



Tree retention in cattle ranching systems partially preserves dung beetle diversity and functional groups in the semideciduous Atlantic forest: The role of microclimate and soil conditions

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Received 27 February 2018; accepted 8 October 2018
Available online 15 October 2018

Abstract

The disturbance of natural environments affects, among others, the diversity of dung beetle assemblages, which could have serious consequences for the ecological processes regulated by these insects. The objective of this study was to evaluate and compare species diversity and functional groups of dung beetle assemblages both in the native forest and in three livestock systems that differed in their structure and composition of vegetation: a livestock system with native trees, a livestock system with exotic trees (*Pinus taeda*), and traditional open pastures, in the semideciduous Atlantic forest of Argentina, in an area previously covered by continuous forest and currently with a heterogeneous landscape of native forest and different land uses. Pitfall traps baited with cow dung were used in the natural forests and the livestock systems studied. A total of 2461 beetles belonging to 38 species were captured. Treed livestock systems showed the highest species richness (⁰D) and diversity (¹D and ²D). Twelve functional groups were identified. The native forest showed the highest functional group richness, while open pastures had the lowest. In general, livestock systems showed a low proportional abundance of telecoprid, diurnal and large beetles. Microclimate (average temperature and humidity) and soil conditions (soil composition: sandy or clayey) were closely associated with the species and functional group composition. Results confirm that cattle ranching with tree retention preserves dung beetle diversity, and suggest that cattle systems without canopy cover have higher impact (negative effects) than silvopastoral systems on both species and functional groups.

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Keywords: Livestock management; Silvopastoral; Exotic trees; *Pinus*

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Introduction

In the last decade, more than 7 million hectares of tropical and subtropical forests have been lost, mostly replaced by agricultural areas (FAO 2016). Currently, livestock ranching occupies 80% of those agricultural land areas worldwide and constitutes one of the main causes of deforestation and biodiversity loss (FAO 2016). One of the direct consequences of cattle raising is the large accumulation of organic matter on the soil surface, since each individual cow produces approximately 9000 kg of feces/year (Losey & Vaughan 2006). The incorporation of cow dung into the soil depends on abiotic factors (such as temperature, rainfall, humidity, soil compaction, etc.) and on the activity of several dung-burying invertebrates, including dung beetles, termites, ants and worms (Riutta et al. 2012). Consequently, the conservation of dung burying animal communities in cattle-raising areas is a key component of the ecological and economic sustainability of cattle production.

Dung beetles (Coleoptera: *Scarabaeinae*) are one of the most diverse and most studied insect taxa worldwide. The dung beetle burial activity improves the soil structure and fertility, decreases parasite incidence, and cleans pasture surface in livestock areas (Nichols et al. 2008). In the last decades, several studies in tropical and subtropical areas have focused on the consequences of forest replacement on dung beetle abundance and diversity, with particular emphasis on cattle systems (Rodríguez, Uchoa, & Ide 2013; Gómez-Cifuentes, Munevar, Giménez, Gatti, & Zurita 2017). Although land use effects on the diversity of dung beetle assemblages depend on the regional context (Escobar, Halffter, & Arellano 2007; Tocco et al. 2013), most previous studies in Neotropical forests have shown that traditional livestock systems (open pastures without trees) have a negative influence on the abundance and richness of dung beetle communities. In contrast, cattle systems retaining a partial tree cover (silvopastoral) show higher richness of the dung beetle community and similarity to that of the native forest (Giraldo, Escobar, Chara, & Calle 2011; Montoya-Molina et al. 2016). Differences between open and silvopastoral cattle systems are probably related to changes in microclimatic and soil conditions (Davis, Van Aarde, Scholtz, & Delpont 2003). In addition, the structure and composition of the canopy and understory vegetation in different silvopastoral systems (native or exotic) influence the diversity of dung beetles (Arellano, León-Córtés, Halffter, & Montero 2013). Forest dung beetles are particularly sensitive to the high temperatures of open pastures (Kenyon, Mayfield, Monteith, & Menéndez 2016). Also, soil compaction and changes in soil properties (pH, organic carbon, etc.) reduce the ability of dung beetles to bury dung and complete their life cycle (Bourg, Escobar, MacGregor-Fors, & Moreno 2016). Additionally, ant parasitic products, extensively used in livestock areas (mainly ivermectin), have a negative influence on dung beetle diversity (Verdú et al. 2018).

While a taxonomic approach to the study of human disturbance on biological communities provides valuable information (richness and composition), the analysis of functional groups, based on species traits (size, foraging strategy, etc.), is more useful to make a direct link between changes in species diversity and ecosystem functioning (Slade, Mann, Villanueva, & Lewis 2007; Nichols et al. 2013) and productivity (Anduaga & Huerta 2007; Lopez-Collado, Cruz-Rosales, Vilaboia-Arroniz, Martínez-Morales, & Gonzalez-Hernandez 2017). Previous studies in livestock systems focusing on functional diversity have shown a loss of functional richness as a consequence of a non-random pattern of species loss according to specific traits (Barragán, Moreno, Escobar, Halffter, & Navarrete 2011; Gómez-Cifuentes et al. 2017).

The aim of this study was to evaluate the potential of livestock areas differing in tree retention (i—with native trees, ii—with exotic trees (*Pinus taeda*), and iii—with traditional open pastures) to preserve the native forest dung beetle taxonomic and functional diversity in the semideciduous Atlantic forest of Argentina. The objectives were: 1) to assess changes in species diversity, species abundance, and composition of both species and functional groups in the different habitats; 2) to relate those changes to microclimatic conditions and soil properties; 3) to identify the species and functional groups that relate to each habitat type. The hypothesis was that livestock systems preserving microclimatic and soil conditions similar to those of the native forest would preserve the native dung beetle species and functional group diversity and that open areas would show a reduction in both species and functional group diversity.

Materials and methods

Study area

This study was carried out in the semideciduous Atlantic forest of Argentina (Fig. 1), one of the most diverse and threatened ecosystems worldwide (Galindo-Leal & de Gusmão Câmara 2003). The study area is located in the subtropical region of the Atlantic forest, and is characterized by a warm climate with temperatures above 20 °C and a cold season between June and August. The humidity is high most of the year, with an average annual rainfall of 2000 mm (Oliveira-Filho & Fontes 2000). The study area extends over approximately 1800 km² and includes heterogeneous landscapes with family farms (25–200 ha) with small pine plantations (mainly *P. taeda*) and annual crops such as corn (*Zea mays*), livestock systems, or plantations of tobacco (*Nicotiana tabacum*) or Yerba mate (*Ilex paraguariensis*) (Izquierdo, De Angelo, & Aide 2008). Also, large areas of native forest in continuous protected areas (Parque Nacional Iguazú, Parque Provincial Urugua-í, and Reserva Privada San Jorge) and forest fragments of different sizes are present in the study area (Izquierdo et al. 2008).

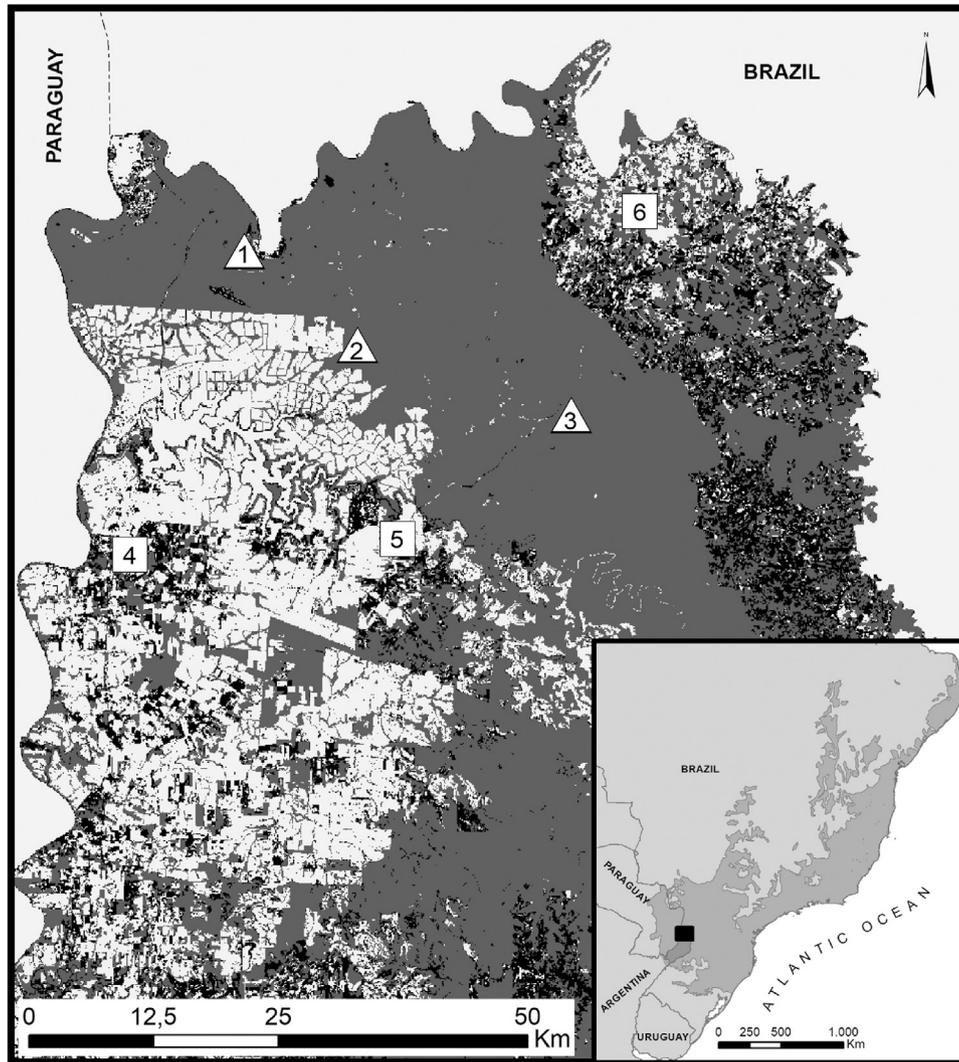


Fig. 1. Study area in the southern Atlantic forest of Argentina. In the main map, native forest remnants are shown in dark gray, agricultural areas in black, and sampling locations in white (squares: livestock systems; triangles: forest control sites). 1. Parque Nacional Iguazú. 2. Forestry company private reserve. 3. Parque Provincial Urugua-í. 4. Esperanza Centro. 5. Gobernador Lanusse. 6. Comandante Andresito. Modified from Zuleta et al. (2015). The inset shows the original distribution of the Atlantic forest ecosystem (dark gray).

Sampling design

Dung beetles were collected in the continuous native forest and three livestock systems: 1) livestock systems with native tree retention, 2) livestock systems with exotic 8- to 15-year-old pine trees (*P. taeda*), and 3) deforested open pastures without trees (OP). A more detailed description of the four habitat types studied is in Supplementary material (see Appendix A). Five replicates of each livestock system and the native forest were selected, separated by at least one kilometer to ensure spatial independence (20 sampling sites in total). Ivermectin and Cypermethrin are extensively used in all sampled areas and the most common cow races in the region are Brahman, Brangus, and Hereford.

To improve the regional representation, cattle system replicates were scattered in three localities separated by an average of 30 km: Esperanza Centro, Gobernador Lanusse,

and Comandante Andresito (see Appendix B: Table 1, Fig. 1). Native forest control sites were located in three sites within the region: Parque Nacional Iguazú, Parque Provincial Urugua-í and a forestry company private reserve (see Appendix B: Table 1, Fig. 1).

Dung beetle sampling

Taking into consideration phenological patterns of dung beetle abundance and composition and to increase the temporal representation of species, two independent dung beetle sampling periods were performed in summer (February) and spring (October) 2015, which are the seasons with highest dung beetle activity (Medina Hernández & Vaz-de-Mello 2009). To capture dung beetles in each of the 20 sampling sites, 10 pitfall traps baited with 100 g of fresh bovine feces (a mixture of different dung from each location) were installed

(200 pitfall traps by period, 400 in total). While the majority of previous studies with dung beetles have used human feces and rotten meat as the main bait (Bourg et al. 2016), in this study, we used bovine feces because the objective was to describe the sub-set of species potentially involved in the manipulation of bovine feces. Traps were separated by 50 m within each replicate and located at least 1 km from the nearest edge to reduce the influence of neighboring environments (Peyras, Vespa, Bellocq, & Zurita 2012). Traps consisted of a plastic container (12 cm in diameter and depth) filled with a solution of water, salt, and detergent to prevent beetles from decomposing (Beiroz et al. 2017). Traps remained open for eight consecutive days during each sampling period and beetles were collected and the bait renewed every 48 h. Captured individuals were preserved in alcohol (80%) and identified to species (or genus and morphospecies) level by using taxonomic keys (Vaz-De-Mello, Edmonds, Ocampo, & Schoolmeesters 2011), consultation with specialists (Dr. Fernando Vaz-de-Mello), and comparison with a reference collection (the entomological collection of the Instituto de Biología Subtropical, Puerto Iguazú, Misiones, Argentina (IBSI Sca)). All the individuals were then stored in this collection (IBSI Sca).

Canopy cover, microclimate and soil conditions

To estimate canopy coverage, we took three pictures (separated by 50 m) from two meters high. Then, vegetation coverage (canopy) was measured using Canopeo app (<http://www.canopeoapp.com>) for android mobiles. To describe the microclimatic conditions, automatic temperature and humidity sensors (HOBO Pro) were installed at ground level throughout the sampling period. The automatic sensors recorded both temperature and humidity every five minutes; daily values were then averaged for the complete sampling period (eight days) to obtain a single value per sampling site. To characterize the soil structure, a composed soil sample (three sub-samples) was collected on each replicate using a soil core sampler (5 cm in diameter and 10 cm in depth) down to 10 cm depth. Soil samples were analyzed at the laboratory to determine: (1) pH, (2) clay content, (3) sand content, (4) silt content, (5) organic carbon (6) relative humidity and (7) bulk density. All soil measures were performed using standard methodologies in Laboratorio de Suelos, Plantas y Ambiente, Universidad Nacional del Sur, Bahía Blanca, Argentina (see Appendix C in Supplementary material).

Estimation of species and functional trait diversity

As a first step prior to diversity analysis, we performed a two-way ANOVA to explore the influence of seasonality (February and October), habitat type, and their interaction on the taxonomic and functional diversity of dung beetles. To evaluate the efficiency of the sampling effort

and the representation of dung beetle communities in each habitat type, sampling completeness was estimated through coverage percentage (C.hat). The latter was used because the representativeness of a sample depends on the number of missing species and their average abundances, which implies a “fair” comparison between sampling sites (Moreno, Barragán, Pineda, & Pavon 2011). To describe and compare the taxonomic diversity of dung beetle assemblages between habitats, we estimated diversity profiles of order q based on the Hill series (0D , 1D and 2D) (Hill 1973), which represent the number of species (0D : species richness) and the number of equally common species, using the relative abundance values of all species, that are required to obtain the same Shannon index-value and Simpson index-value (1D : when all species have a weight proportional to their abundance; and 2D : when dominant species have more weight) (Moreno et al. 2011). Both sample coverage and diversity were estimated using the R-based interactive online version of the software iNEXT (Chao, Ma, & Hsieh 2017).

To estimate functional trait diversity, four traits related to organic matter manipulation were considered: (1) Food relocation (telecoprid, paracoprid and endocoprid species), (2) Daily activity (nocturnal, diurnal and continuous activity), (3) Diet (coprophagous, necrophagous and generalist species) and (4) Biomass (large and small species, based on dry weight) (see Appendix B: Table 2 in Supplementary material).

Data analysis

The canopy coverage (log transformed), microclimatic and soil conditions, alpha diversity, and total abundance and composition of dung beetle assemblages of the native forest and livestock systems were compared through ANOVA and DGC (Di Rienzo, Guzmán, Casanoves) post-hoc comparisons by using the *agricolae* package in R (Mendinburu 2017; R Core Team 2017). We used the DGC multiple comparisons method because this test controls type I error, while maintaining an acceptable statistical power (Di Rienzo, Guzmán, & Casanoves 2002). Species diversity profiles (Hill series: 0D , 1D and 2D) were compared through overlapping confident intervals (5–95%). Normality and homoscedasticity were tested through Shapiro–Wilks and Bartlett tests using the *stats* package (R Core Team 2018) in R (R Core Team 2017).

To compare species composition between habitats and to relate those changes to environmental conditions (soil and microclimate), we performed a multivariate redundancy analysis (RDA), based on the relative abundance of species and explanatory variables (microclimatic and soil conditions) by using the *vegan* package in R (R Core Team 2017; Oksanen et al. 2018). This analysis allowed grouping sampling sites with a similar dung beetle community. Prior to the RDA, a Hellinger transformation (the square root of relative abundance data or environmental variables) was applied to

Table 1. Environmental conditions associated with four habitats (three livestock systems and the native forest) in the southern Atlantic forest of Argentina. Livestock system with native trees (LN), livestock system with pine trees (LP), traditional open pastures (OP) and the native forest (NF). Df: degrees of freedom. TD: transformed data. ANOVA and DGC (Di Rienzo, Guzmán, Casanoves) post-hoc comparisons. Different letters indicate significant differences. p value significance: ** < 0.01. * < 0.05.

Environmental condition	Sites (Df = 3)	NF	LN	LP	OP
Canopy (%) ^{TD}	11.6**	71.9 a	65.2 a	61.4 a	0.0 b
Average temperature (°C)	7.2**	24.7 a	25.1 a	25.5 a	26.9 b
Average humidity (%)	27.9**	97.4 a	95.8 a	95.5 a	89.1 b
pH	1.6	5.8 a	5.5 a	4.9 a	5.1 a
Clay (%) ^{TD}	19.3**	10.4 a	21.1 b	22.0 b	50.9 c
Silt (%)	4.6*	47.6 a	55.8 a	39.0 b	33.1 b
Sand (%)	7.9**	41.5 a	28.7 a	38.9 a	14.4 b
Organic carbon (%)	2.4	3.7 a	3.0 a	2.1 a	3.0 a
Soil relative humidity (%)	1.2	0.3 a	0.3 a	0.3 a	0.3 a
Bulk density (g/m ²)	1.8	2.0 a	2.2 a	2.4 a	2.1 a

species abundance and explanatory variables to standardize data (Legendre & Gallagher 2001), using the *vegan* package (*decostand* function) in *R* (R Core Team 2017; Oksanen et al. 2018). Finally, the statistical significance of the groups formed in the RDA was compared using an ANOVA for redundancy analysis (*anova.cca* function) of the *vegan* package in *R* (R Core Team 2017; Oksanen et al. 2018).

The functional diversity of the native forest and livestock areas was compared using two approaches: 1) grouping species into functional groups according to functional traits, and 2) comparing independent functional traits. Since we chose categorical and numerical traits, a dissimilarity analysis using Gower distance (*gowdis* function) from the *FD* package in *R* (Laliberté & Legendre 2010; R Core Team 2018) was performed to group species into functional groups. Gower's distance is used in cases of categorical and continuous variables and computes distances between pairs of variables over two data sets and then combines those distances to a single value. Categorical traits (food relocation, daily activity and diet) were converted to dummy variables and all variables were transformed by a standardization procedure prior to analysis (t student: residuals/standard deviation). The number of functional groups of each habitat was compared using an ANOVA and DGC post-hoc comparisons using the *agricolae* package in *R* (Mendinburu 2017; R Core Team 2017). Similar to the taxonomic analysis, the influence of environmental variables (soil and microclimatic conditions) on the composition of functional groups was explored through RDA, and the statistical significance of the groups formed was compared through ANOVA for redundancy analysis (*anova.cca* function) of the *vegan* package in *R* (R Core Team 2017; Oksanen et al. 2018). Also, similar to previous RDA, a Hellinger transformation was applied to all variables. Finally, the abundance of independent functional traits was compared through an ANOVA and DGC post-hoc comparisons using the *agricolae* package in *R* (Mendinburu 2017; R Core Team 2017). To reduce the influence of incidental captures, species captured with less than five individuals ($n < 5$) were excluded from the functional analysis.

Results

Environmental conditions

The native forest and silvopastoral systems (both native and exotic) showed higher canopy cover and humidity and lower temperature than open pastures (Table 1). In relation to soil conditions, the native forest exhibited lower clay and higher sand content than open pastures, whereas silvopastoral systems represented an intermediate situation (Table 1).

Species diversity

Species richness and abundance differed between sampling periods (October: $S = 30$, $n = 1733$ and February: $S = 27$, $n = 753$) (see Appendix B: Table 3 in Supplementary material); however, the interaction with habitat type was not significant either for species richness or abundance (see Appendix B: Fig. 1A, B in Supplementary material). Since land use showed similar influence on dung beetle diversity in both periods, we merged the data. Combining both sampling periods, a total of 2486 individuals belonging to 38 species were captured. Most of the individuals were identified to species level (see Appendix B: Table 4 in Supplementary material). The estimator of sampling coverage (C_{hat}) showed that the sampling effort was adequate to capture the majority of species attracted by cow dung (>95%) in all habitats (see Appendix B: Table 4 in Supplementary material). The most abundant species in each habitat were: *Eurysternus parallelus* (Castelnau) ($n = 342$) in the native forest (NF), *Canthon quinque maculatus* (Castelnau) ($n = 380$) in the livestock system with native vegetation (LN), *Eurysternus caribaeus* (Herbst) ($n = 43$) in the livestock system with pine plantations (LP), and *Ontherus sulcator* (Fabricius) ($n = 189$) in open pastures (OP) (see Appendix B: Table 4 in Supplementary material).

The comparison of species richness (0D) showed two distinctive groups: NF, LP and LN with a similarly high number of species (${}^0D = 26, 24$ and 22 , respectively), and OP with the

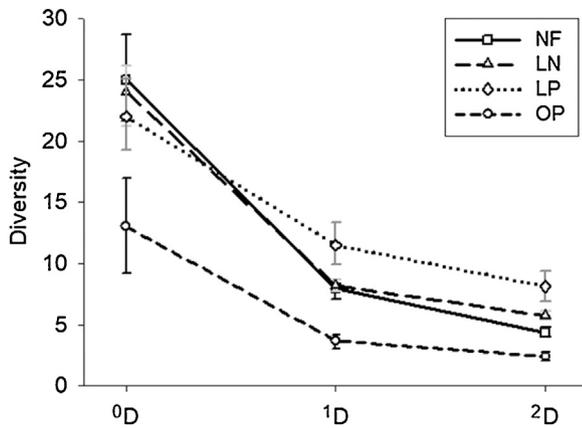


Fig. 2. Diversity profiles (and confident intervals 5–95%) for four habitats types (three livestock systems and the native forest) in the southern Atlantic forest of Argentina. Livestock system with native trees (LN), livestock system with pine trees (LP), traditional open pastures (OP) and the native forest (NF). 0D = Species richness, 1D and 2D “effective species numbers” based on Shannon and Simpson diversity.

lowest richness ($^0D=12$) (Fig. 2). However, species diversity taking into account the relative abundance values of all species showed different patterns. When all species had a weight proportional to their abundance in the community (1D), LP showed the highest diversity ($^1D=11.4$), followed by NF and LN with a similar diversity ($^1D=7.7$ and 8.2 , respectively), and OP with the lowest diversity ($^1D=3.7$); while, when dominant species had more weight (2D), OP had

the lowest diversity ($^2D=2.4$) (Fig. 2). Finally, total abundance was higher and similar in NF and LN than in LP and OP ($F=3.61$, $p=0.03$, see Appendix B: Table 4).

Regarding species composition, the first axis of the RDA explained 58% of the total variation and showed that OP was the habitat with the most distinctive assemblage as compared with the NF and the other livestock systems (see Appendix B: Table 5 (Fig. 3) in Supplementary material). *O. sulcator* was closely associated with OP, which exhibited higher average temperature and clay soil content, and was negatively associated with average humidity. In contrast, *E. parallelus* was closely associated with NF, a habitat positively related to the soil content of sand and organic matter. *C. quinquemaculatus* was associated with LN, which was characterized by higher silt content. Finally, LP was not associated with any species or particular microclimatic or soil condition (see Appendix B: Table 5 in Supplementary material) (Fig. 3).

Patterns of functional groups

Similar to that found for species diversity, the richness and abundance of functional groups differed between seasons (see Appendix B: Table 3 in Supplementary material); however, the interaction was not significant (see Appendix B: Fig. 1C, D in Supplementary material). By using the average value of the Gower coefficient, we obtained 12 functional groups from 24 species in the cluster analysis (see Appendix B: Fig. 2 in Supplementary material). Regarding the richness of functional groups, LN showed the highest number of functional

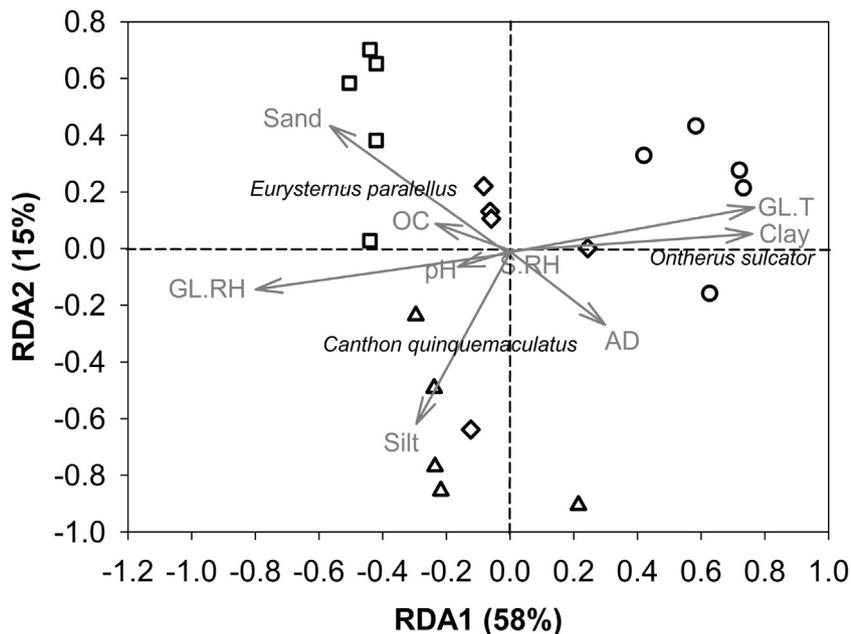


Fig. 3. Redundancy analysis (RDA) based on the species abundance, microclimatic conditions and soil structure in different livestock systems and the native forest in the southern Atlantic forest. Squares: native forest. Triangles: livestock system with native trees. Diamonds: livestock system with pine trees. Circles: open pastures. Species near the center of axis 1 and axis 2 of the RDA are not represented in this figure. GL.T = ground level temperature (average). GL.RH = ground level relative humidity. S.RH = soil relative humidity. OC = organic carbon. AD = apparent density.

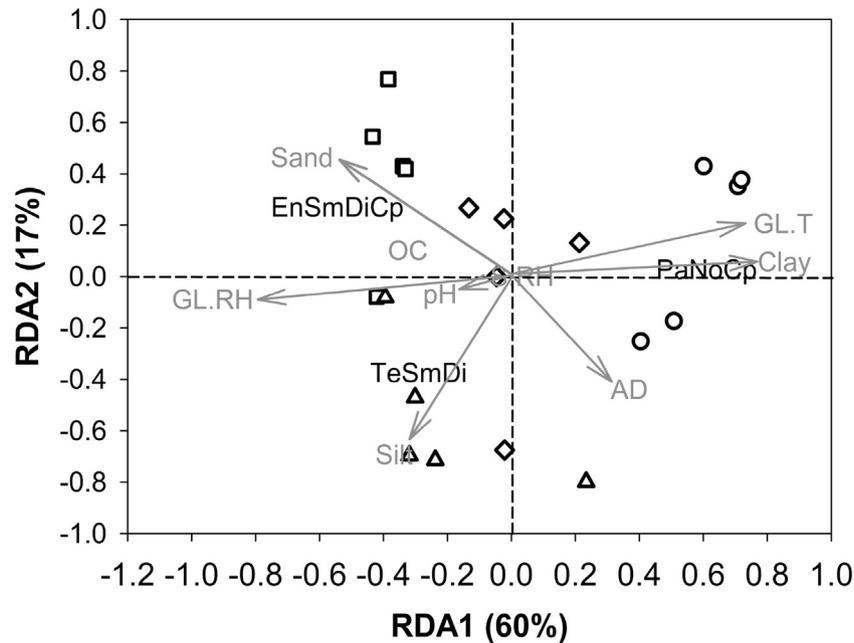


Fig. 4. Redundancy analysis (RDA) based on the relative abundance of functional groups, microclimatic conditions and soil structure in livestock areas and the native forest in the southern Atlantic forest. Squares: native forest. Triangles: livestock system with native trees. Diamonds: livestock system with pine trees. Circles: open pastures. The names of the functional groups are combinations of the following functional traits (categories): food relocation pattern (Pa=Paracoprid, En=Endocoprid, Te=Telecoprid). Biomass (Sm=Small, Lg=Large). Daily activity (Di=Diurnal, No=Nocturnal, Ca=Continuous activity). Diet (Cp=Coprophagous, Np=Necrophagous, Ge=Generalist). Functional groups near the center of axis 1 and axis 2 of the RDA are not represented in this figure GL.T= ground level temperature (average). GL.RH= ground level relative humidity. S.RH= soil relative humidity. OC= organic carbon. AD= apparent density.

groups, whereas OP showed the opposite pattern ($F=10.1$, $p<0.01$, see Appendix B: Fig. 3 in Supplementary material).

Based on the composition of functional groups, the first axis of the RDA (60% of total variation) separated OP from NF, with LN and LP in an intermediate situation (see Appendix B: Table 5 in Supplementary material) (Fig. 4). The paracoprid, nocturnal, and coprophagous (PaNoCp) functional group was associated with higher clay contents and average temperatures in OP. The endocoprid, small, diurnal and coprophagous (EnSmDiCp) functional group was associated with sand contents, typical of the NF; the telecoprid, small and diurnal (TeSmDi) as well as the paracoprid, small, diurnal and coprophagous (PaSmDiCp) functional groups were associated with silt contents closely related to those of LN (Fig. 4). The rest of the functional groups were not clearly associated with any environmental condition or any particular habitat (Fig. 4).

When comparing independent traits, telecoprid, large, diurnal and necrophagous beetles were proportionally less abundant (even absent) in OP than in NF, LN and LP (Table 2). In contrast, paracoprid and nocturnal dung beetles tended to be dominant in OP (however, differences were not significant in either case) (Table 2). In the NF, endocoprid, large, and coprophagous beetles were more abundant (Table 2). Finally, in LN systems, telecoprid, small and diurnal beetles showed higher abundance than in NF, LP and OP (Table 2).

Discussion

Our results support the initial hypothesis that silvopastoral systems (particularly those with native canopy) preserving microclimatic and soil conditions also partially preserve the diversity of species and functional groups of dung beetles. In contrast, open pastures show a drastic decrease in the diversity of both species and functional groups. Previous studies in tropical and subtropical regions with dung beetles have shown similar patterns when comparing the native forest with livestock areas without trees (Kenyon et al. 2016; Costa et al. 2017), but in this study we have further evaluated a gradient of livestock systems that include areas with a canopy of native trees, areas with a canopy of exotic trees, and grazing areas without trees, in a region with a heterogeneous matrix of native forest and different land uses. Therefore, it can be concluded that canopy loss and associated changes in microclimatic conditions and soil properties are probably the main determinants of dung beetle diversity in livestock areas. Canopy cover probably allows dung beetles to use anthropogenic habitats through the regulation of extreme microclimatic conditions, as well as, the improvement of soil conditions (less compaction); also, lower temperature and higher humidity in silvopastoral systems could maintain the water content of dung cow for longer periods than in open pastures, which could increase the

Table 2. Functional traits associated with four habitats (three livestock systems and the native forest) in the southern Atlantic forest of Argentina. Livestock system with native trees (LN), livestock system with pine trees (LP), traditional open pastures (OP) and the native forest (NF). The proportional abundance in each habitat is in italics on the second row of each category. ANOVA and DGC (Di Rienzo, Guzmán, Casanoves) post-hoc comparisons. Different letters indicate significant differences.

Functional traits	Category	NF	LN	LP	OP	F	P
Food relocation pattern	Paracoprids	41.2 a	31.6 a	15.0 a	54.2 a	1.5	0.25
	Endocoprids	92.2 a	58.6 a	14.6 a	4.4 a	2.9	0.07
	Telecoprids	21.4 b	141.8 a	6.8 b	1.0 b	13.5	0.04
Biomass (dry weight)	Small	148.8 a,b	238.6 a	34.6 b	59.6 b	3.6	0.04
	Large	6.0 a	3.4 a,b	1.8 b,c	0.0 c	6.6	<0.01
Daily activity	Diurnal	93.4 a,b	166.8 a	10.0 b	1.8 b	5.0	0.01
	Nocturnal	17.8 a	47.8 a	16.8 a	54.6 a	1.6	0.22
	Continuous activity	43.6 a	17.4 b	9.6 b	3.2 b	7.2	<0.01
Diet	Coprophagous	124.2 a	95.2 a	24.4 a	41.8 a	2.3	0.12
	Necrophagous	25.8 b	126.2 a	6.8 b	1.0 b	4.9	0.01
	Generalist	4.8 a	10.6 a	5.2 a	16.8 a	1.1	0.38

quality of resources (Giraldo et al. 2011). Whereas our results and previous studies have shown negative consequences on dung beetle diversity because of canopy loss (Gries, Louzada, Almeida, Macedo, & Barlow 2011), other studies have shown opposite results (Tocco et al. 2013; Costa et al. 2017). These differences could be associated with different biogeographical histories and the tolerance of species to the microclimatic conditions. In the present study, livestock systems preserving canopy also preserved the functional diversity of the native forest; however, the composition and abundance of species partially differed between them. In contrast, open pastures changed both the functional and taxonomic diversity of species.

Species diversity patterns

Species richness did not vary between the treed livestock systems and the native forest, but when species abundances were included (1D and 2D), dung beetle diversity was lower in the native forest than in the livestock areas with trees. This is because the evenness of the native forest beetle community was low, given that *E. parallelus* was highly dominant (with 43.2% of the total abundance in this habitat), while seven species were rare, accounting for 1% of the total number of individuals found in the native forest. In spite of that, the open pasture had still lower richness and diversity than the native forest and the silvopastoral systems because of the lower number of species and the outstanding dominance of *O. sulcator* (with 60.8% of the abundance) and *Dichotomius sericeus* (Harold) (19.9% of the abundance). The dominance of *O. sulcator* could be explained by the nesting behavior of this paracoprid species, which can build two types of nesting burrows: one close to the soil surface and another one much deeper (10–20 cm) (Sánchez & Genise 2008); the latter could be associated with hyperthermal soils (soil temperatures higher than 22 °C), which are typical of our study

area (Panigatti 2010) and probably implies an advantage for this species. Previous studies in open pastures of Neotropical forests have shown similar results: dung beetle assemblages dominated by a small number of species (probably tolerant to extreme conditions), including exotic species such as *Digitonthophagus gazella* (Fabricius) (Andresen 2007).

Irrespective of the origin of trees (either native or exotic), the silvopastoral systems studied showed small differences in species composition in relation to the native forest, mainly as a consequence of the absence of some forest specialists (such as *Canthon smaragdulus* (Fabricius) and *Canthidium dispar* (Harold)) and changes in the relative abundance of shared species. The main difference between the two livestock systems was related to total abundance: in general, species were much more abundant (almost 10 times) in the native silvopastoral system than in the livestock system with pine trees. In accordance with previous studies, here we showed that livestock systems with native trees create more complex habitats and provide better soil and microclimatic conditions than any other livestock system (Ibrahim, Villanueva, Casasola, & Rojas 2006).

In contrast to silvopastoral systems, large differences were found in species composition between open pastures and the native forest, mainly caused by species loss (especially forest species) and the inclusion of some open habitat species. The results showed that forest species such as *C. smaragdulus*, *Coprophaneus saphirinus* (Sturm), and *Onthophagus catharinensis* (Paulian) – among others – were absent in open pastures, while open habitat species such as *Canthon aff. mutabilis* (Lucas), *O. sulcator*, and *Onthophagus aff. buculus* (Mannerheim) were almost exclusively recorded in this habitat. Dominance was also a remarkable difference between silvopastoral systems and open pastures, given that in silvopastoral systems the dominant species represented less than 30% of total abundance.

Functional group patterns

The loss of functional groups in open pastures was probably associated with changes in the soil structure and microclimatic conditions and specific niche restrictions and behavior of species (such as thermal tolerance and burying strategy). In general, the relative abundance of large, diurnal, necrophagous, endocoprid and telecoprid species decreased from the native forest to open pastures. This low abundance could be explained by the extreme daily temperatures in open pastures and limitations in the thermoregulation mechanisms of forest dung beetles (Verdú, Arellano, & Numa 2006). In addition, the high solar radiation and low humidity in open pastures increase the desiccation rate of dung pats, reducing the availability of resources for species developing inside dung (endocoprids), explaining the low abundance of this group in open pastures (Holter & Scholtz 2007). Additionally, the higher clay content in the soils of open pastures could probably limit the burial capacities and development of telecoprid beetles in these sites and explain the lower abundance of this functional group (Yamada, Imura, Shi, & Shibuya 2007). However, in a previous study, we found a higher proportion of telecoprid species in pastures (Gómez-Cifuentes et al. 2017); this contradictory result may be a consequence of the subset of species considered in both studies. In our previous study, we used human dung and rotten meat to sample the whole dung beetle community, whereas, in this study, the focus was on the cow dung subset of species. In summary, changes in the microclimatic and soil conditions of open pastures probably favor nocturnal, small and paracoprid species and inhibit the use of this habitat by other functional groups. In contrast to open pastures, silvopastoral systems preserved the microclimatic and soil conditions, allowing the development of most of the native forest functional groups.

Management of livestock areas

Our results showed that canopy management in livestock areas plays a key role in the conservation of dung beetles. In contrast, the regulation of the microclimatic conditions and soil erosion, associated with the presence of trees in silvopastoral systems, is probably the main factor allowing the development and survival of dung beetles and the ecosystem functions performed by these taxa (Lobo, Lumaret, & Jay-Robert 1998). Also, silvopastoral systems with native trees and developed understory are spatially heterogeneous, providing more resources and conditions for dung beetles (Neita & Escobar 2012). In contrast, silvopastoral systems with pine trees present a homogeneous tree canopy with less associated vegetation and the absence of understory. While the presence of canopy implies a significant difference in the conservation of the native forest dung beetle community, the conservation of a native canopy and the associated understory preserves not only the richness and composition of the native forest but also the abundance of native species of dung beetles.

Acknowledgments

We wish to thank Ana Munevar, Celeste Guerra, Natalia Vespa, Fernando Foletto and Gisele Jaime for the help in the fieldwork. We also thank Fernando Vaz-de-Mello and his students of the Mato Grosso State University, Brazil, for their help in the identification of dung beetles. We also thank farmers for their hospitality and field lessons, because their knowledge has helped us to understand a lot about livestock management, dung beetle ecology and history of land use. The CONICET, UCAR-MAGyP (BIO 23) and PUE2016 – 22920160100130CO to Dr. M. di Bitteti contributed with financial support, and private owners, the Misiones Ministry of Ecology and the Administration of National Parks (Argentina) granted the necessary permissions.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.baae.2018.10.002>.

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