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Research

Decline of Ecological Functions Performed by Dung Beetles in Areas of Atlantic Forest and Contribution of Rollers and Tunnellers in Organic Matter Removal

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Abstract

The feeding behavior of the Scarabaeinae subfamily has positive implications on ecosystem functioning. We characterize the necrophagous and coprophagous dung beetle assemblages, and we quantify the removal of swine carrion and domestic dog dung in two areas with different degrees of environmental disturbance in an Atlantic Forest remnant located in Florianopolis, SC, Brazil. The experiment was setup at eight sampling points in each area, by installing one control and two collection and removal assessment arenas for collecting necrophagous dung beetles while simultaneously evaluating the removal of carrion (50 g of rotting pork for 48 h). We used the same sample design with 50 g of domestic dog dung for evaluating the coprophagous dung beetle assemblage and dung removal. Our results indicated that necrophagous dung beetles were more sensitive to environmental disturbance owing to a lower richness and changes in species dominance, which resulted in a lower removal in the areas with greater disturbance and lower environmental quality (39.6% carrion removal) in relation to less disturbed areas (75.1% carrion removal). The dung beetle assemblages were similar in structure and removal rates between areas (80% of dung was removed). In assessing the influence of richness, abundance, and biomass of dung beetles on resource removal both for the whole assemblage and for each separate functional guild, only the abundance and biomass of rollers contributed significantly to dung removal. These results highlight the implications of environmental disturbances on the functions of dung beetles, which respond differently according to the resource they use.

Key words: decomposition, ecology, ecosystem service, functional guild, Scarabaeinae

Dung beetles have been used in various ecological investigations with great potential for response (as seen in the revisions of Nichols et al. 2007, 2008), including the execution of ecological functions and maintenance of ecosystem services (Slade et al. 2007, Dangles et al. 2012). These services can be understood as any activity performed by a living organism that interferes with natural processes, such as, for example, nutrient cycling, soil formation and maintenance, pollination, seed dispersal, and biological control (Myers 1996, Daily 1997). Through their ecological functions, organisms provide elements for the functioning of systems and directly or indirectly generate benefits for the human population, also known as ecosystem services, which can be measured and economically valued (environmental services; De Groot et al. 2002, Millennium Ecosystem Assessment [MEA] 2005). Within the ecosystem services, dung beetles are a part of regulatory functions through the removal of carcasses and dung for feeding and nidification. This feeding behavior has direct effects on the decomposition of organic matter and nutrient cycles (Halffter and Matthews 1966) and is strongly associated with other ecological functions, such as secondary seed dispersal (Andresen 2001, 2003; Vulinec 2002), soil aeration, and biological control of flies (Braga et al. 2012, 2013). As nutrient cycling and soil formation are primarily associated with ecosystem functioning, the functions that interfere with these processes were hierarchically categorized into support ecosystem functions, which is the basis of other functions, reinforcing its importance in maintaining ecosystems and human well-being (MEA 2005).

The subfamily Scarabaeinae (Coleoptera: Scarabaeidae) comprises >7,000 species (ScarabNet 2016), primarily of copronecrophagous habit. Coprophagy, a habit of eating dung from other animals, evolved with the vertebrates, initially dinosaurs (Chin and Gill 1996), but after the diversification of mammals, it is strongly associated with this group (Scholtz et al. 2009, Nichols et al. 2009, Barlow et al. 2010, Culot et al. 2013). Some species of dung beetles may present some degree of specificity or preference for one type of dung; however, most prefer dung of omnivorous mammals (Filgueiras et al. 2009, Amézquita and Favila 2010, Whipple and

Hoback 2012, Puker et al. 2013, Bogoni and Hernández 2014). As for necrophagy, the association of this feeding behavior with dung beetles is a recent evolutionary process, driven by the absence of large mammals concurrently with the relative scarcity of other groups of insects that could compete for decaying flesh (Halffter and Matthews 1966, Scholtz et al. 2009). This shift in diet may have been facilitated by the similarity between carrion composition and omnivorous dung, as well as the high nitrogen concentration in decaying flesh (Hanski and Cambefort 1991). Dung beetles can also be generalists and opportunists, feeding on a range of available items, such as decomposing fruits (Scholtz et al. 2009). As for resource reallocation behavior for feeding or nidification, dung beetles can be classified into three functional guilds: tunnellers (paracoprids), which relocate resources directly underneath the source, burying them in subterranean galleries; the rollers (telecoprids) relocate their resources into balls for feeding and nidification, which are then rolled and buried at a certain distance from the source; and dwellers (endocoprids), which use the resource directly at the source (Halffter and Matthews 1966, Halffter and Edmonds 1982).

The importance and implications of dung beetles and their ecological and functional characteristics in maintaining ecosystem services have been investigated by quantifying the removal of dung (Klein 1989; Horgan 2001, 2005, 2008; Andresen 2003; Anduaga 2004; Anduaga and Huerta 2007; Slade et al. 2007; Amézquita and Favila 2010; Dangles et al. 2012; Kudavidanage et al. 2012; Braga et al. 2013; Gollan et al. 2013), and less commonly, carcass removal (Klein 1989, Horgan 2008, Amézquita and Favila 2011). Empirically, reduced dung beetle diversity is associated with habitat loss or modification (Spector 2006; Gardner et al. 2008a,b), which directly involves the reduction or loss of ecological functions and ecosystem services provided by this group. This relationship occurs because species differ in their capacity to obtain resources, measured by removal, which generates distinct patterns in the performance of ecological functions and thus, on ecosystem services. In addition, the execution of these functions is positively related to biomass, body size of the organisms (Nervo et al. 2014), and the complementarity of species and functional guilds (Slade et al. 2007). These ecological characteristics are negatively compromised in degraded environments owing to a reduced diversity.

Dung beetles are important for the maintenance of regulatory and support function within the ecosystem services. The diversity of this group interferes positively in these functions, but is compromised by the alteration of the environmental quality. Therefore, an important step in elucidating the dynamics of the nutrient cycle and the implications of the decomposition process is to understand qualitatively how these insects respond to subtle variations in environmental quality. Thus, the objective of this study was to characterize the assemblage of dung beetles associated with carrion and dung in two areas, which differ in the degree of environmental disturbances within a remnant of the Atlantic Forest in southern Brazil. Simultaneously, we aimed at assessing the ecological function of removal, according to feeding behavior and functional guilds. We quantified the removal of swine carrion and domestic dog dung made by these assemblages, quantitatively describing the actions of tunnellers and rollers in the execution of these functions. In this study, we had two predictions—the first was that regardless of the resource offered, whether carrion or dung, communities would be less diverse in more disturbed environments, and the second prediction was that communities with less diversity would have their ecological function reduced.

Materials and Methods

Study Area

The study was conducted in the Municipal Park of Lagoa do Peri, MPLP (between 27° 42′30″ and 27° 46′30″ south latitude and between 48° 30′00″ and 48° 33′30″ west longitude), located in Florianopolis, Santa Catarina Island, SC, Brazil. The regions' climate has characteristics inherent to the Brazilian southern coastline, and according to the Köppen criteria, the climate classification is Cfa (humid subtropical climate), with no dry season and hot summers. Situated in the subtropical intermediate zone, the MPLP belongs to the humid mesothermal group "C," with an average monthly temperature of > 3 °C and <18 °C in the coldest months, and an average monthly temperature of > 22 °C in the hottest month (Santos et al. 1989).

The MPLP was created in 1981 (Lei Municipal number 1.828/81), regulated in 1982 (Decreto Municipal number 091/82), and administrated by the Municipal Foundation of the Florianopolis Environment (Fundação Municipal do Meio Ambiente de Florianópolis [FLORAM]), possessing around 20 km^2, which were zoned into the biological reserve area, cultural landscape area, and recreation area. The biological reserve area is home to a large remnant of Atlantic Forest with different stages of regeneration, and hilltops are still home to primary forest remnants. Agriculture and logging practices were common in the past and promoted intense deforestation in MPLP. However, owing to the reduction of these activities, the MPLP is now made up of a mosaic of forest in different stages of regeneration (Santos et al. 1989, Cardoso et al. 2008). In this study, two areas were chosen owing to the park's history—one area was located in the park's northern region (Area +P) and the other area in the park's southeastern region (Area −P)—the two areas are about 3 km apart and separated by a lagoon (for a map see Supp. Fig. 1 [online only]).

Environmental Characterization of the Study Areas

A characterization study was carried out to characterize the differences in environmental quality of the two areas investigated in August 2014. In this characterization, we included the floristic composition, the structural attributes of vegetation (tree height, basal area, canopy diameter, canopy length, crown percentage, and canopy cover), and some soil characteristics (percentage of exposed soil, percentage of litter, percentage of green cover, and soil penetrability). For this characterization, three 100-m^2 plots were established ~200 m apart within each area. Thus, 125 individual trees belonging to 40 species were registered, where both areas are found in the intermediate stages of regeneration, with some species indicating advanced regeneration stages (Conselho Nacional do Meio Ambiente [CONAMA] number 4/94). In Area +P, 23 tree species were found, 14 of which were unique and 11 species made up >70% of the importance value index (IVI). In Area −P, 27 tree species were found, of which 16 were unique and nine species were responsible for >62% of the IVI. Ten species were common to both areas; however, only three (*Pera glabrata*, *Casearia sylvestris*, and *Machaerium stipitatum*) presented an IVI >10% in both areas (for tree species list see Supp. Table 1 [online only]). Therefore, these assemblages are different in species composition, which was confirmed by the 25% similarity value, measured using the Jaccard similarity index.

With regards to structural parameters of the vegetation and soil, the percentage of canopy and canopy cover were greater in Area +P, and the percentage of leaf litter and soil penetration force were greater in Area −P (Figs. 1 and 2). The field data combined with the history of use of these two areas permitted the classification of Area +P as an area more preserved, with a lower degree of environmental disturbance.

Table 1. Necrophagous and coprophagous dung beetle species collected from two areas of Atlantic Forest with different environmental disturbances on the Island of Santa Catarina, Florianópolis, SC, Brazil, during summer of 2013 and 2014: Area +P area more preserved; Area −P area with a higher degree of environmental disturbance

Behavior—species	Biomass (g)[a]	Size (mm)[a]	Necrophagous			Coprophagous			Total
			Area +P	Area −P	Total	Area +P	Area −P	Total	
Tunnellers									
Canthidium aff. *trinodosum* (Boheman, 1858)	0.012 (±0.004)	2.8 (±0.7)	2	1	**3**	2	3	**5**	**8**
Coprophanaeus saphirinus (Sturm, 1826)	0.856 (±0.228)	17.6 (±2.2)	17	5	**22**	2	0	**2**	**24**
Dichotomius sericeus (Harold, 1867)	0.341 (±0.084)	12.4 (±1.1)	72	123	**195**	205	259	**464**	**659**
Phanaeus splendidulus (F., 1781)	0.434 (±0.088)	16.1 (±0.5)	0	0	**0**	5	0	**5**	**5**
Uroxys sp.	0.006 (±0.002)	2.0 (±0.1)	0	1	**1**	9	62	**71**	**72**
Rollers									
Canthon luctuosus (Harold, 1868)	0.042 (±0.007)	5.4 (±0.4)	5	0	**5**	1	0	**1**	**6**
Canthon rutilans cyanescens (Harold, 1868)	0.137 (±0.035)	9.0 (±0.8)	13	8	**21**	152	114	**266**	**287**
Deltochilum morbillosum Burmeister, 1848	0.208 ((±0.034)	9.6 (±0.7)	18	0	**18**	0	0	**0**	**18**
Deltochilum multicolor Balthasar, 1939	0.469 (±0.067)	13.7 (±1.1)	37	62	**99**	0	2	**2**	**101**
Deltochilum rubripenne (Gory, 1831)	0.296 (±0.042)	11.9 (±0.9)	21	0	**21**	0	0	**0**	**21**
Dweller									
Eurysternus parallelus Laporte, 1840	0.155 (±0.198)	7.5 (±6.6)	0	0	**0**	4	5	**9**	**9**
Abundance			**185**	**200**	**385**	**380**	**445**	**825**	**1210**
Richness			**8**	**6**	**9**	**8**	**6**	**9**	**11**

[a] Biomass and average individual length (±SD).

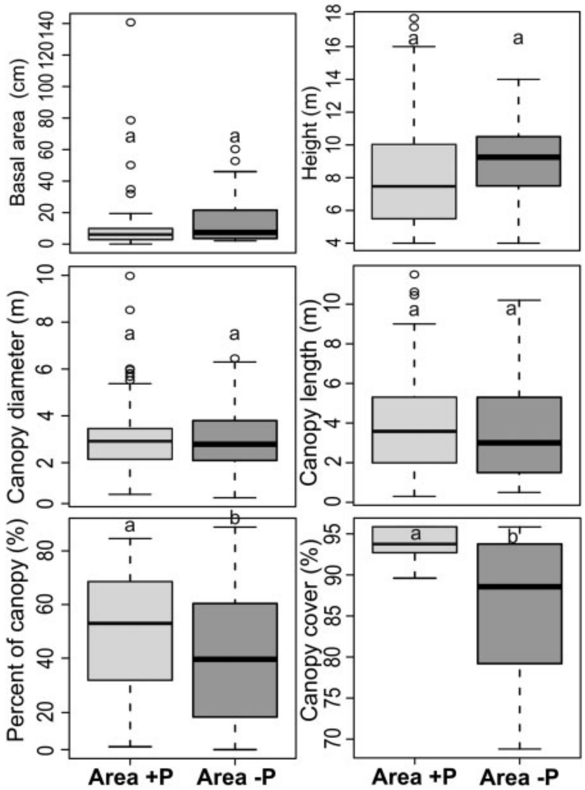

Fig. 1. Structural attributes of the vegetation in two Atlantic Forest areas with different degrees of environmental disturbances, Island of Santa Catarina, Florianopolis, Brazil. Area +P, area with a lower degree of environmental disturbance; Area −P, area with greater degree of environmental disturbance. Different letters indicate significant differences ($P < 0.05$).

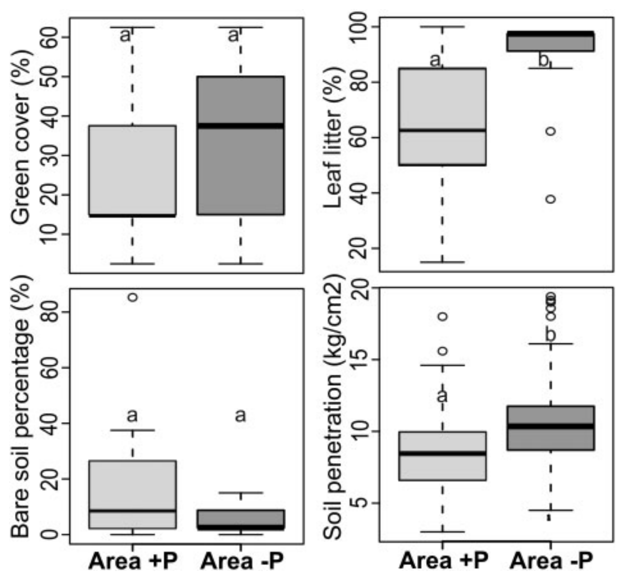

Fig. 2. Soil attributes in two Atlantic Forest areas with different degrees of environmental disturbances, Island of Santa Catarina, Florianopolis, Brazil. Area +P, area with a lower degree of environmental disturbance; Area −P, area with greater degree of environmental disturbance. Different letters indicate significant differences ($P < 0.05$).

Area −P, as it was more open, had more compacted soil, and is used more intensely by tourists in relation to Area +P, was classified as an area with a higher degree of environmental disturbance, and thus, a lower environmental quality.

Scarabaeinae Collection and Carrion and Dung Removal Data

In each area, eight sampling points were established that functioned as replicates separated by ∼100 m. For each sampling point, three collection and removal assessment arenas were installed, separated by 10 m. For each sampling point, one of the three arenas was the control, differing from the others because its opening was sealed with vole tissue to prohibit access to the insects. The data from the other two arenas effectively assessed were added, increasing the sampling quality. The collection and assessment arena consisted of a 1.5-liter plastic pot buried and filled with sifted soil up to ∼5 cm from the edge; this margin served to retain the allocated material and the telecoprids within the arena. To protect each arena from the rain, a plastic cover was suspended over each arena, and to avoid the action of vertebrates, a wire mesh with a 10- by 10-cm opening surrounded each arena (Supp. Fig. 2A [online only]).

The experiments for capturing necrophagous dung beetles (attracted by carrion) and evaluation of removal were conducted simultaneously using 50 g of rotting swine meat in each arena in November and December 2013. After that, at the same points in January 2014, the capture of coprophagous dung beetles (attracted by dung) and removal evaluation was conducted using 50 g of domestic dog dung per arena, which was previously stained with an odorless edible liquid blue dye (40 ml/kg; Supp. Fig. 2B [online only]). This technique, which does not interfere with the attraction of dung beetles nor in its manipulation of the offered resource (Batilani-Filho and Hernández 2016), was used to facilitate the quantification of dung removed by different functional guilds. The dung is more easily confused with the soil, especially omnivore dung that has a similar brown, beige, yellowish coloration. The carrion, owing to its texture and fragment size processed by the beetles (usually seen by the naked eye), does not mix easily with the soil within 48 h and therefore can be found more easily without the need for staining. The domestic dog dung was used as an easy-to-obtain resource and has high attractiveness, similar in attraction efficiency to capture dung beetles compared with native omnivorous mammalian resources. In both cases (carrion or dung), the baited arenas were exposed in the field for 48 h, then the dung beetles within each arena were collected, identified, and the average weight and size were measured for the living organisms. Afterwards, the collected organisms were sent to the Laboratory of Terrestrial Animal Ecology (LECOTA) at UFSC.

At the end of the 48 h of the field experiment, to obtain the removal data, the remaining resource was separated and weighed into three categories: 1) surface or unused resource, weight that was subtracted from the initial amount (50 g per arena) to obtain the amount in grams of the resource removed; 2) allocated or removed by rollers, which consisted of balls made with the resource and buried or retained in the protection margin of the arenas; and 3) allocated or removed by tunnellers, which corresponded to the amorphous material buried in subterranean galleries. These three categories were applied in the quantification of the removal of the two resources, carrion and dung. Despite the presence of beetles from the dweller guild, their role in removal was not measured because they feed directly on the resource with not reallocation. These three categories had their values corrected by subtracting the value lost in the control arenas that were simultaneously exposed at each of the sampling points.

Data Analysis

In each area, the unit analyzed was each sampling point ($n = 8$ per area), so resource removal and dung beetle data from the two arenas at each point were combined. Assemblage and removal data were compared between areas separately for the necrophagous dung beetles assemblage (defined as the dung beetle species attracted to swine carrion) and the coprophagous dung beetles assemblage (defined as the dung beetle species attracted to domestic dog dung), as well as carrion and dung removal. For each area, the observed species richness was recorded, and to verify the sampling efficiency of the collections, we made a relation percentage with the estimated richness using the estimators ACE and Chao 1, taking into consideration the abundance of species (Magurran 2004, Colwell et al. 2012).

Table 2. Ecological attributes of necrophagous and coprophagous dung beetle assemblages in two areas of Atlantic Forest with different environmental disturbances on the Island of Santa Catarina, Florianópolis, SC, Brazil

Assemblage ecological measures	Necrophagous		Coprophagous	
	Area +P	Area −P	Area +P	Area −P
Richness	8	6	8	6
Abundance	185	200	380	445
Total biomass	71.4	76.9	95.6	101.8
Richness estimators				
ACE	8.0	6.0	8,0	8.2
Chao1	8.0	6.0	8,0	7.0

The richness, abundance, and biomass (average of three repetitions of the individual wet weight of each organism obtained with a precision scale) of dung beetles were compared between the areas through a *t*-test. Subsequently, to compare these attributes, i.e., richness, abundance, and biomass between functional guilds and between areas, a two-way ANOVA with a post hoc pairwise Tukey test was applied (Crawley 2007), where area and functional guilds were the factors. Abundance and biomass data of coprophagous beetles were transformed with log $x + 1$, and necrophagous beetle data were not transformed. To compare community structure between areas, species abundance and biomass were square root transformed, and an ANOSIM test was conducted from a Bray–Curtis distance matrix (Clarke 1993, Warton et al. 2012).

Resource removal (carrion or dung) by each assemblage (necrophagous or coprophagous dung beetle community) was compared between areas through a *t*-test. Additionally, a two-way ANOVA with a post hoc pairwise Tukey test was used to compare relocated resource between functional guilds and areas (Crawley 2007). To assess which assemblage attributes are more important for resource removal, we used species richness, abundance, and biomass as predictor variables, and their independent effects on resource removal were obtained through a hierarchical partition analysis (Chevan and Sutherland 1991). The same procedure was adopted to verify how the different functional guilds affect resource removal, using richness, abundance, and biomass of tunnellers and rollers as predictor variables, and again their independent effects on this function were obtained through hierarchical partitioning. In both cases, the models were evaluated based on R^2_{dev}, and the significance of the effect of each predictor variable was obtained through a randomization test with 999 iterations (Mac Nally 2000, 2002; Braga et al. 2013).

All analyses were performed using R 3.0.1 (R Core Team 2014) with the packages *vegan* (Oksanen et al. 2013) and *hier.part* (Walsh and Mac Nally 2013), and when needed, residuals were evaluated for normality and homoscedasticity (Crawley 2007).

Results

Structure and Ecological Attributes of the Dung Beetle Assemblage

In total, 1,210 dung beetles from 11 species were collected—five tunneller, five roller, and one dweller species (Table 1). Only the area with a lower degree of disturbance had unique species, which were *Canthon luctuosus* (Harold, 1868); *Deltochilum morbillosum* Burmeister, 1848; *Deltochilum rubripenne* (Gory, 1831); and *Phanaeus splendidulus* (F., 1781). The total observed species

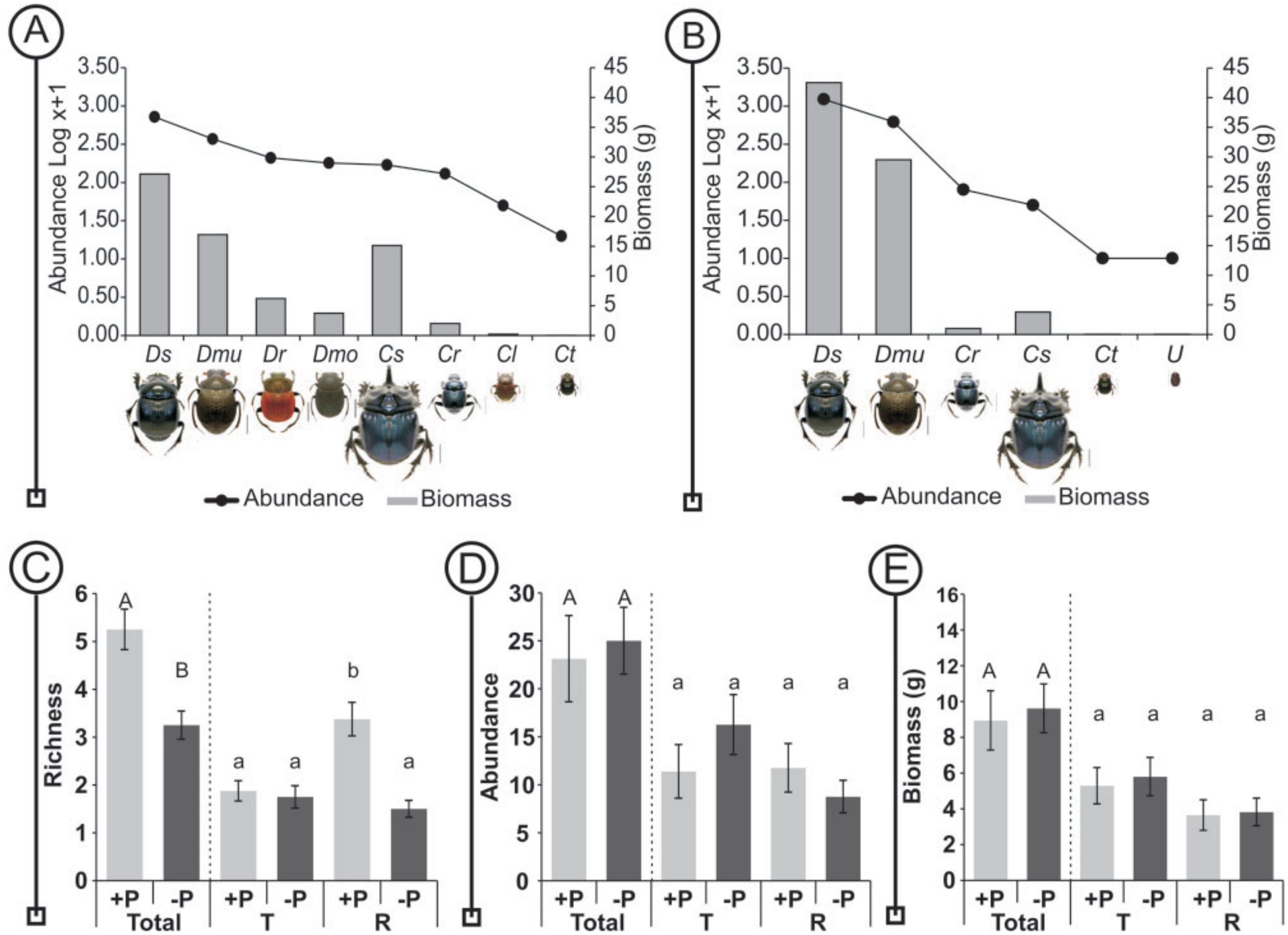

Fig. 3. Abundance distribution (log x + 1) and total biomass (g) of necrophagous dung beetle species in two Atlantic Forest areas with different degrees of environmental disturbances, Island of Santa Catarina, Florianópolis, Brazil. (**A**) +P, most preserved area; (**B**) –P, most disturbed area; Ct, *Canthidium* aff. *trinodosum*; Cl, *Canthon luctuosus*; Cr, *Canthon rutilans cyanescens*; Cs, *Coprophanaeus saphirinus*; Dmo, *Deltochilum morbillosum*; Dmu, *Deltochilum multicolor*; Dr, *Deltochilum rubripenne*; Ds, *Dichotomius sericeus*; and U, *Uroxys* sp. Average (**C**) richness, (**D**) abundance, and (**E**) biomass per sampling point (±SD) for the same necrophagous dung beetle assemblage; T, tunneller; and R, roller.

richness was greater in the less disturbed area, both for dung beetles attracted to carrion (Area +P: S = 8; $N = 185$; Area –P: S = 6; $N = 200$), and dung (Area +P: S = 8; $N = 380$; Area –P: S = 6; $N = 445$; Table 1). In the necrophagous dung beetle assemblage, the number of observed species, in both study areas, was 100% of that estimated by ACE and Chao 1 richness estimators. In the coprophagous dung beetle assemblage, sampling efficiency was 100% in the least disturbed area, and 75% (ACE) and 86% (Chao 1) in the area with greater disturbance. Thus, it is estimated that the area with a lower degree of disturbance had two necrophagous species and one coprophagous species more than the area with a higher degree of environmental disturbances (Table 2).

The necrophagous dung beetle assemblage was dominated by *Dichotomius sericeus* (Harold, 1867) (40%), *Deltochilum multicolor* Balthasar, 1939 (20%), *Deltochilum rubripenne* (Gory, 1831) (11%), *D. morbillosum* (10%), and *Coprophanaeus saphirinus* (Sturm, 1826) (9%) in the area with lower degree of environmental disturbance (Fig. 3A). In the area with higher degree of disturbance, only *D. sericeus* (61%) and *D. multicolor* (31%) were dominant in terms of number of individuals, and represented 96.7% of the total assemblage biomass in this area (Fig. 3B). Thus, there were significant differences in assemblage structure between the study areas when abundance was taken into account (ANOSIM, $R = 0.310$; $P < 0.05$), as well as when biomass was considered (ANOSIM, $R = 0.26$; $P < 0.05$). Average species richness was significantly higher in the area with the least degree of environmental disturbance; the necrophagous dung beetle community had higher richness per sampling point in relation to the area with higher degree of disturbance ($t = 3.62$; $P < 0.01$; Fig. 3C). This difference was owing to the contribution of rollers that showed, on an average, more species in the less disturbed area ($F = 10.55$; df = 1; $P < 0.01$; Fig. 3C). There were no significant differences between areas for either abundance ($t = 0.30$; $P = 0.76$; Fig. 3D) or biomass ($t = 0.30$; $P = 0.77$; Fig.3E), and the same results were observed for functional guilds (abundance: $F = 2.02$; df = 1; $P = 0.16$; Fig. 3D and biomass: $F = 0.03$; df = 1; $P = 0.86$; Fig. 3E).

The coprophagous dung beetle assemblage was dominated by *D. sericeus* representing 54% of individuals in the least disturbed area and 58% in the disturbed area, and *C. rutilans* with 40% and 25% of individuals in least and most disturbed area, respectively (Fig. 4A, B). Thus, the coprophagous dung beetle assemblage structure was similar between areas in terms of both abundance (ANOSIM, $R = 0.01$; $P = 0.36$) and biomass (ANOSIM, $R = 0.03$; $P = 0.33$). Average species richness attracted to dung was similar in the areas, with no significant difference between them ($t = 0.44$; $P = 0.66$; Fig. 4C). In addition, no significant differences were found between

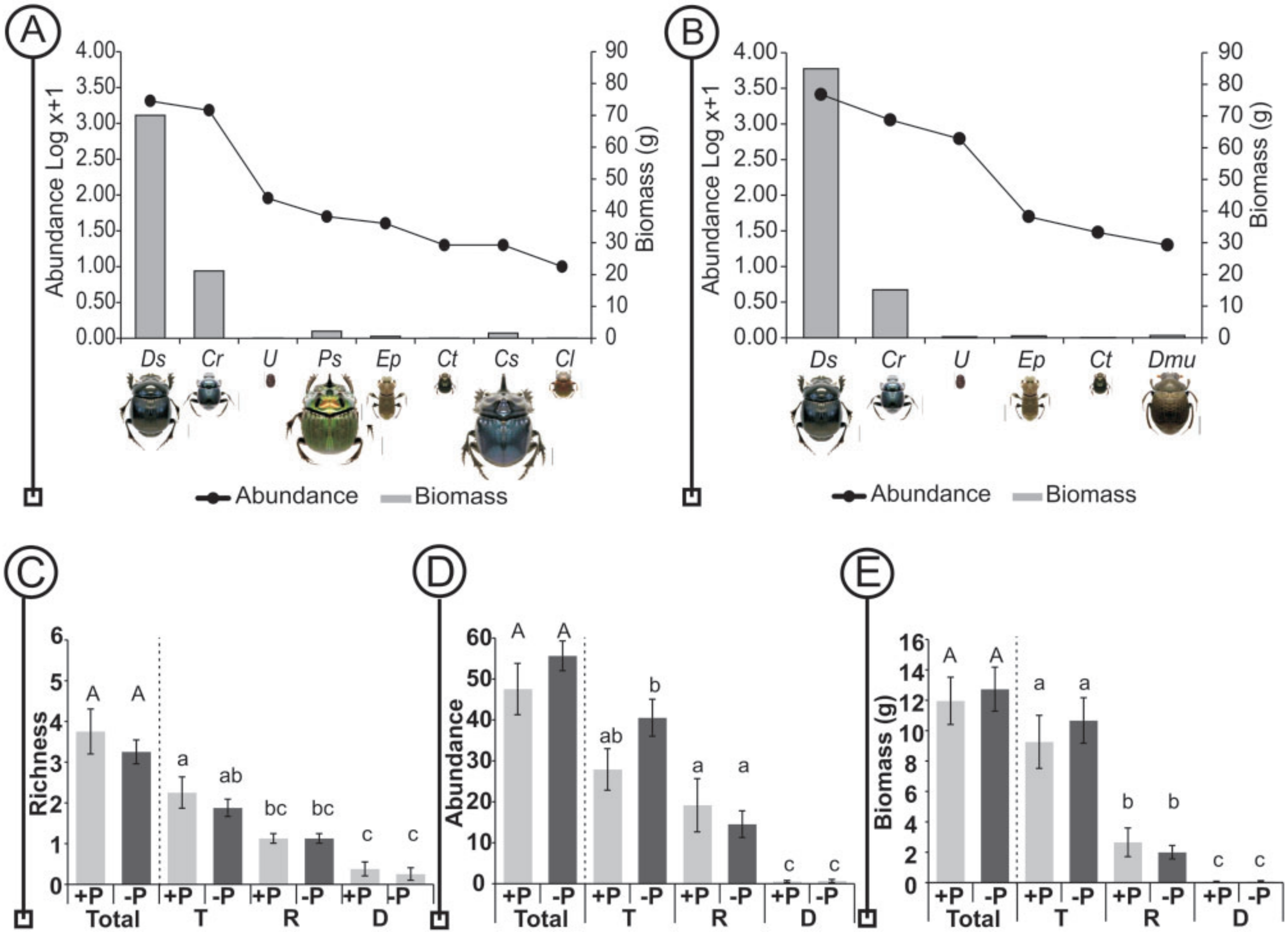

Fig. 4. Abundance distribution (log x + 1) and biomass (g) of coprophagous dung beetle species in two Atlantic Forest areas with different degrees of environmental disturbance, Santa Catarina Island, Florianópolis, Brazil. (**A**) +P, most preserved area; (**B**) −P, most disturbed area; Ct, *Canthidium* aff. *trinodosum*; Cl, *Canthon luctuosus*; Cr, *Canthon rutilans cyanescens*; Cs, *Coprophanaeus saphirinus*; Dmu, *Deltochilum multicolor*; Ds, *Dichotomius sericeus*; Ep, *Eurysternus parallelus*; Ps, *Phanaeus splendidulus*; and U, *Uroxys* sp. Average (**C**) richness, (**D**) abundance, and (**E**) biomass per sampling point (±SD) for the same coprophagous dung beetle assemblage; T—tunneller; R—roller; and D—dweller.

areas for either abundance ($t = 1.01$; $P = 0.33$; Fig. 4D) or biomass ($t = 0.22$; $P = 0.82$; Fig. 4E). Contrary to what happened with the necrophagous dung beetle assemblage, the average species richness of tunnellers attracted to dung was greater than that of the other functional guilds ($F = 29.45$; df = 2; $P < 0.01$; Fig. 4C). Tunnellers had also higher average abundance than other functional guilds, especially in the area with higher degree of disturbance ($F = 74.76$; df = 2; $P < 0.05$; Fig. 4D), and higher average biomass in both areas ($F = 86.90$; df = 2; $P < 0.05$; Fig. 4E).

Carrion and Dung Removal

Necrophagous dung beetles in the least disturbed area removed on an average 75.1 ± 24.6 g of carrion per sampling point, from a total of 100 g offered, which was twice the removal performed by the community in the most disturbed area, with an average of 39.6 ± 24.0 g of carrion removal per sampling point ($t = 2.92$; $P = 0.01$; Fig. 5A). Carrion removal was carried out mainly by tunnellers, with higher removal in the least preserved area, but the results were marginally nonsignificant ($t = 2.03$; $P = 0.06$; Fig. 5A). The difference between the total material removed and allocated by the tunnellers may be attributed to feeding and fragmentation of the resource, which is performed by insects of all guilds—the difference between the total removed and allocated by the functional guilds cannot be quantified owing to the particle size.

Dung removal was similar in both areas, with an average of 80.8 ± 10.7 g removed in the least disturbed area and an average of 81.5 ± 13.4 g removed in the most disturbed area ($t = 0.12$; $P = 0.90$) from a total of 100 g offered (Fig. 5B). Tunnellers relocated, on an average, 22.1 ± 19.9 g in the least disturbed areas and 26.1 ± 20.9 g in the most disturbed area, while rollers relocated on an average 13.0 ± 6.2 g and 12.5 ± 6.0 g, respectively. Thus, although there were no differences between areas in the amount of dung removed by each functional guild ($F = 0.11$; df = 1; $P = 0.74$), paracorpids removed more than double of dung compared with the rollers ($F = 4.53$; df = 1; $P = 0.04$; Fig. 5B). The interaction between the two factors, area and functional guild, was not significant ($F = 0.17$; df = 1; $P = 0.67$).

The hierarchical partition analysis showed that only a small part of the variation in carrion removal was explained by the measured community attributes ($R^2_{\text{dev}} = 0.07$), as well as functional guilds ($R^2_{\text{dev}} = 0.16$), and the effect of all these factors was not significant (Fig. 6A,B). Similarly, community attributes (richness, abundance, and biomass) did not significantly explain the variation in dung removal ($R^2_{\text{dev}} = 0.35$; Fig. 6C). However, roller abundance (34.2%) and biomass (29.2%) have the largest independent effects on dung

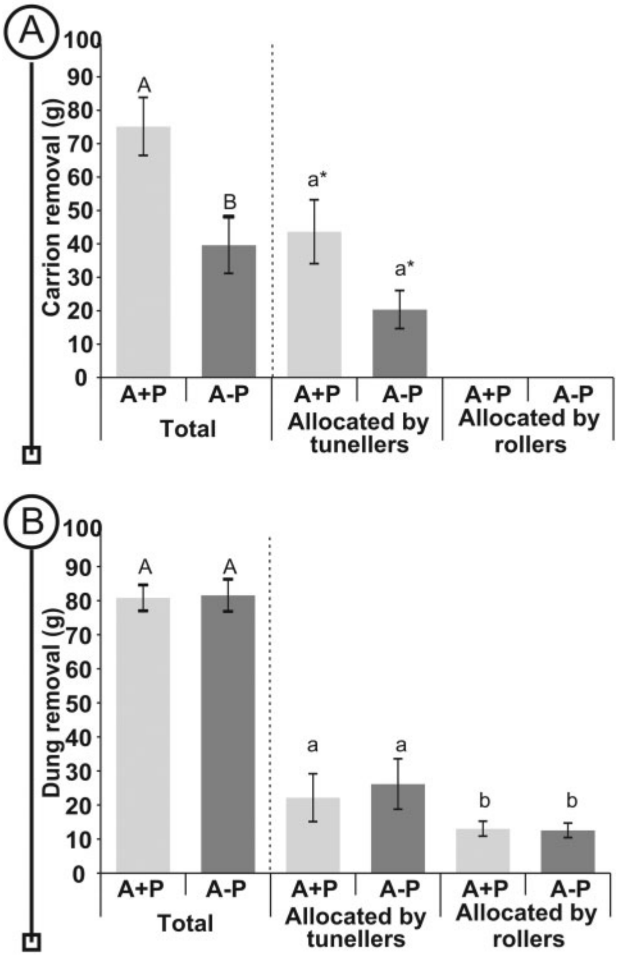

Fig. 5. (**A**) Carrion and (**B**) dung removal per sampling point (average ± SD) in two Atlantic Forest areas with different degrees of environmental disturbance, Santa Catarina Island, Florianópolis, Brazil. A + P, most preserved area; A−P, most disturbed area. Letters indicate significant differences, uppercase to evaluate removal and lowercase for evaluation of carrion relocation by different functional guilds.*Marginally nonsignificant ($P = 0.06$).

removal, having a positive and significant effect on this function ($R^2_{\text{dev}} = 0.72$; $P < 0.05$; Fig. 6D).

Discussion

Studies assessing the removal of both carrion and dung, as the one presented here, are the basis for understanding aspects of decomposition and nutrient cycling of animal-derived organic matter in forest ecosystems. Moreover, elucidating which ecological characteristics of dung beetle assemblage and functional guilds are important for the execution of those ecological functions can help in conservation strategies. This type of information indicates the capacity of key elements, such as the dung beetles, in the maintenance of ecosystem services. Our results reveal the elevated functional capacity of dung beetles, mainly the coprophagous dung beetles function in regulation and support of ecosystem services, as in 48 h and independent of environmental quality, these insects removed almost all the offered resources (80%). The removal of carcass was influenced by subtle differences in environmental disturbance of the areas; however, in the least disturbed environment, the necrophagous dung beetles had the same performance as the coprophagous dung beetles (75% of the offered resources in 48 h). These data are especially important in Atlantic forest environments that are in conservation or regeneration, because when dung beetles bury carrion and dung, they contribute significantly to the transfer of nutrients to the soil. This transfer of nutrients is owing to the fragmentation of the resource carried out by the beetles, which promotes soil microbial activity increasing nutrient availability for plant uptake (Galbiati et al. 1995, Hanafy 2012), performs biological control and soil aeration (Braga et al. 2012, 2013), as well as secondary seed dispersal, which can contribute to a seedlings successful reproduction (Vulinec 2002, Andresen 2003, Nichols et al. 2008), and consequently, to the regeneration of environments.

Our study demonstrates that changes in environmental disturbance have differentiated implications on species that use different resources. Thus, the function of carrion removal is more compromised with environmental changes than that of dung removal, owing to a loss of species and structural changes in necrophagous dung beetle assemblage. In the most disturbed area, not only were there fewer species, but it also showed an accentuated pattern of dominance, which was reflected in the lower removal of carcass (39.6%) in relation to the less disturbed area (75.1%). According to the theory of redundancy, loss of some species would not compromise the functioning of the ecosystems owing to the existence of more than one species performing the same ecological role (Walker 1992, Lawton and Brown 1993). In dung and carcass removal studies, Amézquita and Favila (2010, 2011) observed that the loss of some species was offset by an increase in abundance and biomass of other species. Thus, owing to functional redundancy, even with reduced species richness, the rate of dung removal was similar between research areas, as there were no differences in abundance or total biomass of dung beetles. Other studies also suggest that this mechanism, which compensates in abundance and biomass with the loss of some species, may be able to maintain decomposition rates and therefore not changing the functioning of the ecosystem (Rosenlew and Roslin 2008). However, our results show that this compensation in abundance and biomass is not effective enough in degraded areas of the Atlantic Forest, and the loss of some necrophagous roller species changed the community structure and significantly compromised the removal of carrion in the most disturbed area.

The coprophagous dung beetle assemblage and the removal of dung were similar between investigated areas, as even with lower tunneller richness in the most disturbed area, both abundance and total biomass of the assemblage were similar. This dynamic suggests that when the absence of other species does not result in a structural difference between communities, the compensation mechanism becomes relevant (Amézquita and Favila 2010, 2011). These differences in food resource removal between necrophagous and coprophagous dung beetles suggest that assemblages respond differently to environmental changes and different factors constrain the communities (Amézquita and Favila 2011, Dangles et al. 2012). The greater sensitivity of necrophagous dung beetles was also reported in other removal studies (Klein 1989, Horgan 2008, Dangles et al. 2012), and may be related to the transience and unpredictability of this type of resource in relation to dung, as the defecation pattern of vertebrates may be more predictable in space and time (Amézquita and Favila 2011). On the other hand, coprophagous dung beetles and dung removal show more pronounced responses in the extremes of altered gradients or environmental quality (Klein 1989, Andresen 2003, Anduaga 2004, Amézquita and Favila 2010, Braga et al. 2013).

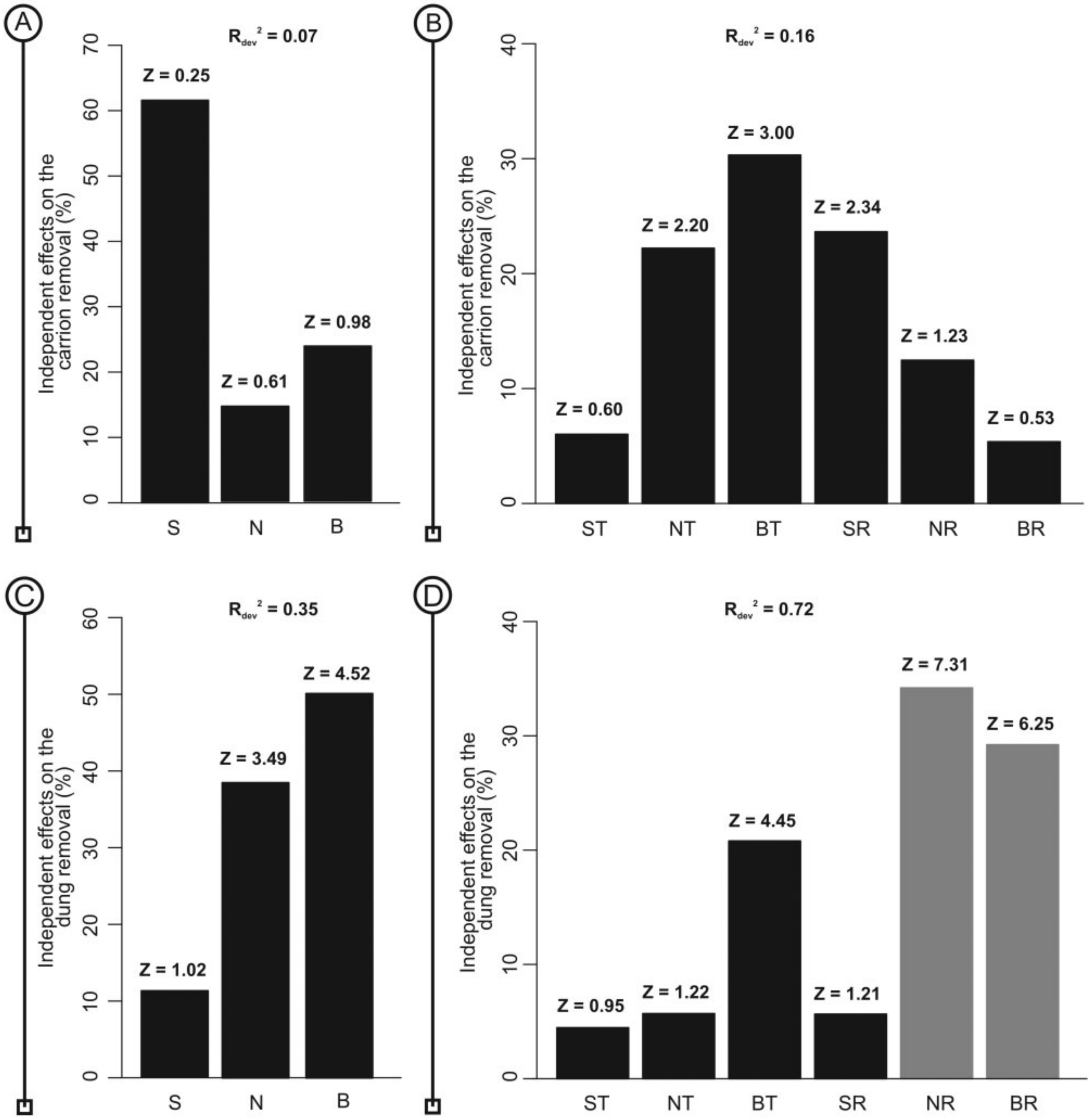

Fig. 6. Hierarchical partitioning analysis for variation of removal with: (**A**, **C**) percentage distribution of the independent effects of the community's structural attributes, (**B**) functional guilds of necrophagous dung beetles, and (**D**) functional guilds of coprophagous dung beetles. Gray bars represent significant effects on structural attributes ($P < 0.05$); R^2_{dev} is the total variation in data explained by the model; S—richness; N—abundance; B—biomass; ST—tunneller richness; NT—tunneller abundance; BT—tunneller biomass; SR—roller richness; NR—roller abundance; and BR—roller biomass.

While breaking down the dung beetle assemblage and analyzing ecological attributes of functional guilds in our hierarchical partitioning models, we were able to get a good representation of variation in dung removal (72%), and roller abundance and biomass were significant variables in this function. The rollers, especially diurnal rollers, such as *Canthon rutilans cyanescens* (Harold 1868), a dominant species in the coprophagous dung beetle assemblage in this study, belongs to the functional group least efficient in removal (Slade et al. 2007). However, the maximum capacity of this function is observed when various functional groups act together (Slade et al. 2007, Dangles et al. 2012). Furthermore, when the total biomass of small beetles is similar to larger beetles, it is possible to observe the same removal capacity, and when these small beetles are abundant, the capacity of removal is increased (Dangles et al. 2012). These observations explain the importance of abundance and biomass of rollers in the hierarchical partitioning model. This also suggests that other characteristics of the species, in addition to body size and functional guild, may positively influence removal capacity (Nervo et al. 2014).

As for tunneller insects, these were the ones who most allocated the resource in both areas, and dung beetles with this behavior are commonly reported as the most efficient in this function

(Andresen 2003; Anduaga 2004; Slade et al. 2007; Amézquita and Favila 2010, 2011; Dangles et al.2012; Braga et al. 2013; Nervo et al. 2014). Even though only the ecological attributes of the rollers were identified as relevant in removal, it is important to note that tunnellers are more efficient in soil aeration and secondary seed dispersal (Vulinec 2002, Andresen 2003, Braga et al. 2012), functions which are associated with removal but are not executed similarly when equivalent biomass and abundance are observed (Vulinec 2002, Slade et al. 2007, Braga et al. 2013). Therefore, the complementarity between functional guilds and species is necessary to maintain all the ecological functions linked to dung beetles.

The species of dung beetles have different periods of activity (Hernández 2002), and when the resource is placed during the day, as was done in our study, the diurnal species may benefit (Amézquita and Favila 2011). However, the rollers dung beetles represented by the dominant species *C. rutilans*, a diurnal species, relocated less than the tunnellers, which were represented by the dominant species *D. sericeus* (Harold, 1867), a nocturnal species. The least amount of dung relocated by the rollers may occur owing to nonexclusive factors: because they have lower total biomass, and biomass in this group significantly increase removal rates; because they are slower than tunnellers in using resources (Andresen 2003, Anduaga 2004) owing to time spent in possible combats and other type of interactions at the dung deposit during the resource relocation (Favila 1988, Chamorro-Florescano and Favila 2008, Chamorro-Florescano et al. 2011). Even though they allocate less dung and do not allocate carcass, the rollers assist in the removal while feeding and fragmenting these resources. This fragmentation, which is part of the resource readily available in smaller particles in soil and is carried out by all the guilds, may be observed in the difference between total removed by the assemblage and the allocated material.

The results of the study show partial agreement with our predictions, as only the necrophagous dung beetles were sensitive to subtle differences in habitat quality, displaying a loss in diversity that compromised the removal of carrion. In addition, we can conclude that within the coprophagous dung beetles, rollers abundance and biomass are the most important attributes for dung removal, although in both cases—removal of carrion or dung—tunnellers relocated more material in the soil.

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