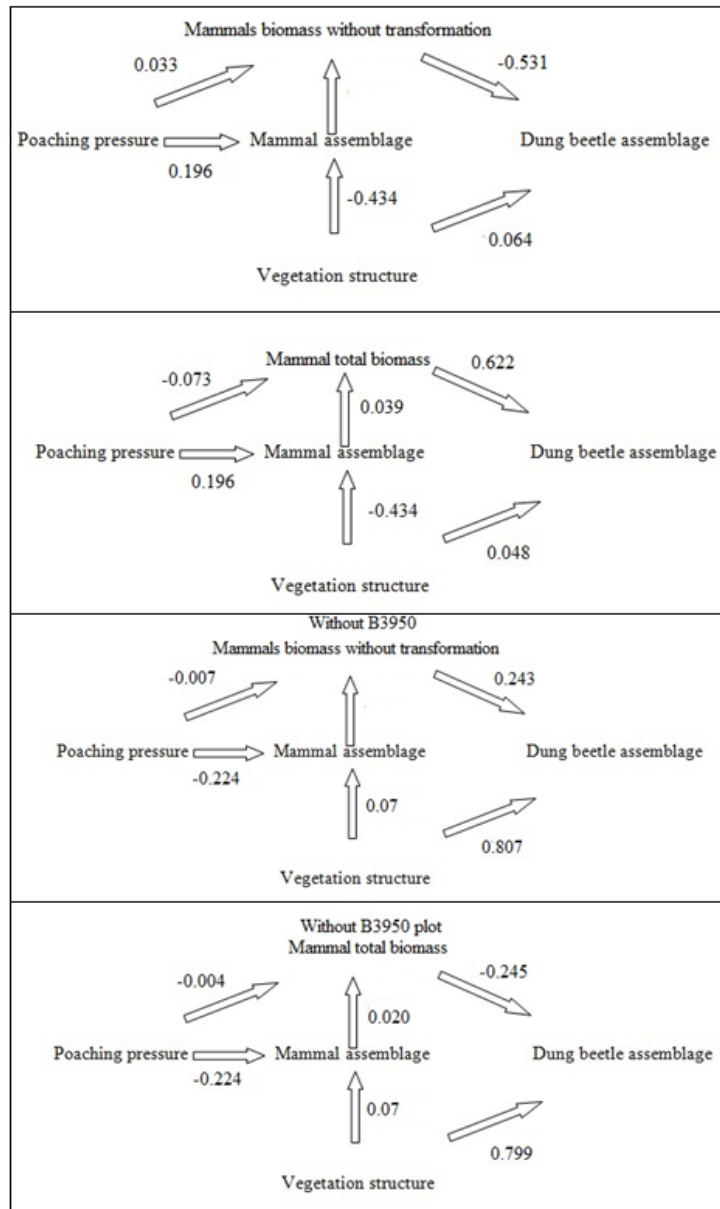
Source: The author, 2018.

Legend: P corresponds to plots where the proportion of paracoprid dung beetles were higher, T corresponds to plots where the proportion of telecoprid dung beetles were higher, and T/P where those plots where the proportion of telecoprids and paracoprids were similar.

Poaching effect

The coefficients used in the path analysis indicate the direct contribution of one variable at another as showed in Figure 17. The total results for each path, at each model are in table 8. When we considered all plots and without the three plots, total biomass and biomass without transformation had the major effect on dung beetle assemblage. Without B3950 plot, the vegetation had the strongest effect on dung beetle assemblage. The effect of poaching in all cases was negligible (Table 9).

Figure 17- Path analysis diagrams showing the direct and indirect effects of mammal assemblage and biomass, vegetation structure and poaching pressure in dung beetle assemblage.



Source: The author, 20

Table 9 - Path analysis results showing the total effect of vegetation, poaching and mammal biomass on dung beetle assemblage, considering direct and indirect paths. The bold numbers indicate the paths that had the greatest effects.

| Plots | Models | Vegetation effect | Poaching effect | Biomass effect |
|---------------------|--------------------------------|-------------------|-----------------|----------------|
| All plots | Total Biomass | -0.387 | 0.017 | 0.491 |
| | Biomass without transformation | -0.386 | 0.007 | 0.685 |
| Without B3950 plot | Total Biomass | 0.799 | 0.002 | -0.245 |
| | Biomass without transformation | 0.803 | 0.012 | 0.243 |
| Without the 3 plots | Total Biomass | 0.037 | -0.04 | 0.622 |
| | Biomass without transformation | 0.035 | -0.004 | -0.531 |

Source: The author, 2018

4. DISCUSSION

We found 36 species of dung beetles and it corresponds to 27.9% of the species recorded at the Reserve and identified by specialists (Martins et al, 2016, p. 353). A similar number of species (34) was found on previous work at the area (Lima, 2013), but we found four species that were not recorded at previous works at the same area, *Atheucus pygidiale*, *Canthidium clypeale*, *Canthon ibarragrassoi* and *Ontophagus haematophus*.

We also found an introduced invasive species, *Digitontophagus gazella* (previously known as *Ontophagus gazella*) at plot B3950, which is an African beetle introduced in Brazil by EMBRAPA in order to control the horn fly (*Haematobia irritans*) (Miranda et al., 1990; Bianchin et al., 1998). The only one individual of *Digitontophagus gazella* was found in B3950, a plot that is located on the border of RNV close to a farm. Cattle can be seen eventually within the reserve, which would explain the presence of *Digitontophagus gazella* (Srbek-Araujo et al., 2014).

Lima (2013) had a total abundance of 9039 individuals recorded at the Reserve but in a different area of study. The two most common species found at his work were *Dichotomius sericeus* (2214 individuals) and *Aphengium sordidum* (1926 individuals), but the two species were not found at our work. They were followed by *Canthon staigi* (1926 individuals) that was our most abundant species. Tavares (2018) also found *Canthon staigi* and *Dichotomius irinus* as the most abundant species in their studies at another site of Atlantic forest, corroborating our results.

The *Dichotomius schiffleri* found in our work is an endangered species and also an environmental quality indicator because is highly sensitive to degraded areas (Vaz-de-Mello et al., 2001; Vieira et al., 2011). This species was recorded in Ilha de Guriri, Linhares (ES) and is considered to inhabit areas of well preserved restinga, an ecosystem restricted to litoraneous Atlantic forest (Vaz-de-Mello et al., 2013). Few specimens were recorded in large lowland forest fragments (>2000 ha) (Vaz-de-Mello et al., 2013). The large abundance (374) of this species in the present study and its occurrence in 17 out of 21 plots suggest that Vale Natural

Reserve is an area with a good state conservation, despite of the high incidence of poaching on medium and large mammals.

The medium and large mammal species found at the study represented 50% of the species recorded at the Espírito Santo State (Moreira et al., 2008) and 63% of the medium and large mammals previously recorded at the reserve (Srbek & Kierulff, 2016). Despite the short sampling time of the photographic traps, with only 12 months, the proportion of medium and large mammals species found was similar to the ones found by Ferregueti et al. (2017a) during 13 months at the same area and by Srbek-Araujo (2013) during four years of study at the Linhares-Sooretama protected area block.

Ferregueti et al. (2017a) found differences in abundance, species richness and in the structure of medium and large mammals in different vegetation sites at the same area of our study. The authors also found that areas that were closest to water resources showed higher mammals species richness. This could explain why the Barra Seca, a plot close to the water showed high numbers of mammal occurrences and species richness. However, dung beetle richness (7) and abundance (13) were not high in Barra Seca, a grassland habitat.

The tapir is the species with higher biomass and it was found at all plots surveyed. *Tapirus terrestris* was surveyed at the same area and showed still viable population with an abundance estimate of 200 ± 33 individuals (Ferregueti et al, 2017b). In our work, we found that in areas with high tapir biomass, we have less dung beetle species richness and abundances. This could be explained by two reasons: 1) there is so much tapir dung available that the dung beetles were not attracted to our bait, or 2) that there is some sort of specificity of dung beetles with tapir's dung, so few species were observed in areas with high mammal biomass.

Our results for mammal and dung beetle richness and abundances were very similar, with B3950 being the plot with lower numbers. B3950 plot is quite distinct from the others, with many discrete numbers and therefore considered an outlier. Being so distinctive, both with dung beetles and mammals, the best models considering B3950 were the ones with mammal-related covariates.

When B3950 is taken out of the analyzes, the dung beetles assemblage becomes structured by the vegetation, separating open (Barra Seca and Paraju) and closed vegetation

areas (all the others). Dung beetles are known to be influenced by vegetation cover and by soil type and consequently insolation (Nealis, 1976), where open areas have more insolation than more forested ones and it could lead to dung desiccation. Not coincidentally, the most common functional group in the open areas were the paracoprides (tunnelers). Five out of eight species of dung beetle (*Atheucus squalidus*, *Canthon sp*, *Dichotomius geminatus*, *Dichotomius nisus* and *Trichillum externepunctatum*) occurred only in Barra Seca and Paraju plots. Probably, these species are adapted exclusively to this kind of environment.

When the results are focused only in forested areas (the model without the three plots), the dung beetle assemblage structure is intimately related to the mammals. However, neither the occurrences nor the transformed biomass explained the dung beetle assemblage structure, probably because it is not how many mammals of each species or the proportion of their biomass that affect the dung beetles but the total amount of biomass from the animals occurring at each plot. The total amount of biomass seems to affect more than the biomass without transformation and it was expected that when higher the biomass, higher were the feces amount and bigger the resources for the dung beetles.

Considering the results, when we analyzed all plots, the dung beetle species richness was positively related with mammal richness, but when we took all three plots out of the analyzes, mammal biomass explained richness and abundances of dung beetle species but, in a negative way. Therefore, the greater the occurrence of *Tapirus terrestris*, *Mazama americana* and *Tajacu pecari*, the smaller are the abundance and richness of dung beetles, refuting our hypothesis.

The association between dung beetles and mammals can be corroborated by several studies (Barlow et al., 2007; 2010; Estrada et al., 1998; Andresen & Laurence, 2007) but Culot et al (2013) showed specifically that areas with large mammal biomass allowed to maintain a more even distributed dung beetle community, corroborating that it is not the species that matter, but the total amount of mammal biomass. We found strong relationship with mammal biomass, although they were negative, contrary to what we expected.

According to our hypothesis, poaching pressure should have a negative effect on dung beetles. Nevertheless, we were not able to find any indirect effect of poaching on the dung

beetles. This could have happened because the measurements that we used (minimum distance of a poaching record) probably were not adequately and it could be more interesting to use the abundance of poaching around the plot. However, our model is only conceptual because mammals and dung beetles are not univariate variables but a reduced axes of composition and abundance.

Indirect effects, such as poaching, are difficult to predict and could be ambiguous and would be better determined experimentally (Didham *et al.*, 1996; Wright, 2003; Hamer *et al.*, 2005). Andresen & Laurence (2007) found that the abundance of dung beetles was found to decline with the decrease of mammal abundances in overhunted areas but were not able to evaluate if it was the overall availability of dung or if it was the dung of a particular taxon.

From our results, we can infer that when comparing all plots with different vegetation types, it is the vegetation that structures the dung beetle assemblages, mostly because such environments are very different in their composition. However, when we compare only forested areas, the mammal total biomass is the main reason that structures the dung beetles assemblages.

We recorded presence of endangered (Louzada *et al.*, 1996; Vaz-de-Mello *et al.*, 2001) and invasive species of dung beetles and also some others never recorded at the area. These shows how important are constant surveys to continue the monitoring of the reserve. Dung beetles reflect other taxon diversity and are good indicators of faunal diversity (Barlow *et al.*, 2007). We suggest that further studies continue at the area to help understand if there is any specificity among the dung beetle's species and the mammal dungs.

Our work corroborated the hypothesis that dung beetles are intimately connected to medium and large mammals and also by the vegetation structure. Further analysis could improve our understanding of that relationships and if there are any specificities among certain mammals dungs and dung beetles species.

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