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Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure

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Abstract Dung beetles feed and nest in mammal feces, are influenced by habitat quality and have limited dispersal ability. We hypothesized that dung beetle community structure is affected by mammal composition, habitat structure, and spatial distance, and that these predictors vary among the functional groups in communities. Dung beetles and mammals were sampled using pitfall traps and camera traps, respectively, at 15 Atlantic Forest sites between 2005 and 2013. Habitat structure was described using the point-quadrant method. We utilized descriptive ecological values and used variation partitioning to identify

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predictors of dung beetle community composition both as a whole, and after organizing the community into functional groups. We recorded 43 dung beetle species and 28 mammal species. Mammal and dung beetle species richness were positively correlated. Mammals and habitat explained the majority of the variation among dung beetle communities, and explanatory values varied substantially when using the functional group approach. Our results indicate that mammals are, indeed, important drivers of dung beetle community structure. Individually, or in combination with habitat structure, mammal composition explained 40 % of the total variation in dung beetle data, i.e., the abundance and species composition of dung beetles and mammals covary. However, herbivorous mammals, medium-sized mammals and omnivorous mammals numerically contributed more than did other groups to the explanation of variation in dung beetle guilds. Habitat structure was an important determinant for dung beetle functional group abundance, and spatial distance influenced covariation between dung beetles and mammals. Thus, the integrity and maintenance of ecological processes in the Atlantic Forest may be dependent on these groups, and further fragmentation, habitat loss and defaunation may increase the sensitivity of this already reduced and threatened biome.

Keywords Atlantic Forest · Biodiversity · Community ecology · Defaunation · Co-decline

Introduction

Biodiversity is under threat as a result of habitat fragmentation and loss of natural areas caused by human activities (Foley et al. 2005; Pardini et al. 2010; Cassano et al. 2012). The decline of animal species and populations (defaunation) is a specific type of biodiversity loss that has recently gained the attention of researchers (Canale et al. 2012; Brocardo et al. 2013; Dirzo et al. 2014; Bogoni et al. 2016). Defaunation levels are reaching critical thresholds in many cases that are affecting broader ecosystem diversity and function (Barnosky et al. 2012; Cardinale et al. 2012). The decline of wildlife populations and associated cascade effects (such as food production) also threaten human well-being (Dirzo et al. 2014).

Selective defaunation results from a combination of factors related to hunting, and decreases with fragmentation of natural areas (Galetti and Dirzo 2013; Kurten 2013; Bogoni et al. 2016). The effects of defaunation operate on various levels, influencing ecosystems through a gradient of ecological processes from plant reproductive performance (e.g., seed dispersal and predation) to animal behavior (e.g., movement and dietary patterns) (Culot et al. 2013; Galetti and Dirzo 2013). These effects influence populations, community-level dynamics and structure in the short term, and can promote evolutionary changes in the long term (Galetti and Dirzo 2013). Thus, selective defaunation is expected to have cascading effects upon all other organisms (Kurten 2013). The overexploitation of wild populations is a significant threat to the survival of many mammals worldwide (Wiederholt et al. 2010; Canale et al. 2012). This issue is particularly important in the Atlantic Forest biome, where there are 298 mammal species and a high degree of endemism ($\sim$90 species) (Paglia et al. 2012).

Dung beetles (Coleoptera: Scarabaeinae) use mammal feces and carcasses as primary food and nesting resources (Halffter and Matthews 1966) so are intimately associated with mammalian fauna (Barlow et al. 2007, 2010; Culot et al. 2013) because they. Thus, mammalian species richness strongly influences dung beetle species richness and abundance, as well as community structure (Barlow et al. 2007, 2010). Evidence suggests that the cascading effects of mammalian defaunation are leading to a decline in dung beetle species richness and abundance as a result of resource shortages. (Nichols et al. 2009; Culot et al. 2013). Dung beetles, like other detritivores, do not control the rate at which their food resources become available or regenerate; instead they depend on the rate at which other forces supply them (Pimm 1982).

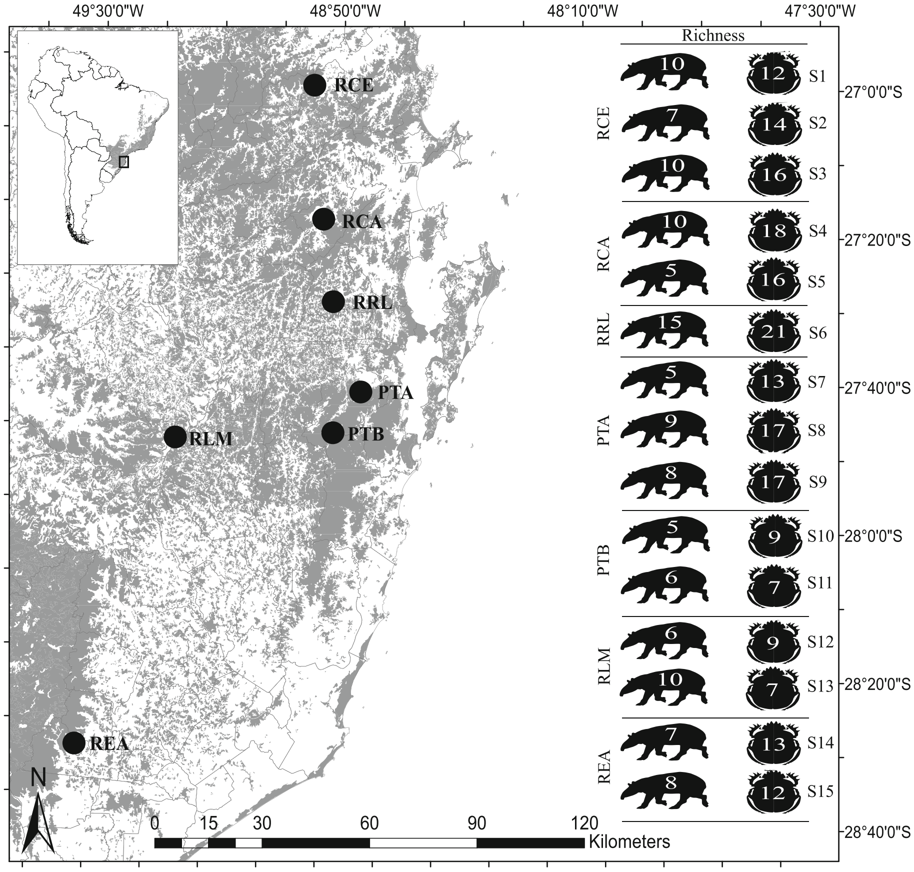

Fig. 1 Schematic map of the spatial variation in mammal richness (represented by the *Tapuris terrestris* silhouette) and dung beetles (represented by the dung beetle silhouette) from 15 Brazilian subtropical Atlantic Forest sites. From north to south: S1, S2 and S3 were located within Reserva Particular do Patrimônio Natural (RPPN) Chácara Edith (RCE); sites S4 and S5 were within RPPN Caraguatá (RCA); S6 was within RPPN Rio das Lontras (RRL); S7, S8 and S9 were located within Parque Estadual da Serra do Tabuleiro (PEST; Area A) in the municipality of Santo Amaro da Imperatriz (PTA); S10 and S11 were in PEST (Area B) in the municipality of São Bonifácio (PTB); S12 and S13 were in the RPPN Leão da Montanha (RLM); and S14 and S15 were located within the Reserva Biológica Estadual do Aguaí (REA). The database for the map was obtained from the Ministério do Meio Ambiente- Brazil (http://mapas.mma.gov.br/mapas/aplic/probio/datadownload.htm), Empresa Catarinense de Pesquisa Agropecuária (http://ciram.epagri.sc.gov.br/mapoteca/), and the Nature Conservancy (http://maps.tnc.org/gis_data.html). Details in green correspond to the Atlantic Forest remnants in the study area in 2011–2012 (according to the foundation SOS Mata Atlântica: http://mapas.sosma.org.br/)

Dung beetles can be utilized directly and indirectly as biodiversity indicators due to their close relationship with mammals (Halffter and Favila 1993). Their short life cycle, broad distribution, high abundance, and rapid responses to environmental alterations (such as changes in community structure) mean they can also be used as ecological indicators (Favila and Halffter 1997). A decline in dung beetle species richness often occurs in areas that have suffered environmental degradation, particularly loss of habitat (Barlow et al. 2007; Hernández et al., 2014). For example, declines have been documented in response to forest conversion at both local and regional scales (Nichols et al. 2013a), and primarily affect species with larger body sizes (Nichols et al. 2013b). Establishing relationships between species distribution and environmental characteristics is a major goal of ecology, and such relationships are likely to be important predictors of community structure, (Peres-Neto et al. 2006; da Silva and Hernández 2014, 2015). For example, changes to spatial and biogeographic conditions may influence or limit organism dispersal, thereby altering the composition of biological communities (Holyoak et al. 2005; da Silva and Hernández 2014, 2015).

Our study of subtropical Atlantic Forest was based on the importance of the relationship between mammals and dung beetles in, as well as the role of habitat structure and spatial distance in dung beetle community structure. Our aims were: (1) to evaluate whether mammal and dung beetle communities covary, and whether there is a positive relationship between them with respect to species richness; (2) to elucidate the individual and combined contributions of mammal composition, habitat structure, and spatial distance to explaining the variation in subtropical Atlantic Forest dung beetle communities; and (3) to assess whether these factors vary when communities are evaluated using a functional group approach.

Materials and methods

Study areas

We conducted this study at 15 sites in a quasi-continuum of subtropical Atlantic Forest with varying habitat structure, located across six protected areas of Serra Geral in Santa Catarina, Brazil (27°05′, 27°35′S; 48°20′, 48°55′W) (Fig. 1; Supplementary Material 1). The study region is located within the humid subtropics (Cfa and Cfb climate types according to the Köppen-Geiger classification) but has defined seasons. Rainfall is distributed throughout the year, with an annual rainfall average of ca. 1700 mm. Annual temperatures vary widely (between −10 and 40 °C), with an annual average between 11 and 19 °C (Peel et al. 2007). The study region contains dense rainforest vegetation (Dense Ombrophilous Forest) and Araucaria Forest (Mixed Ombrophilous Forest) (Instituto Brasileiro de Geografia e Estatística (IBGE) 1992).

Sampling

Dung beetles: response variables

We sampled dung beetles in the hot months of the year, i.e. in November and December 2009 and February and March 2010 (at sites S1, S2, S3, S7, S8 and S9), and in the same months in 2012–2013 (for sites S4, S5, S6, S10, S11, S12, S13, S14 and S15) because these period provide favorable conditions for this group of organisms (Hernández and Vaz-de-Mello 2009).

At each site, we used ten pitfall traps arranged as five pairs for collecting coprophagous and necrophagous dung beetles. Each pair of traps consisted of one filled with water and detergent solution baited with human feces (10 g), and another containing the same solution baited with decomposing pork meat (15 g). Individual traps in a pair were 10 m apart (see Supplementary Material 2), and pairs of traps were placed at least 50 m apart to decrease the influence of other sets of traps when sampling Scarabaeinae (Larsen and Forsyth 2005) The traps were installed >100 m inside in forest areas to avoid border zones and with a minimum distance of 10 m from streams. Traps remained in the field for 48 h. Body sizes of collected beetles were determined and categorized as follows: large (L), mean weight $\geq$ 0.1 g; medium (M), > 0.009 and $\leq$0.09 g; and small (S), $\leq$ 0.009 g prior to oven drying at 50 °C for 48 h. A random selection of ten individuals per species per area were then weighed (on a precision balance). Total biomass was calculated by multiplying the average species weight by the number of individuals of that species at each site.

Species of dung beetle where more than one individual was collected were also categorized into functional groups as follows: coprophagous (C), $\geq$ 80 % of individuals collected in traps with feces; necrophagous (N), $\geq$ 80 % of individuals captured collected in traps with rotting flesh; and generalists (G), when the percentage of capture is roughly equivalent using both types of bait (Halffter and Arellano 2002). Published information was used to classify the trophic category of species where fewer than ten individuals were collected (Hernández 2007; Almeida and Louzada 2009; Campos and Hernández 2013). Resource relocation behavior (paracoprid, telecoprid or endocoprid) was classified according to standard practices (Halffter and Edmonds 1982).

Specimens were identified at the Seção de Entomologia da Coleção Zoológica at the Universidade Federal do Mato Grosso (UFMT) and deposited in the Coleção Entomológica do Centro de Ciências Biológicas at the Universidade Federal de Santa Catarina (UFSC).

Mammals, habitat structure, and spatial distance: predictor variables

Presence-absence data on mammal species were collected from each site from 2005 to 2011 using camera traps. We distributed a total of 33 camera traps (Model: Tigrinus ® 6.0C), with one to four traps per site that were spatially distributed among areas to cover different habitat types. These traps were installed in trees at 30–40 cm above ground level, and were intentionally placed on trails (both narrow and wide) and paths naturally used by mammals. The traps were checked for functionality and maintained approximately every 30 days and remained in the field for between 31 and 138 days.

Presence-absence data were used due to limitations imposed by differences in sampling effort among sites (Espartosa et al. 2011). Pearson's correlation analysis was performed to analyze the relationship between species richness and the number of camera traps per site per day [$r = -0.07$; $p = 0.82$]. The results showed that variation in sampling effort did not affect mammal species richness. We acknowledge that the animal community observations are not 100 % accurate regardless of the method(s) used and, in most cases, not every species present will be detected (Schmidt 2005). Furthermore, detection efficiency is limited for some species because mammals vary in physiology and lifestyle (Lyra-Jorge et al. 2008; O'Connell et al. 2011). Cricetidae (small rodents) were excluded from our analyses for these reasons and because of identification difficulties. Mammals in different trophic guilds influence dung beetle community structure in different ways (Estrada et al. 1993, Filgueiras et al. 2009, Marsh et al. 2013; Bogoni and Hernández 2014) so mammal communities were organized into guilds by trophic habit and body size for analyses using functional approaches (see below) (Parera 2002; Reis et al. 2006; Magioli et al. 2015). Thus, for body size classification, the following criteria were used: small mammals, adult body size $\leq$1.2 kg; medium mammals, adult body size $<$1.2 and $\geq$10 kg; and large mammals, adult body size $>$10 kg (according to Paglia et al. 2012).

Habitat structure among sites was described by measuring various vegetation and environmental characteristics. We used an adapted point-quadrant method (Brower et al. 1998), which includes placing a cross-shaped dowel between the first, third and fifth pair of traps at each site to outline four quadrants (northeast, southeast, southwest and northwest). We measured the following parameter in each quadrant: circumference at breast height (CBH, $\sim$1.4 m) for the trees closest to the center cross-point with CBH $\geq$ 16 cm; circumference at ankle height (CAH) for shrubs closest to the center point with CAH $\geq$ 5 cm and with height $\geq$ 1 m; distance, height, and crown diameter for trees and shrubs closest to the center point; green and woody lianas (CAH $\geq$ 5 cm) closest to the center point (i.e., the distance from the center and CAH) and litterfall height in each quadrant by placing a 1 m square constructed of plastic pipes on the ground. Green area and litter cover percentages in each square were visually estimated as one of the following percentage classes: 0–5, 6–25, 26–50, 51–75, 76–95 and 96–100. The percentage of canopy cover in four directions was visually estimated using a 10 cm^2 square placed 40 cm from the observer's eye at an inclination of 20° in relation to the zenith and classified in the same percentage classes aforementioned The average elevation above sea level of each site was considered as an environmental variable. Finally, we calculated the linear spatial distance between sites using geo-referenced data obtained by GPS, which was transformed into a truncated distance matrix.

Data analysis

Initial analysis of the dung beetle community data was undertaken using the descriptive parameters species richness, abundance, biomass, and body size. We constructed rarefaction curves and calculated the Chao1 richness estimator for dung beetle communities (Colwell et al. 2012). Mammal communities were described by diversity index, such as total richness and functional groups' richness.

We performed a principal coordinate analysis of neighborhood matrices (PCNM) to determine significant spatial components obtained from the distance matrix among sites Analyses were also conducted using geo-referenced area values but only the site-scale analysis results are reported here because the two methods had compatible results. We selected only positive PCNMs according to spatial autocorrelation obtained via the Moran index (Borcard et al. 2004, 2011). The PCNMs represent the spatial relationships among sampling sites and, therefore, can be also used as predictors of variation among sites (Borcard et al. 2004).

We conducted variation partitioning through redundancy analysis (RDA) to evaluate the percent contribution (both individual and combined) of each group of predictor variables [including mammal composition (resource), habitat structure, and linear distance (derived from PCNMs)] to explain the variation in dung beetle community composition, abundance, biomass, and body size (Legendre and Legendre 1998; Borcard et al. 2011; Legendre et al. 2012). The variation was partitioned by selecting a subset of (significant) predictor variables based on the complete mammal data set and non-multi-collinear habitat data and using the forward selection method proposed by Blanchet et al. (2008) to reduce the likelihood of type-I errors. These analyses were performed in two ways: (1) using a full predictor (mammal composition) and response (dung beetle) dataset; and (2) using the subset of mammal composition and dung beetle abundance data after it had been organized into functional groups.

Variation partitioning performs RDAs for all predictors then one-by-one for each set of predictors individually, removing effects of other predictors (e.g. RDA for mammals removes the effects of habitat and distance; RDA for habitat removes the effects of mammals and distance) (Peres-Neto et al. 2006). The proportions of variation explained by the predictors are represented by adjusted r^2 (adj. r^2) in accordance with Ezekiel's correction (Peres-Neto et al. 2006), where values are expressed as percentages.

We used a Hellinger transformation in the variance partitioning to correct for asymmetry in dung beetle abundance and biomass (Borcard et al. 2011). All other analyses were performed without data transformation. Significance ($p \leq 0.05$) tests were based on 1000 permutations, and analyses were performed in R 3.0.1 (R Core Team 2013) using the Vegan (Oksanen et al. 2013) and Packfor (Dray et al. 2013) packages.

Results

Dung beetles

We collected 4120 dung beetles from 43 different species (Supplementary Material 3). The number of species per site varied between seven (S11 and S13) and 21 (S6) (Fig. 1). Sixteen species (37 % of the total) were coprophagous, ten (23 % of the total) were necrophagous, nine (21 %) were generalist. We were not able to classify the remaining

Table 1 Mammal richness, estimated (Chao 1) richness (Est. Rich.), abundance, and total biomass (g) of dung beetles in 15 Brazilian subtropical Atlantic forest sites located in protected areas of Serra Geral in Santa Catarina, Brazil

Area	Site	Mammals	Dung beetles			
		Richness	Richness	Est. rich.	Abundance	Biomass (g)
RPPN Chácara Edith (RCE)	S1	10	12	12	253	31.9
	S2	7	14	18.5	167	26.7
	S3	10	16	16.7	365	65.3
RPPN Caraguatá (RCA)	S4	10	18	20.6	127	16.9
	S5	5	16	20.5	212	18.1
RPPN Rio das Lontras (RRL)	S6	15	21	39	430	90.5
P.E. Serra do Tabuleiro (PSA)	S7	5	13	16	261	21.3
	S8	9	17	17.7	519	57.8
	S9	8	17	23.2	475	40.5
(PSB)	S10	5	9	15	200	6.2
	S11	6	7	9	99	3.2
RPPN Leão da Montanha (RLM)	S12	6	9	9	371	10.1
	S13	10	7	7	206	5.8
ReBio Aguaí (REA)	S14	7	13	17.5	271	55.7
	S15	8	12	15	164	32.9

eight species (19 %) due to low sample size (∼1 individual). Fifteen species (41 %) were large-sized, 19 (28 %) were medium-sized, and nine (31 %) were small-sized. Eighteen species (42 %) were paracoprids, 15 species (35 %) were telecoprids, two (4 %) were endocoprids, and eight (19 %) were not identifiable. Total abundance among sites varied from 99 (S11) to 519 (S8) individuals. Biomass varied from 3.2 g (S11) to 90.6 g (S6), and observed species richness varied from 54 to 100 % compared with estimated (rarefied) richness (Table 1). Species rarefaction curves showed sufficient dung beetle community sampling (Fig. 2; Supplementary Material 4) at all sites except for S4, S10 and S11 [although only S10 had less than 75 % of the estimated richness (Table 1)]. Abundance varied strongly among sites, however variation in species richness was not high. The 95 % confidence intervals and estimated richness showed the lowest species richness occurred at sites S11 and S13 (seven species each), and S10 and S12 (nine species each).

Mammals, habitat structure, and spatial distance

We recorded 646 mammals from 28 species and 16 families, including one exotic species [the European hare *Lepus europaeus* (Pallas, 1778)] (Supplementary Material 5). Richness among the 15 sites varied from five to 15 species (Table 1). Total species richness included six carnivores (ranging from 1–5 per site), 13 omnivores (2–9 per site), and nine herbivores (1–4 per site). Seven large mammals (0–3 per site) were recorded, 17 medium (4–11 per site), and four small-sized mammals (0–2 per site).

Habitat structure varied among sites, particularly in green ground-cover percentage and woody-liana basal area. Other parameters with high variation were generally multicollinear with each other or with elevation. The average elevation of our sites was 984 meters above sea level (m.a.s.l.) (range 124–1108 m.a.s.l.) (Supplementary Material 1). The linear distance between sites within an area was at least 800 m, with a mean of 1500 m.

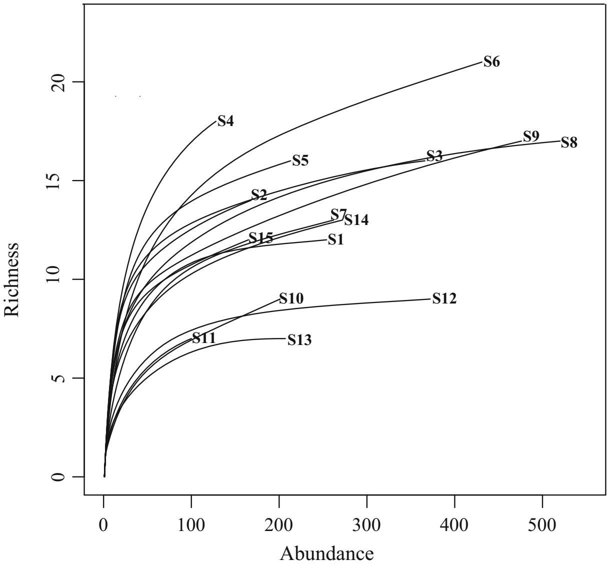

Fig. 2 Rarefaction curves of dung beetles species from 15 Brazilian subtropical Atlantic Forest sites. Site abbreviations as in Fig. 1

Ecological relationships and variation partitioning

Forward selection using complete community data varied according to response variable (dung beetle composition, abundance, biomass and/or body size). Overall, 11 mammal species (4–7 per site) were selected, including *Dasyprocta azarae* (Azara's agouti; found in 25 % of sites), *Procyon cancrivorus* (crab-eating raccoon; found in 60 % of sites), *Cerdocyon thous* (Crab-eating fox), and *Dasypus novemcinctus* (nine-banded armadillo) (both found in 80 % of sites). Percentage of green cover and elevation were significant predictors of the habitat variables and spatial vectors derived from PCNMs, and ranged from one and three (positive and significant, according to response variable). Variation partitioning using only these significant predictors indicated that 20 % of the total variation in dung beetle composition was explained by mammal composition and spatial distance, whereas 14 %

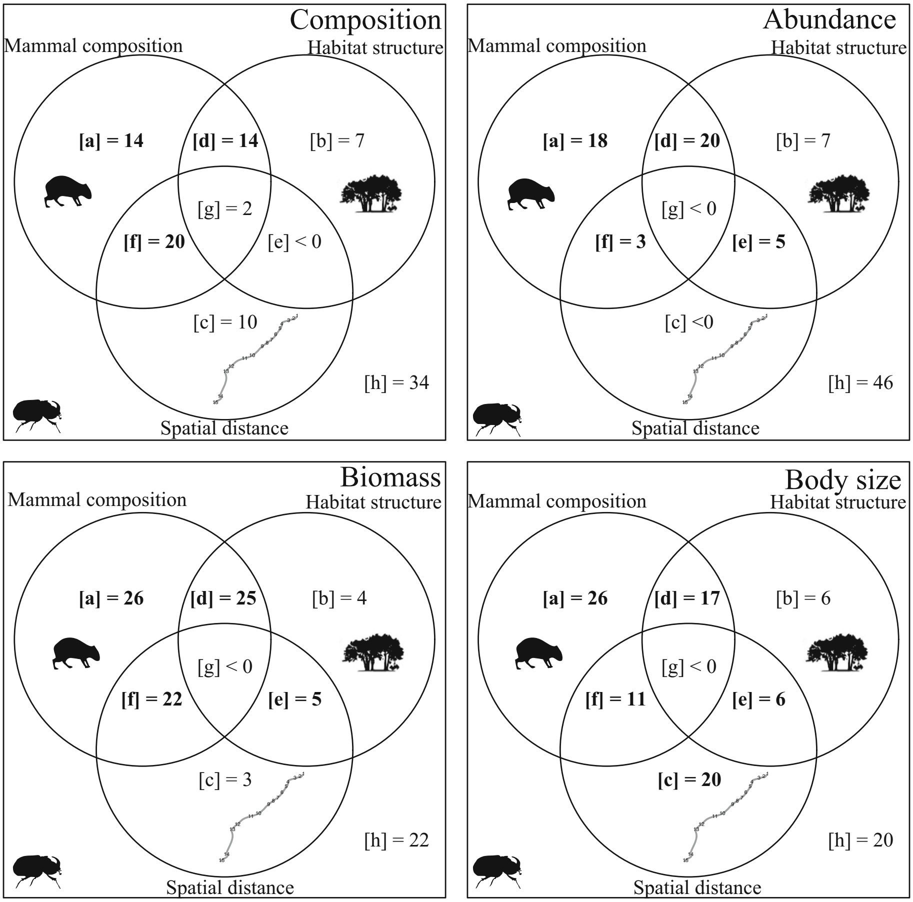

Fig. 3 Variation partitioning analysis for dung beetle community structure in 15 Brazilian subtropical Atlantic Forest sites. Beetle composition, abundance, and total and average biomass were analyzed in relation to proportion explained by the explanatory variables. *Red* values are statistically significant at $p \leq 0.05$. **a** mammals; **b** structural complexity of habitats (habitat); **c** spatial distance (space), **d** mammals and complexity; **f** mammals and spatial distance; **g** all the factors together, and **h** residual

was explained by mammal composition and 14 % by both mammal composition and habitat structure. Mammals and habitat explained 20 % of the variation in dung beetle abundance, and 18 % was exclusively attributed to mammals. Mammals explained 26 % of the variation in biomass, and mammals and habitat together explained 25 %, while 22 % was explained by mammals and spatial factors. Mammals explained 26 % of the variation in dung beetle body size, spatial factors explained 20 %, and mammals and habitat together explained 17 % (Fig. 3; all values in Supplementary Material 6).

Analysis of the functional groups using variation partitioning indicated that the largest contributors to dung beetle abundance in different trophic guilds were habitat (26.5 % on average), herbivores (13 % on average) and medium-bodied mammals (10 % on average) (Fig. 4). Reinforcing this pattern, variation in habitat best explained the presence of coprophagous (C), necrophagous (N), and generalist beetles (G) (on average 25, 25 and 44 %, respectively) (Fig. 4a). Dung beetle body size was best explained by the presence of herbivorous and omnivorous mammals (19 and 13 %, respectively). The main predictors for variation in the numbers of large beetles (L) were herbivore presence (33 %) and

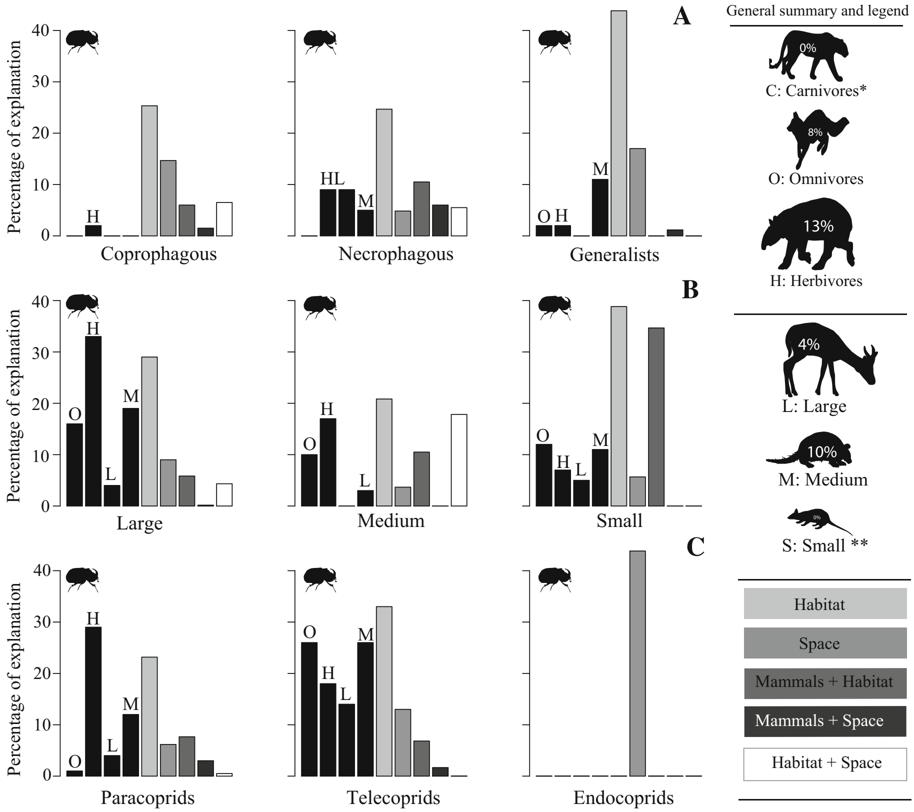

Fig. 4 Summary (obtained by means) of the partitioned variation involving mammal functional groups, habitat, and spatial distance in explaining the variation in abundance of dung beetle functional groups. **a** dung beetle trophic guild; **b** dung beetle body size; and **c** dung beetle relocation resource behavior. For a complete list of values see Supplementary Materials 6. *Asterisk* Carnivores and small mammals showed had no predictive value; *double asterisk* Except Cricetidae

habitat (29 %). The main predictors for the numbers of medium-sized beetles (M) were habitat (21 %) and herbivore presence (17 %). For small-sized (S) beetles, habitat was the main predictor (39 %, Fig. 4b). The behavioral-guild (resource relocation types) results showed that the presence of herbivores is the most important factor for paracoprid presence (29 %), habitat is most important factor for telecoprid presence (33 %) and the presence of endocoprids is affected mainly by spatial distance (44 %) (Fig. 4c; Supplementary Material 7).

Discussion

The main result of this study is that mammal composition and habitat structure, mainly acting together, can explain much of the variation in dung beetle communities. The functional-group approach revealed that the explanatory values vary substantially depending on the response variable analyzed. Several studies have shown the importance of mammals for dung beetle communities, yet have also highlighted unresolved issues involving the congruence of these two groups (e.g. Nichols et al. 2009; Culot et al. 2013). Our results generally agree with the importance of mammals for dung beetle community structure. Mammal composition, either individually or in combination with habitat structure, explains 40 % of the total variation in the dung beetle data. Furthermore, we observed that herbivorous, medium-sized and omnivorous mammals explained most of the variation in dung beetle guild, especially in abundance of medium- to large-sized dung beetles, and abundance of paracoprids and telecoprids. Our overall results utilizing different approaches may contribute to our understanding of recent issues, such as cascade dynamics along detritivore foodwebs (Schmitz et al. 2010), trait-defined cascade structures (Nichols et al. 2013a), scale-dependence and habitat contributions on structuring dung beetle communities (da Silva and Hernández 2014, 2015), transcending biome boundaries. For example, they could be used to generate predictions about the distinct effects of habitat, mammal composition, and mammal-guild functional imbalances upon dung beetle communities.

Changes in mammal composition, including defaunation (mainly in large mammal species), can lead to potentially serious secondary effects like decreased dung beetle abundance and secondary seed dispersal (Culot et al. 2013; Galetti and Dirzo 2013; Nichols et al. 2013b). In general, near-equilibrium in dung beetle species abundance is best achieved when local mammal communities have a large biomass (Barlow et al. 2007, 2010; Gardner et al. 2008a; Culot et al. 2013), i.e., when dung beetle community dynamics are not driven only by smaller mammal species. Hanski and Cambefort (1991) also found that beetle (species) size is strongly influenced by mammal composition, as well as spatial proximity. There is a greater proportion of small-bodied beetles in situation where large mammals are absent (Nichols et al. 2013b). Therefore, biomass data may provide a better picture of the processes leading to changes in community structure than just species counts, since body size is directly proportional to the amount of resources consumed and body mass is associated with population responses across different habitats (Peters 1983; Nichols et al. 2013b).

Habitat quality has direct effects on mammal composition and abundance (Goulart et al. 2009; Cassano et al. 2012), as well as dung beetle community structure (Barlow et al. 2007; 2010; Gardner et al. 2008b; Nichols et al. 2013b). However, a trade-off between resource availability and environmental quality must also be considered (i.e., greater availability in lower habitat quality). Our findings show that resources (mammals) are more important for full dung beetle communities, and habitat characteristics are more important for functional group configuration. Many dung beetle species have generalist feeding behavior (Hanski and Cambefort 1991) and human feces are the main bait used for trapping dung beetles (Larsen et al. 2006), so observed dung beetle abundance is expected to be more influenced by mammal composition, whereas species composition might be more affected by habitat characteristics (Hanski and Cambefort 1991; Hernández and Vaz-de-Mello 2009; Campos and Hernández 2013).

Dung beetle functional groups have been found to respond differently to habitat quality (Davis 1996) and forest conversion (Nichols et al. 2013b). These results emphasize the need to go beyond simple examination of diversity-habitat relationships and to move towards understanding the functional consequences of different habitats (Slade et al. 2011). In particular, there is some evidence of complementarity, facilitation, and resource sharing between different functional groups, and also different responses to habitat types (Hernández 2002; Slade et al. 2007; Hernández et al. 2011). Functional guild studies show that the majority of dung beetle species have opportunistic-feeding behavior, where individuals utilize a wide variety of resource types (Hanski and Cambefort 1991). Atlantic Forest dung beetles are preferentially attracted to omnivorous mammal feces (Filgueiras et al., 2009; Bogoni and Hernández 2014) independent of trophic guild (except necrophagous); nevertheless community structure remains linked to the nutritional quality of the resource (Bogoni and Hernández 2014). Here, we found that herbivores contributed to variation dung beetle community structure more than other groups, which is not uncommon in the Neotropics (Hanski and Cambefort 1991).

The functional group approach of the current study enhances the explanatory value of determining habitat characteristics (with regard to variation in abundance of dung beetle functional groups) by highlighting two important issues: (1) there will be significant changes in dung beetle communities if the mammal community has functional unbalances (e.g. loss of carnivores), since all mammal communities had strong predictive potential; and (2) dung beetle communities are strongly influenced by habitat quality, followed by food resource availability. Our species richness results also show that both dung beetle and mammal alpha diversity was low, with a decrease in dung beetle richness at the higher elevations. In Atlantic Forest areas, it is expected that mammal alpha and beta diversity are similar (Eduardo 2011). On the other hand, dung beetle alpha diversity in these areas is generally low, while beta diversity is usually high (Hernández and Vaz-de-Mello 2009; Campos and Hernández 2013; da Silva and Hernández 2014). Variation in community richness at different spatial scales is common, and the metrics for analyzing these variations are well documented and discussed (Colwell et al. 2012). Our data and results contribute to the knowledge of subtropical Atlantic Forest fauna, which is an area that is typically under-sampled and where species richness and distribution data are lacking (Cáceres et al. 2007). We conclude that all factors evaluated in this study are important for the integrity and maintenance of ecological processes in the Atlantic Forest. These processes can be affected by fragmentation, habitat loss, and defaunation, further increasing the sensitivity of this reduced and threatened biome.

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