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Spatial variation of dung beetle assemblages associated with forest structure in remnants of southern Brazilian Atlantic Forest



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ABSTRACT

The Brazilian Atlantic Forest is one of the world's biodiversity hotspots, and is currently highly fragmented and disturbed due to human activities. Variation in environmental conditions in the Atlantic Forest can influence the distribution of species, which may show associations with some environmental features. Dung beetles (Coleoptera: Scarabaeinae) are insects that act in nutrient cycling via organic matter decomposition and have been used for monitoring environmental changes. The aim of this study is to identify associations between the spatial distribution of dung beetle species and Atlantic Forest structure. The spatial distribution of some dung beetle species was associated with structural forest features. The number of species among the sampling sites ranged widely, and few species were found in all remnant areas. Principal coordinates analysis indicated that species composition, abundance and biomass showed a spatially structured distribution, and these results were corroborated by permutational multivariate analysis of variance. The indicator value index and redundancy analysis showed an association of several dung beetle species with some explanatory environmental variables related to Atlantic Forest structure. This work demonstrated the existence of a spatially structured distribution of dung beetles, with significant associations between several species and forest structure in Atlantic Forest remnants from Southern Brazil.

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Introduction

Tropical forests host most of the earth's biodiversity, and provide several benefits to human beings through the provision of economic goods and ecosystem services (Gardner et al., 2009). In contrast, the maintenance of biodiversity and ecosystem processes associated with it depend on effective conservation initiatives, which are major challenges to conservationists and decision makers (Gardner et al., 2009; Rands et al., 2010; Tabarelli et al., 2010). There are many barriers to the creation of effective conservation policy decisions, including lack of established conservation practices tailored to different local conditions, a paucity of basic information on species abundance, distribution and conservation status, and perhaps most importantly, the potentially large number of unknown species (Pimm et al., 2014). Such shortcomings in our knowledge about species identity and local or regional distribution are referred to as Linnean and Wallacean shortfalls (Whittaker et al., 2005). Some of these gaps can be filled by connecting important issues such as the fulfillment of basic studies (e.g. associations

between species and environmental conditions) in order to contribute to the knowledge on species distribution and also to the potential to discover new species. Furthermore, these studies can bring new information on spatial distribution of species associated with the variation in environmental conditions, which may be taken into consideration in planning conservation initiatives.

In Brazil, Atlantic Forest hosts a large part of the biodiversity of South American rainforests (Myers et al., 2000; Tabarelli et al., 2005) and was the second largest rainforest type in South America, covering about 150 million hectares of the Brazilian coast, northeastern Argentina and southeastern Paraguay (Tabarelli et al., 2005; Ribeiro et al., 2009; Vieira and Gardner, 2012). Historically, the Brazilian coast has always had the highest human population and industrial concentration and, thus, the Atlantic Forest has been affected by the growth and development of the country over the last five centuries (Dean, 1996), mainly in the last century. The Atlantic Forest is currently the most endangered Brazilian ecosystem in terms of biodiversity conservation (Myers et al., 2000). Recent studies indicate that only 12% of its original area remains, much of it fragmented with a high degree of isolation, and most in an intermediate state of regeneration (Ribeiro et al., 2009). Regardless, the fragments are usually of different sizes and exist in a heterogeneous matrix, consisting mainly of areas being

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used for various agriculture and forestry purposes. These features make the Atlantic Forest a very heterogeneous ecosystem, housing species with different environmental requirements (Aleixo, 1999).

The study of the diversity–environmental heterogeneity relationship of organisms that have key ecological functions and can be used as ecological indicators, such as dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), is a first step to support biodiversity conservation initiatives and management of ecosystem processes in tropical forests. Dung beetles are detritus-feeding insects that aid in organic matter decomposition and nutrient cycling (Halffter and Matthews, 1966; Hanski and Cambefort, 1991; Simmons and Ridsdill-Smith, 2011) by burying and consuming portions of feces, animal carcasses and rotting plant matter, thereby making the nutrients in these materials available to the ecosystem once again (Nichols et al., 2008). These insects construct tunnels in the soil, increasing aeration and water infiltration. They also bury eggs of cattle parasites (e.g., flies and nematodes) and secondarily disperse fruit seeds previously consumed by mammals on which they feed (Andresen and Feer, 2005; Nichols et al., 2008).

Dung beetles have been used as a tool for monitoring environmental changes in tropical forests because they are sensitive to fragmentation, disturbance and habitat loss (Klein, 1989; Halffter and Favila, 1993; Davis et al., 2001; Nichols et al., 2007; Gardner et al., 2008b; Korasaki et al., 2013; Viegas et al., 2014) and because they respond positively to increased restoration time in tropical forests (Davis et al., 2003; Audino et al., 2014; Bett et al., 2014; Hernández et al., 2014). However, few studies have identified important associations between dung beetle species and small changes in forest features (e.g. Hernández and Vaz-de-Mello, 2009; Campos and Hernández, 2013; da Silva and Hernández, 2014). Most studies investigate the Scarabaeinae community response when there is a clear environmental change, such as forest vs. open habitats (Lopes et al., 2011; Costa et al., 2013; Silva et al., 2014), forest vs. monocultures (Gardner et al., 2008b; Barlow et al., 2010), or distinct vegetation formations (Almeida and Louzada, 2009; da Silva et al., 2013).

Changes in environmental conditions in small spatial extents may be key drivers of compositional and structural differences in dung beetle communities in tropical forests (Feer, 2013; da Silva

and Hernández, 2014, 2015a; Medina and Lopes, 2014). Changes in dung beetle communities affect their ecological functions, and hence proper ecosystem functioning (Vulinec, 2002; Andresen, 2003; Horgan, 2005; Slade et al., 2007; Gardner et al., 2008b; Kunz and Krell, 2011; Slade et al., 2011; Braga et al., 2012, 2013). In addition, these beetles are correlated with other taxa, particularly mammalian fauna (Barlow et al., 2007; Culot et al., 2013). Thus, the evaluation of the spatial distribution of dung beetle fauna, which combines ease of identification and low-cost and standardized sampling methods (Gardner et al., 2008a), may contribute to research concerning effectiveness of conservation management, especially in a heterogeneous environment as the Atlantic Forest.

The aim of this study was to determine whether small differences in forest structure affect the local distribution of Scarabaeinae dung beetles in remnants of Atlantic Forest in southern Brazil. We predict that dung beetle fauna will show spatial differences in relation to structural features of the Atlantic Forest.

Material and methods

Study area

The study was performed in four large, non-contiguous areas of Atlantic Forest in Santa Catarina state, southern Brazil (Fig. 1). Two areas are located on the Island of Santa Catarina: Peri Lagoon Municipal Park (PER, 27°42' and 27°46' S; 48°32' and 48°30' W, area of ca 75 km²) and Permanent Protection Areas of Ratoles (RAT, 27°30' and 27°32' S; 48°30' and 48°27' W, area of ca 73 km²), both located in Florianópolis city. Other two areas are located on the mainland near the Brazilian Atlantic coast: Anhatomirim Environmental Protection Area (ANH, 27°22' and 27°26' S; 48°35' and 48°33' W, area of ca 56 km²) located in Governador Celso Ramos city, and Permanent Protection Areas of Itapema (ITA, 27°02' and 27°05' S; 48°38' and 48°35' W, area of ca 175 km²) located in Itapema city. The Island of Santa Catarina is approximately 54 km (north–south length) with a maximum width of 18 km, with a total area of 424.4 km². The distance between the island and mainland varies, with a minimum distance of 500 m and maximum around 10 km. Despite the conversion of forest for agricultural, livestock and forestry activities,

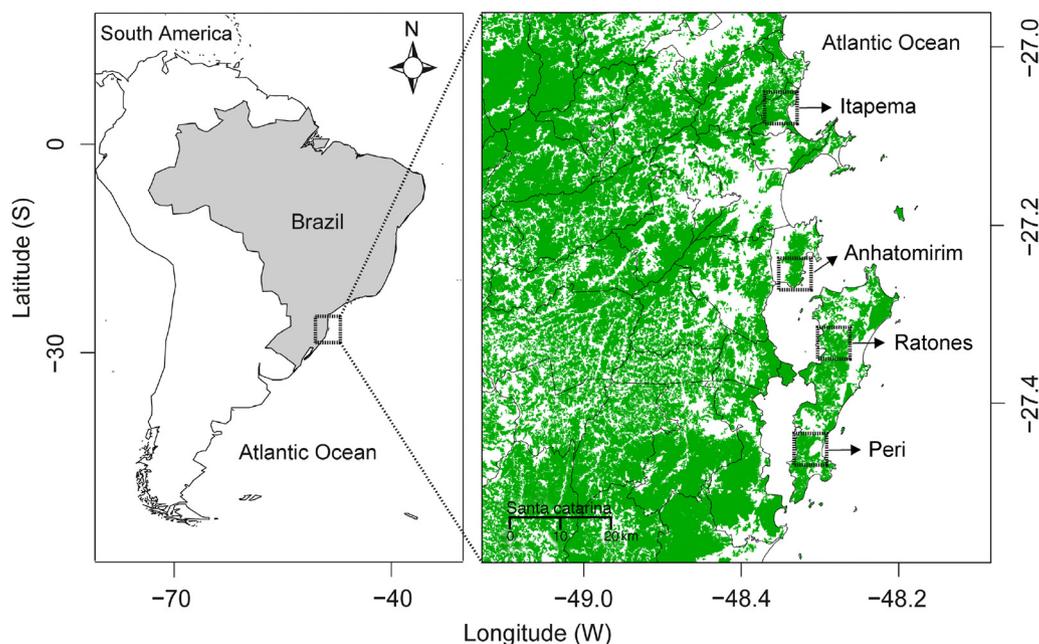


Fig. 1. Map of the Atlantic Forest remnants where dung beetles were sampled during January and February 2012. Anhatomirim Environmental Protection Area in Governador Celso Ramos city; Permanent Protection Areas of Itapema city; Peri Lagoon Municipal Park in Florianópolis city; Permanent Protection Areas of Ratoles in Florianópolis city.

the state of Santa Catarina in southern Brazil still contains the third highest Atlantic Forest area among the states, with 17% of its original cover; it also contains the third largest Atlantic Forest remnant (Ribeiro et al., 2009). Regardless, the fragments are usually of different sizes and exist in a heterogeneous matrix, consisting mainly of areas being used for various agriculture and forestry purposes. Over the decades there have been several conflicts of interest regarding these areas, primarily related to illegal occupation and lack of public administration oversight.

All sampled areas contain dense ombrophilous forest (Veloso et al., 1991) within the Atlantic Forest biome, with vegetation in different stages of succession. According to the Köppen classification (Peel et al., 2007) the climate is Cfa, humid subtropical (mesothermal) with hot summers (average 25 °C), no dry season and well distributed rainfall throughout the year averaging around 1500 mm annually (Veloso et al., 1991). The altitude of the sampled sites ranged between 28 and 265 m asl. The distance between the protected areas ranged between 13.5 and 71 km, and the distance among sampling sites within areas varied between 500 m to several kilometers (ca 6 km).

Dung beetle sampling

Dung beetles were sampled at each of the four study areas at five different sampling sites per area located on hillsides near rivers. Baited pitfall traps were used for sampling dung beetles. Each sampling site consisted of 10 traps distributed in pairs, with each pair spaced 50 m apart. A minimum distance of 50 m decreases the risk of influence of other sets of traps on sampling of dung beetles (Larsen and Forsyth, 2005). Our work was carried out before the new trap spacing proposed by da Silva and Hernández (2015b) where they found that 100 m are more appropriate to reduce interference between baited pitfall traps in sampling dung beetles. Paired traps were spaced 5–10 m apart. Each pair of traps was considered a sampling unit, and all traps remained in the field for 48 h.

The traps consisted of plastic containers (15 cm diam. × 20 cm depth) buried with their edge level with the ground. A rain guard was placed above the traps to prevent trap overflow and to support the bait. Traps contained a solution of water and detergent (300 mL) for catching fallen beetles. Traps contained two different bait types, including human feces and rotting flesh (30 g) (i.e., to attract coprophagous and necrophagous species, respectively). The baits were individually wrapped in thin cloth and tied in the central portion of the rain guard. All beetles collected were sorted, mounted on entomological pins and dried in an oven (60 °C for 72 h) then weighed. They were identified by experts (Fernando Vaz-de-Mello and David Edmonds) and deposited in the Entomological Collection of the Centro de Ciências Biológicas at the Universidade Federal de Santa Catarina, Brazil. The samplings were performed during the summer of 2012 (January and February). This period is characterized by high regional temperatures, as well as being the period of greatest dung beetle abundance in southern Brazil (Hernández and Vaz-de-Mello, 2009; da Silva et al., 2013).

Forest structure

For each area, forest structure was described by 15 environmental variables, which were tested for influence on dung beetle distribution. Variation in tree features, such as density, height and canopy cover, can change microclimatic conditions that may affect dung beetles (Feer, 2008, 2013). Furthermore, the physical structure of the forest floor, such as increased leaf litter, can affect the nesting activities of some guilds of dung beetles (Nichols et al., 2013). Measurement of variables was performed using the adapted point-centered quarter method (Cottam and Curtis, 1956). Briefly,

a plastic cross was placed in the center of each pair of traps (i.e., at each sampling point), dividing the sampling point into four quadrants (northwest, southwest, southeast and northeast). Tree, shrub and soil environmental variables were measured in each quadrant as follows: (A) circumference at breast height when diameter at breast height [DBH] >5 cm, (B) height, (C) top diameter and (D) distance from the nearest tree to the center of cross, (E–H) repeated same measures for shrubs when circumference at ankle height when DBH <5 cm and with a minimum height of 1 m, (I) land slope, (J) altitude, (K) canopy cover, (L) percentage of leaf litter cover, (M) green (vegetation up to 1 m height) cover, (N) exposed soil, and (O) height of leaf litter. Additional information on the methods used and environmental measures can be found in Appendices A and B.

Data analysis

The sampling effort was verified by smoothed species accumulation curves using data of the number of individuals for each sampling site and area. The data were extrapolated two times in relation to the number of samples per site (Colwell et al., 2012). Species richness was compared graphically between sampling sites and areas using the rarefaction method. The estimated species richness was obtained by using Chao 1 estimator (and its confidence interval) that it takes into account the abundance of species. We used the EstimateS 9.1 program for these analyses (Colwell, 2013).

We performed a principal coordinates analysis (PCoA) to map the similarity between sites regarding to composition (presence data), and assemblage structure based on abundance and biomass of dung beetle assemblages, and also regarding to environmental conditions. These analyses were based on Bray–Curtis dissimilarity, and abundance and biomass data were square root transformed prior to analysis. A permutational multivariate analysis of variance (PERMANOVA) was used to test for significant differences in dung beetle assemblages and environmental variables between sampling areas. PCoA and PERMANOVA were performed in R 3.1.1 program (R Core Team, 2014) and Primer 6 with PERMANOVA+ package (Clarke and Warwick, 2005; Anderson et al., 2008), respectively. We used Mantel tests to correlate dung beetle dissimilarity matrices (composition, abundance and biomass) with the environmental dissimilarity matrix. Biotic data were based on Bray–Curtis dissimilarity while abiotic data were based on Euclidean distance. These analyses were computed in R 3.1.1 program (R Core Team, 2014) using *vegan* package (Oksanen et al., 2013) with 999 permutations.

The Multivariate Regression Tree analysis (De'ath, 2002) was used to identify habitat types that were similar in environmental conditions and in dung beetle species composition. A set of clusters were constructed by repeated binary splits of the environmental dataset (15 environmental variables) to produce nodes as homogeneous as possible with respect to the dung beetle abundance and biomass (species-by-sites dataset) as response variables. We kept all environmental variables after the collinearity between them has been tested (see Appendix A). MRT analysis was computed in R 3.1.1 program (R Core Team, 2014) using the *mvpart* package (De'ath, 2006).

The Indicator Value Index – IndVal (Dufrene and Legendre, 1997) was used to assess possible associations of dung beetle species with features of sampling areas identified by MRT analysis (De Cáceres and Legendre, 2009). The IndVal method combines the degree of specificity of an ecological status, presenting the percentage of occurrence and significance for each species independently (McGeoch et al., 2002). This analysis was performed in R 3.1.1 program (R Core Team, 2014) using the *indicspecies* package (De Cáceres, 2013) with 999 permutations, using data for dung beetle abundance.

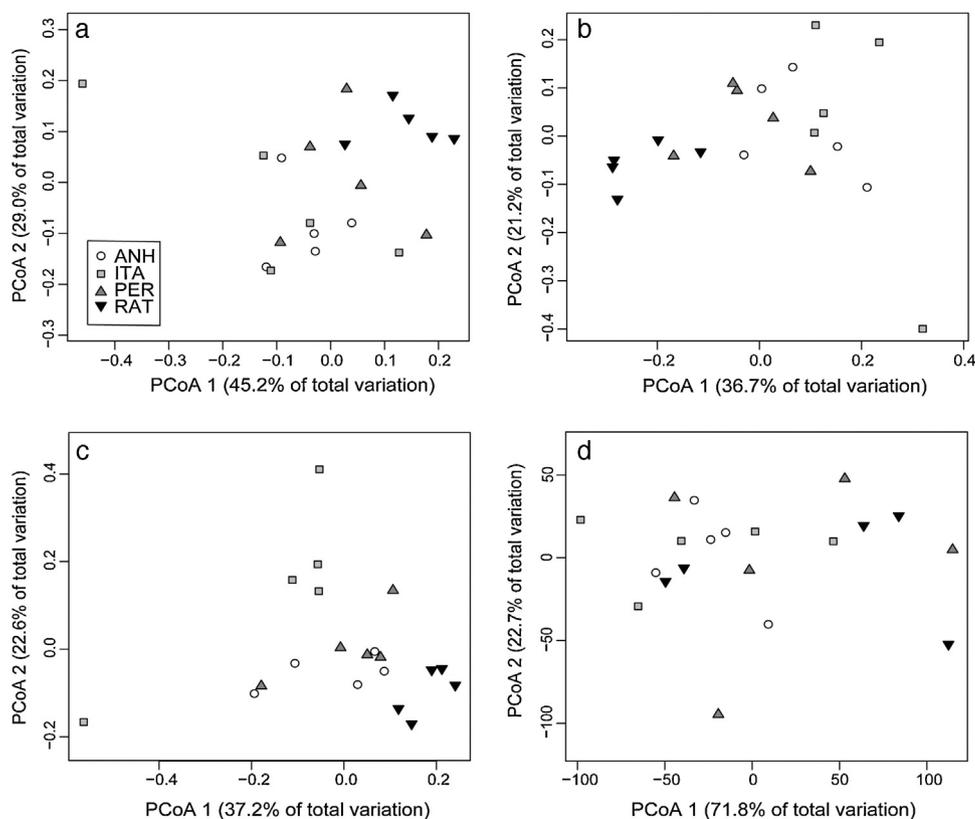


Fig. 2. Principal coordinates analysis (PCoA) of dung beetle species based on Bray–Curtis similarity and environmental variables based on Euclidean distance. The analysis was performed using presence–absence (a), abundance (b) and biomass (c) data of dung beetles, and 15 environmental variables (d). ANH: Anhatomirim Environmental Protection Area; ITA: Permanent Protection Areas of Itapema; PER: Peri Lagoon Municipal Park; RAT: Permanent Protection Areas of Ratones.

Redundancy analysis (RDA) was used to verify the linear relationship between dung beetle abundance and biomass and forest structure. Abundance and biomass data were Hellinger-transformed prior to the analysis in order to eliminate the disparity between values (Legendre and Gallagher, 2001). The Pearson correlation coefficient was used to correlate the RDA-axes and environmental variables.

Results

We collected a total of 3004 Scarabaeinae beetles belonging to 21 species (Appendix C). Most extrapolated species accumulation curves (except for site A of Peri, site E of Ratones, and Ratones as whole) reached the asymptote (Appendix D). Similar patterns were found for species accumulation curves for each area, which demonstrates the success in sampling dung beetle assemblages (Appendix D). The rarefied species richness showed differences in the number of species between sites and areas sampled (Appendix E). This difference was greater for ITA and PER. According to the species richness estimator Chao 1, based on the abundance, there were an estimated capture of species richness between 70% and 100% for the sampling sites (Appendix E), with averages above 88.2% in each of the four areas.

Dichotomius sericeus (Harold, 1867), *Canthon rutilans cyanescens* Harold, 1868, and *Canthidium* aff. *trinodosum* (Boheman, 1858) were the most abundant species, representing 71 percent of the total individuals captured (Appendix C). Only eight species (38.1%) were found in all four areas. The number of species per site ranged between 5 and 14. Only one species occurred in all sampling sites (*C. rutilans cyanescens*). Three species were sampled in at least 19 sites (*Deltochilum morbillosum* Burmeister, 1848, *Deltochilum multicolor* Balthasar, 1939, and *D. sericeus*). Five species were responsible for

92.8% of the total dung beetle biomass (*D. sericeus*, *Coprophanaeus saphirinus* (Sturm, 1826), *C. rutilans cyanescens*, *D. multicolor* and *D. morbillosum*) (Appendix C).

In general, PCoA analyses explained more than 58% of total variation in dung beetle assemblages. According to the PCoA species composition (presence–absence), species abundance and species biomass showed a spatial distribution according to the forest areas sampled (Fig. 2a–c). The dissimilarity values between sites within the same area were higher for dung beetle abundance and biomass (Table 1). PERMANOVA results confirmed the differences visually observed for composition (Pseudo- $F=3.199$; $p=0.001$), abundance (Pseudo- $F=4.053$; $p=0.001$) and biomass (Pseudo- $F=3.138$; $p=0.001$). PCoA analysis explained 94.5% of total variation in environmental variables (Fig. 2d). PERMANOVA results showed that there are differences in environmental conditions between them (Pseudo- $F=3.083$; $p=0.001$). Mantel tests showed that only dissimilarity between dung beetle abundance and environmental variables among sites was associated (Mantel test = 0.299; $p=0.010$).

Multivariate Regression Tree analysis using environmental variables as predictors split the dung beetle abundance distribution into four groups, which explained 66.2% of the variation (Fig. 3a). The environmental variables that showed higher similarity of dung

Table 1
Mean dissimilarity of dung beetle datasets between sites within the same area. Dissimilarity was based on Bray–Curtis. Standard deviation is in parenthesis.

	Composition	Abundance	Biomass
Anhatomirim	16.3 (6.8)%	44.5 (12.3)%	41.7 (16.0)%
Itapema	35.3 (18.9)%	54.4 (12.9)%	60.2 (21.9)%
Peri	29.1 (9.4)%	46.3 (14.6)%	45.6 (16.7)%
Ratones	17.5 (3.8)%	33.2 (10.9)%	25.1 (10.1)%

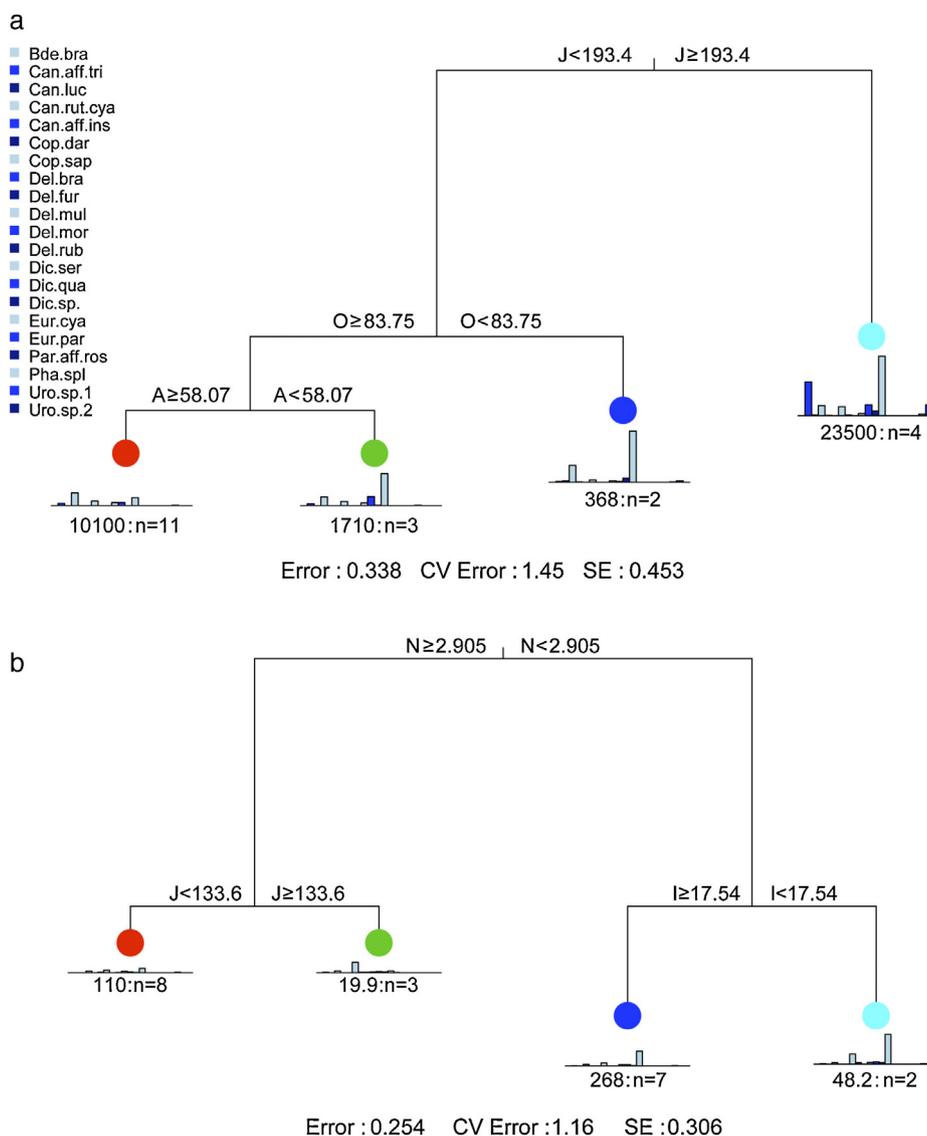


Fig. 3. Multivariate Regression Tree (MRT) analysis of the dung beetle abundance (a) and biomass with environmental variables as predictor variables. Environmental variables: A, basal area of trees; I, land slope; J, altitude; N, height of leaf litter; O, canopy cover. Species names are abbreviated and can be found in legend of Fig. 4 and in Appendix C. Bar charts at the terminal leaves of the regression tree represent species abundance means. The order of bars in each bar chart are the same and follows the sequence of names showed at left.

beetle composition based on abundance were altitude, canopy cover (in sites with lower altitudes) and basal area of trees (in sites with lower altitudes and higher canopy cover). For biomass, MRT analysis also split the dung beetle biomass distribution into four groups, which explained 74.6% of the variation (Fig. 3b). The environmental variables that showed higher similarity of dung beetle composition based on biomass were height of leaf litter, land slope (in sites with lower height of leaf litter) and altitude (in sites with higher height of leaf litter). The Principal Component Analysis resulting from MRT analyses for abundance and biomass can be found in Appendix F.

Several dung beetles species were significantly associated with some environmental feature, according to the results of the IndVal analysis (Table 2). Seven species were associated to sites with higher values of altitude, which occurred mainly in Ratonés and Peri. Only *Paracanthion* aff. *rosinae* Balthasar, 1942 was associated to sites with lower values of basal area of trees, which occurred mainly in Peri.

Redundancy analysis constrained 27% of the dung beetle abundance in relation to the explanatory variables (Fig. 4a). The first and

second canonical axes were significant and accounted for 67.7% of the constrained variance. The first axis (RDA1, $F = 13.982$; $p = 0.001$) accounted for 44.8% of the variance, and was positively correlated with leaf litter height ($r = 0.46$), green cover ($r = 0.38$) and distance of shrubs ($r = 0.26$); it was negatively correlated with altitude ($r = -0.82$), shrub height ($r = -0.20$) and shrub basal area ($r = -0.20$). The second axis (RDA2, $F = 7.167$; $p = 0.001$) accounted for 22.9% of

Table 2

IndVal analyses of dung beetle species with significant associations with some environmental features (see Multivariate Regression Tree analysis for values).

	IndVal	p-Value	Environmental feature
<i>Canthidium</i> aff. <i>trinodosum</i>	0.971	0.003	Higher altitudes
<i>Canthon</i> <i>luctuosus</i>	0.837	0.022	Higher altitudes
<i>Deltochilum</i> <i>brasiliense</i>	0.985	0.001	Higher altitudes
<i>Deltochilum</i> <i>morbillosum</i>	0.858	0.045	Higher altitudes
<i>Deltochilum</i> <i>rubripenne</i>	0.934	0.003	Higher altitudes
<i>Dichotomius</i> <i>sericeus</i>	0.876	0.043	Higher altitudes
<i>Paracanthion</i> aff. <i>rosinae</i>	0.939	0.011	Lower basal area of trees
<i>Uroxys</i> sp. 1	0.990	0.001	Higher altitudes

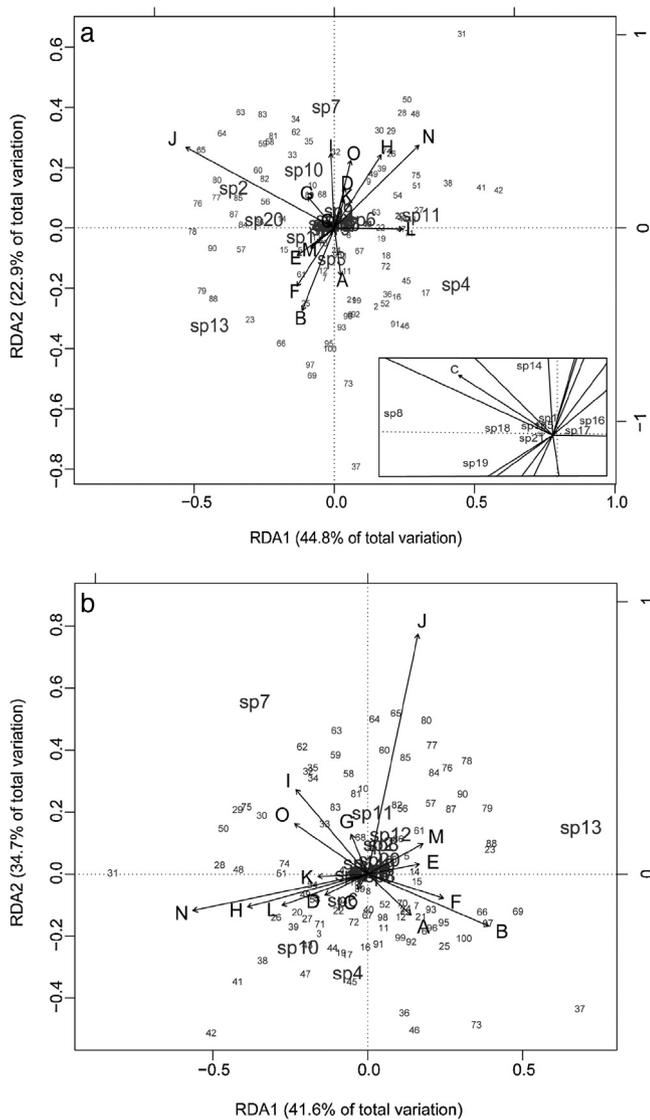


Fig. 4. Redundancy analysis ordination for dung beetle abundance (a) and biomass (b) constrained by environmental variables. Triplot with explanatory variables, species and samples: sp. 1: *Bdelyrus braziliensis*; sp. 2: *Canthidium* aff. *trinodosum*; sp. 3: *Canthon luctuosus*; sp. 4: *Canthon rutilans cyanescens*; sp. 5: *Canthonella* aff. *intriata*; sp. 6: *Coprophanaeus dardanus*; sp. 7: *Coprophanaeus saphirinus*; sp. 8: *Deltochilum brasiliense*; sp. 9: *Deltochilum furcatum*; sp. 10: *Deltochilum morbillosum*; sp. 11: *Deltochilum multicolor*; sp. 12: *Deltochilum rubripenne*; sp. 13: *Dichotomius sericeus*; sp. 14: *Dichotomius quadrinodosus*; sp. 15: *Dichotomius* sp.; sp. 16: *Eurysternus cyanescens*; sp. 17: *Eurysternus parallelus*; sp. 18: *Paracanthion* aff. *rosinae*; sp. 19: *Phanaeus splendidulus*; sp. 20: *Uroxys* sp. 1; sp. 21: *Uroxys* sp. 2; A: basal area of first tree; B: height of first tree; C: top diameter of first tree; D: distance to first tree; E: basal area of first shrub; F: height of first shrub; G: top diameter of first shrub; H: distance to first shrub; I: land slope; J: altitude; K: leaf litter cover; L: green cover; M: exposed soil; N: height of leaf litter; O: canopy cover; 1–25: ANH sampling points; 26–50: ITA sampling points; 51–75: PER sampling points; 76–100: RAT sampling points.

the variance, and was positively correlated with leaf litter height ($r=0.42$), altitude ($r=0.41$), land slope ($r=0.38$), distance of shrubs ($r=0.37$), canopy cover ($r=0.34$) and distance of trees ($r=0.20$); it was negatively correlated with tree height ($r=-0.42$), shrub height ($r=-0.30$) and tree basal area ($r=-0.24$).

Redundancy analysis on dung beetle biomass constrained 27.5% of total variance in relation to the explanatory variables (Fig. 4b). The first and second canonical axes were significant and accounted for 76.3% of the constrained variance. The first axis (RDA1, $F=13.281$; $p=0.001$) accounted for 41.6% of the variance, and

was positively correlated with tree height ($r=0.44$), shrub height ($r=0.27$) and percentage of exposed soil ($r=0.20$); it was negatively correlated with shrub distance ($r=-0.44$), land slope ($r=-0.26$), percentage of green cover ($r=-0.31$), height of leaf litter ($r=-0.64$), and canopy cover ($r=-0.26$). The second axis (RDA2, $F=11.082$; $p=0.001$) accounted for 34.7% of the variance, and was positively correlated with land slope ($r=0.31$) and altitude ($r=0.88$).

Analyses of species distribution plots (Fig. 4a) indicated that abundance of *C. aff. trinodosum* and *Uroxys* sp. 1 were associated to sites with higher altitude values and lower green (vegetation) cover values. *C. rutilans cyanescens* was associated to sites with lower altitude values, small-sized trees, higher leaf litter height and green (vegetation) cover values. *C. saphirinus* was associated to sites with higher sized trees, canopy cover and land slope values. *D. multicolor* was associated to sites with higher values of green (vegetation) cover and leaf litter height, while *D. morbillosum* was associated to sites with higher altitude and wide-crowned shrubs. *D. sericeus* was associated to sites with higher sized trees and lower values of leaf litter height. Analyzing the biomass (Fig. 4b), *C. saphirinus* was associated to sites with higher altitude, land slope and canopy cover. *D. morbillosum* was associated to sites with higher leaf litter height, green cover and distance of shrubs, while *D. sericeus* showed an opposite pattern.

Discussion

The results indicate significant differences in species richness, assemblage structure based on abundance and biomass, as well as in the composition of dung beetles between remnant sites of the Atlantic Forest, and that these differences are associated with the distribution of environmental characteristics of remnants along the spatial gradient studied. We also found that abundance and biomass of dung beetles respond differently to environmental variation, which is related to differences in species composition between sampled sites, as demonstrated by PCoA analysis.

Different historical processes of anthropogenic occupation and land use may have produced these associations. However, several other mechanisms and processes may be associated with patterns of species distribution (species richness, composition, abundance and biomass) due to isolation and fragmentation of areas and the mainland-island landscape (da Silva and Hernández, 2014), as well as differences in current human activity among areas and neutral processes. Furthermore, dung beetles are very dependent on mammals as a main food resource (Culot et al., 2013), and mammal populations can also be negatively affected by fragmentation (Canale et al., 2012; Santos-Filho et al., 2012), as well as by human-driven defaunation that occurred on the Island of Santa Catarina (Graipel et al., 2001). Historically, sea level of the Atlantic Ocean was lower and the island and mainland were united during the last ice age (~10,000–100,000 years ago), which probably enabled migration of species between the areas of the mainland to the island (Klein et al., 2006). With the increase in sea level (~10,000 years ago) and urbanization (in the last century), several areas of forests became fragmented and isolated, a common scenario in current Atlantic Forest areas (Tabarelli et al., 2005; Klein et al., 2006; Ribeiro et al., 2009). These large fragments now act as “islands”, with isolated communities and low dispersal and colonization rates (May et al., 2013), especially of organisms that are severely affected by forest fragmentation and habitat loss. These characteristics can adversely affect the long-term conservation of biodiversity and related ecological processes.

In addition to the historical processes, the IndVal and RDA analyses of dung beetle species distribution indicated that several species showed some degree of association with environmental characteristics of forest structure among areas. *C. aff. trinodosum*, *Canthon*

luctuosus Harold, 1868, *Deltochilum brasiliense* (Castelnau, 1840), *D. morbillosum*, *Deltochilum rubripenne* (Gory, 1831), *D. sericeus* and *Uroxys* sp. 1 were associated to sites with higher altitude values (IndVal), while *C. rutilans cyanescens* showed an opposite response (RDA). Altitude ranged between 28 and 265 m asl among sites, a common feature of the southern Brazilian Atlantic Forest (Ribeiro et al., 2009). Altitude is an important feature for dung beetle distribution as highlighted by Escobar et al. (2005) in the Colombian Andes. However, we expected that altitude in our study might be a proxy that represents an environmental variable we did not measure, such as soil type, soil penetrability, soil texture, or other variable describing soil condition, which influences dung beetle distribution in our sampled areas. These soil conditions may be related to a greater or lesser distance from the sampling site to the sea.

Our results (RDA) also showed that *C. saphirinus* was associated to sites with greater trees, canopy cover, land slope and altitude. *D. multicolor* was associated to sites with greater green (vegetation) cover and leaf litter height. *D. morbillosum* was also associated to sites with higher leaf litter height, green cover and wide-crowned shrubs. *D. sericeus* was associated to sites with larger sized trees and lower values of leaf litter height, green cover and distance of shrubs. Hernández and Vaz-de-Mello (2009) and Campos and Hernández (2013) also showed that some of these features (size and distance of trees and shrubs, percentage of leaf litter, green cover and exposed soil) were also important determinants of dung beetle distribution in Atlantic Forest areas in São Paulo and Santa Catarina, respectively. Increased leaf litter is expected to affect negatively the nesting activities of some roller species (Nichols et al., 2013), but our results did not explicitly show such association. However, height of leaf litter was highlighted as an important environmental condition for the distribution of dung beetle biomass in our study. Dung beetle species associated to sites with higher or smaller sized trees or shrubs may be affected by related microclimatic variation (Feer, 2008), which may influence reproductive aspects of species (Martínez and Vásquez, 1995). Differences in environmental characteristics across study sites and areas may represent the degree of change, or the status of succession of the forest structure in Atlantic Forest remnants. In general, the distribution of dung beetles along different environmental characteristics may show discrete associations with particular biotypes within the landscape (Davis et al., 2001; Viegas et al., 2014), and evidence suggests that species richness, abundance and biomass are negatively impacted in disturbed habitats (Gardner et al., 2008b). These environmental characteristics are also expected to affect the distribution of some mammalian species (Culot et al., 2013) and, therefore, the intake of food resources for dung beetles.

Differences in environmental conditions (e.g. habitat disturbance) indirectly affect the ecological functions of dung beetles by affecting their community attributes (e.g. species richness, abundance and biomass) (Braga et al., 2013). Several studies have highlighted the relationship between community attributes and ecological functions (Andresen, 2002; Bang et al., 2005; Slade et al., 2007). In addition, some species may have their demographic dynamics altered by poor environmental conditions. Therefore, differences in dung beetle distribution across different spatial extents associated with differences in environmental conditions may be affecting the ecological functions, as well as community structure, even within the same fragment of forest. The differences in environmental conditions found within the same fragment reflect the current stage of the Atlantic Forest: isolated and small fragments composed by second-growth forests in early to medium stages of succession (Metzger et al., 2009).

This work demonstrated the existence of significant associations between several species of dung beetles and the environmental structure of Brazilian Atlantic Forest remnants at local and regional

scale. Species composition and structure based on abundance and biomass of dung beetle assemblages were also associated with structural features of the studied habitats. This result reveals the importance of spatial distribution of these areas for the maintenance and conservation of dung beetle species, as well as for the response of these species to environmental changes. We expect that providing basic information on species distribution and community structure may be useful in the evaluation and monitoring of the protected Brazilian Atlantic Forest remnants.

The spatial distribution and the occurrence of spatially structured environmental characteristics of Atlantic Forest remnants can host a high gamma diversity of dung beetles. Because these insects show responses similar to several other taxa (Barlow et al., 2007; Culot et al., 2013), we expect that the remnants in this study contribute to the maintenance of wildlife of several taxonomic groups of organisms. We know that both the mammal community and environmental heterogeneity influence the distribution of dung beetle assemblages. Knowing the relative importance of these two factors is a demand for future studies on factors influencing the spatial distribution of dung beetles.

Conflicts of interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.rbe.2015.11.001](https://doi.org/10.1016/j.rbe.2015.11.001).

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