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Differences in Coprophilous Beetle Communities Structure in Sierra de Minas (Uruguay): a Mosaic Landscape

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Abstract
Coprophilous beetles represent an abundant and rich group with critical importance in the functioning of terrestrial ecosystems. Most coprophagous beetles have a stenotopic distribution in relation to vegetation types. Because of this, they are usually very sensitive to environmental changes and are considered well suited as bioindicator organisms. The aim of this study was to analyze variations in coprophilous beetle assemblages in natural and anthropogenic habitats. Coprophilous beetle communities were sampled monthly for 1 year using pitfall traps baited with cow dung, in native xeric upland forests, 15-years-old plantations of *Pinus elliottii* and pastures in Sierra de Minas, Lavalleja, Uruguay. A total of 7,436 beetles were caught and identified to species or morphospecies level. The most abundant families were Aphodiidae, Scarabaeidae, and Staphylinidae. Differences in species richness, abundance, Shannon index, evenness, and dominance were detected between habitats. Abundances of most frequent families were significantly higher in both kinds of forests. Species richness and diversity of Aphodiidae and Staphylinidae were higher in forests, while Scarabaeidae showed the highest richness and diversity in pine plantations. Species composition significantly differed between habitats. *Uroxys terminalis* Waterhouse and *Ataenius perforatus* Harold typified the assemblages in native forests and pine plantations and also discriminated both communities because of their differential pattern of abundance between habitats. Typifying species in pastures were *Onthophagus hirculus*, *Ateuchus robustus* (Harold), and *Ataenius platensis* Blanchard. Habitat type had a strong effect on the coprophilous beetle community structure and composition.

Introduction

Beetles attracted by mammal droppings comprise a small number of families with coprophagous, predators, saprophagous, and mycophagous species (Hanski 1991). Coprophagous beetles, mainly Scarabaeidae, Aphodiidae, and Geotrupidae, use dung as food and as a substrate for oviposition and feeding by their larvae (Hallfter & Edmonds 1982). Predatory beetles like Staphylinidae and Histeridae participate as indirect regulators of the decomposition process by feeding on fly larvae, which stimulate the metabolism of bacteria, the main organism responsible for organic matter decomposition (Stevenson & Dindal 1987). Dung beetles play various roles in the food web and nutrient flow in ecosystems, particularly in the reduction of decomposing materials such as carrion, rotting plant materials, and dung through burial and feeding, thus converting biomass, conserving energy, and recycling nutrients (Horgan 2008). Activities related to these functions have further beneficial consequences to the ecosystem, which can be considered as secondary functions.

Dung beetle communities comprise species with special ecological requirements due to the ephemeral and patchy nature of feces (Hanski 1991). Habitat characteristics influence the microclimate surrounding dung pats, so habitat selection by beetles often occurs. This selection takes place at two spatial scales: the dropping itself and its immediate surroundings (microhabitat), and the larger area which includes the soil type, vegetation type, and mammals (macrohabitat) (Hanski & Cambefort 1991, Jankielsohn *et al* 2001). At the macrohabitat scale, the distribution of dung beetles is influenced most strongly by soil type (Doube 1991, Davis 1996) and vegetation type (Davis 1994). Changes in vegetation influence on different factors in the microhabitat (i.e., the dung pat) and also on factors around the dung pat, such as breeding space in the soil. Moreover, temperature, moisture content, and consistency of the dung are influenced by changes in the macrohabitat (Jankielsohn *et al* 2001). Thus, the composition and structure of beetle communities tend to differ among habitat types due to differential selection by species (Spector & Ayzama 2003, Durães *et al* 2005, Caballero *et al* 2009).

Many studies assessed the responses of dung beetle assemblages, mainly Scarabaeidae, to landscape structure in remnant natural and modified habitats or across different natural ecosystems in tropical zones (Durães *et al* 2005, Nichols *et al* 2007, Arellano *et al* 2008, Horgan 2008). However, there are no comparative studies directed to analyze variations in the structure of coprophilous beetle assemblages between different natural and anthropogenic habitats in the temperate Neotropical region. In particular, effects of forestry practices on dung beetle diversity have not been assessed. Studies conducted in Pampean region have been scarce and restricted to open pastures grazed by cattle (Cabrera Walsh & Cordo 1997, Morelli *et al* 2002). The purpose of this study is to evaluate the local variations in abundance, species richness, diversity, and composition of coprophilous beetle communities in contrasting habitats: native forests, pastures, and exotic pine plantations. Considering that: (a) distinct types of feces have differential spatial distribution (large and moist cattle dung pats prevail in open habitats and exotic plantations, whereas no ruminant herbivore, omnivore, and carnivore dung prevail in native forests) and (b) habitat specificity among coprophilous beetles is very high in relation to vegetation cover and soil type, we expect to find differences in coprophilous beetle communities between habitats, and we predict that species richness and diversity will be higher in native habitats (upland forest and pastures) than in pine plantations.

Material and Methods

Study site and sampling design

The study was undertaken in Sierra de Minas, a low hill system (<600 m asl) in Eastern Uruguay (Department of Lavalleja) that forms the "Sistema de Serranías del Este", a natural mosaic landscape with different habitat types. The matrix is dominated by pastures interspersed with rocky outcrops and small size patches (<5 ha) of xeric upland forests, shrublands, and riparian gallery forests. Anthropogenic activities in the past (deforestation and livestock grazing practices) led to contract the woodland patches and to narrow the gallery forests. During the last 30 years, new patches represented by pine and eucalyptus plantations have been introduced, causing the reduction and fragmentation of the pasture matrix. Since 1987, native forests are protected by law in Uruguay: the reduction of forest patches has stopped, and therefore the "Sistema de Serranías del Este" still enjoys a species-rich vertebrate fauna, including several species of small and medium mammals, birds, and reptiles (Evia & Gudynas 2000). Mammals are mainly represented by brown brocket deer (*Mazama gouazoubira* Fischer), some procyonids, mustelids, foxes, and "armadillo" species, and many species of opossum and rodents (Achaval *et al* 2004). Additionally, grasslands are grazed by bovine cattle and sheep.

The sampling was made 5 km south of Aguas Blancas (route 81, km. 105–112) within an area of 450 ha (34°30'S; 55°20'W to 34°30'S; 55°19'W). Three habitats were selected: xeric upland forests (UF), open pastures (OP), and pine plantations (PP). (1) UF are characterized by a dense vegetation of xerophyte stunted and gnarly shrubs and trees, ca 1–3 m tall, with closed canopy, ferns and epiphytes associated. (2) OP are used for cattle grazing and are defined by narrow corridors (1.5 ha) with riparian forests on one side and pine forests on the other. *Axonopus* spp., *Paspalum* spp., *Vulpia australis*, and *Stipa charruana* are commonly found in pastures. (3) PP of *Pinus elliottii* have been established 15 years ago on previously open pastures, covering ca 1.5 ha in the study area. They are used as refuge for cattle, causing the accumulation of manure on the soil. Those plantations were adjacent to open pastures and 1–2 km away from the native forest habitats. All sampling sites had little deep clay-slimy soil. Two independent replicates of each habitat, located 1 km apart, were surveyed monthly from May 2002 to April 2003.

Coprophilous beetles were sampled using the model of pitfall traps (CSR model) described by Lobo *et al* (1988) and Veiga *et al* (1989). Each trap consisted of a plastic bucket (12 cm diameter and 10 cm depth) buried with the rim level with the ground and filled with a solution of formaldehyde (10%) and a drop of detergent. The bait (350 g of fresh cow

dung) was placed on a metallic grid, 5-cm mesh. In each site, a transect was set up in the middle of the habitat and three pitfall traps were located at 20-m intervals. A total of 216 traps were used for analyses. The traps were deployed for a week following the method of Baz (1988). Although it has been demonstrated that attractiveness of dung pats for dung beetles (Scarabaeoidea) decrease markedly after 3 days, it also has been demonstrated that Histeridae and Staphylinidae predator species reach a great number of individuals in droppings between 3 and 8 days old (Desière 1987, Lobo 1992). Leaving the baited traps exposed for a week guarantees the capture of predatory species.

In the laboratory, captured insects were sorted, counted, and identified to the species or genus taxonomic level or morphospecies. All individuals were stored dry and deposited as voucher specimens at the Sección Entomología, Departamento de Biología Animal of the Facultad de Ciencias (Uruguay).

Statistical analyses

Species richness and abundance for each trap were used to compute the following ecological indices (Magurran 1989), using PAST (Hammer *et al* 2001): (1) species diversity (Shannon $H' = -\sum p_i \ln p_i$; $p_i = n_i/N$; where n_i is the number of individuals of each species in the sample and N is the total number of individuals in the sample); (2) evenness (Pielou, $E = H'/H_{max}$; $H_{max} = \ln S$, being S the total number of species in the sample); and (3) dominance (Berger-Parker, $d = N_{max}/N$, being N_{max} the number of individuals of the most abundant species in the sample). Between-habitat and seasonal differences in abundance, species richness, and diversity indices were evaluated through two-way ANOVA using habitat and season of the year as main factors.

Species accumulation curves for each habitat were built using EstimateS 8.2 (Colwell 2009), with randomized sample order. Mean richness values were estimated after 100 randomizations. Total richness in each habitat was estimated by extrapolation of the species accumulation curve, using Chao 1 estimator:

$$S_1^* = S_{obs} + (a^2/2b)$$

where S_{obs} is the observed number of species in a sample, a is the number of observed species that are represented by only a single individual in that sample (singletons), and b is the number of observed species represented by two individuals in that sample (doubletons) (Colwell & Coddington 1994).

Differences in abundance, richness, and diversity for the most frequent families (abundance ≥10% of total capture)

were also evaluated between habitats through one-way ANOVA because in this case, our main goal was not to detect significant differences among seasons but rather differences between habitats. Staphylinidae beetles were categorized in two groups: coprophagous (Oxytelinae) and predators (the remaining subfamilies, including parasitoids) (Caballero *et al* 2009). Variables were log-transformed when necessary to fulfill ANOVA assumptions of normality and homocedasticity. All statistical analyses were run using the R statistical software (R Development Core Team 2008).

Spatial ordination of species was determined by non-metric multidimensional scaling (nMDS), performed on a Bray–Curtis dissimilarity matrix and using root–root transformed data from a species×sampling unit matrix (Clarke 1993). We only considered species with more than 10 individuals of the families with well-known coprophilous behavior. Non-standardized data were used to preserve site-specific characteristics and responses. The trophic level position of each species was used to identify functional feeding guilds in the nMDS ordination in order to provide additional insights about the structure of beetle assemblages. Tests for differences in structure and composition of assemblages between habitats were done using analysis of similarities (ANOSIM), which uses ranks of Bray–Curtis dissimilarities. Similarity percentages (SIMPER) were calculated to estimate the average contribution of each species to the similarity (typifying species) and dissimilarity (discriminating species) between habitats. All these analyses were carried out using PRIMER v5 (Clarke & Gorley 2001).

Results

A total of 7,436 beetles of 47 species belonging to 10 families were captured (see "Electronic supplementary material", Appendix 1). All families collected, except Nitidulidae, Corylophidae, Leiodidae, and Ptilidae, which represented <1.5% of the total catch, had well-known coprophilous behavior (Desière 1987, Hanski 1991, Lobo 1992, Cabrera Walsh & Cordo 1997, Brousseau *et al* 2010). Staphylinidae was the most speciose family (24 species) followed by Scarabaeidae (6 species), whereas the remaining families were represented by only one to five species (Electronic Supplementary Material 1). The most abundant families were Aphodiidae, Scarabaeidae, Staphylinidae, and Histeridae, which represented, respectively, 66%, 18%, 10% and 4% of the total abundance. Species accumulation curves tended to stabilize in PP (Fig 1) and estimated richness using Chao 1 indicated that PP was completely sampled ($S_{obs} = S_1^* = 27$ species), whereas 92% of the estimated number of species were captured in UF ($S_{obs} = 36$ species; $S_1^* = 39 \pm 3$) and in OP ($S_{obs} = 28$ species; $S_1^* = 31 \pm 3$).
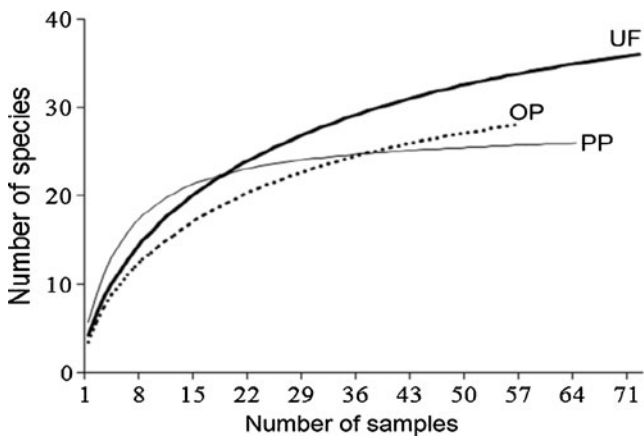
Fig 1 Species accumulation curves of coprophilous beetles recorded in each habitat (*UF* xeric upland forest; *OP* open pasture; *PP* pine plantation).

Coprophilous beetle abundance, species richness, diversity, evenness, and dominance significantly differed between habitats and seasons, as well as in the habitat× season interaction (Table 1). Concerning between-habitat

variations, abundance was significantly higher (Tukey test, $P<0.05$) in PP (62.6±7.16 ind/trap) than in UF (24.6±2.64 ind/trap) and in OP (4.7±0.58 ind/trap) (Fig 2a). Species richness (Fig 2b) in PP and in UF were similar (4.1±0.39 and 4.1±0.29, respectively) and significantly higher than in OP (2.1±0.20) (Tukey test, $P<0.05$). UF showed higher diversity and evenness ($H'=0.9±0.06$ and $E=0.7±0.30$) than OP ($H'=0.6±0.06$ and $E=0.5±0.44$) and PP ($H'=0.7±0.06$ and $E=0.5±0.31$) (Fig 3a, b). The dominance was significantly higher in PP ($d=0.6±0.03$) than in OP ($d=0.5±0.04$) (Tukey test, $p<0.05$), reaching intermediate values in UF ($d=0.6±0.03$) (Fig 3c).

Concerning between-season variations, all community descriptors were highest in austral summer, intermediate in spring and autumn, and significantly lowest in winter (Tukey test, $P<0.05$). This held true for all descriptors, including abundance (February: 63.0±18.17 ind/trap), species richness (January=5.6±0.80), diversity (December: $H'=1.2±0.12$), evenness (January: $E=0.8±0.04$), and dominance (April: $d=0.7±0.05$). Diversity in autumn also significantly differed from those found in spring and summer (Tukey test, $P<0.001$). The Berger-Parker index did not differ

Table 1 Results of 2-way ANOVA for the effect of habitat and season on: abundance (number of individuals/trap), species richness (number of species/trap), Shannon diversity index (H'/trap), Pielou index, and Berger-Parker index of coprophilous beetle assemblages.

Significant differences are highlighted in bold.

Source of variation	Degrees of freedom	Mean squares	*F* value	*P* value
Abundance				
Habitat (1)	2	76.75	57.11	**<<0.001**
Season (2)	3	22.52	16.76	**<<0.001**
1×2	6	3.06	2.28	**0.04**
Error	204	1.34		
Richness				
Habitat (1)	2	6.24	19.59	**<<0.001**
Season (2)	3	6.93	21.76	**<<0.001**
1×2	6	0.71	2.22	**0.04**
Error	204	0.32		
Shannon index				
Habitat (1)	2	2.25	1.07	**<<0.001**
Season (2)	3	4.30	10.29	**<<0.001**
1×2	6	0.56	1.21	**0.01**
Error	204	0.19		
Pielou index				
Habitat (1)	2	0.80	6.30	**<0.01**
Season (2)	3	0.55	4.60	**<0.01**
1×2	6	0.15	1.26	<0.27
Error	204	0.12		
Berger-Parker index				
Habitat (1)	2	0.30	3.59	**0.03**
Season (2)	3	0.03	0.30	0.82
1×2	6	0.13	1.59	**0.15**
Error	204	0.08		

Fig 2 Mean (± SE) values of **a** abundance and **b** species richness of coprophilous beetles in pitfall traps located in xeric upland forests (*UF*), open pastures (*OP*), and pine plantations (*PP*). *Different letters on bars* indicate significant differences between habitats.
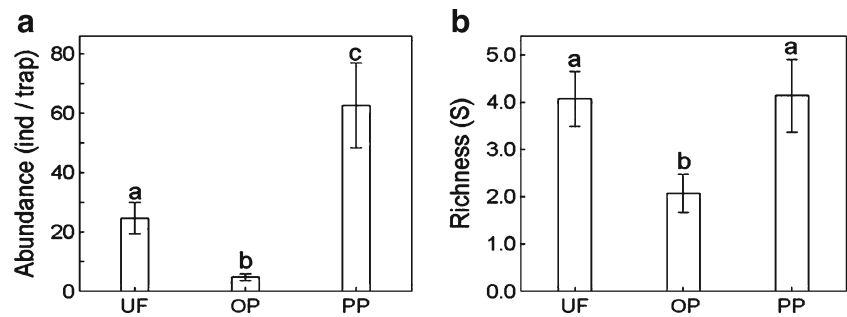
between seasons, even though it tended to be higher in autumn.

The significant "habitat×season" interaction for abundance, richness, and diversity means dependence of one factor over another, and this was reflected in different patterns of seasonal variation in response variables among habitats (Fig 4). In UF, abundance was significantly higher in spring and summer than in winter, peaking in September. OP showed consistently low abundance in autumn, spring, and summer, and the lowest value in winter, but significant differences were not found between seasons. In PP, abundances were significantly higher in autumn and summer (peaking in February and March) than in winter, reaching an intermediate value in spring (Fig 4a). Species richness and diversity (Fig 4b, c) were significantly highest in spring and summer in UF, reaching the highest levels in December. In OP, both parameters were highest in summer and autumn, peaking in March. In PP, species richness showed the highest value in summer, peaking in January, while diversity was higher in spring and summer, peaking also in January. In all the three habitats analyzed, species richness and diversity were lowest in winter. Evenness had similar patterns of seasonal variation among habitats, increasing from winter to summer.

All community parameters of Aphodiidae, Scarabaeidae, and Staphylinidae (not Oxytelinae) significantly differed between habitats (Table 2). In Aphodiidae, abundance was significantly higher in PP than in the other two habitats and it was also significantly higher in UF than in OP. Species richness, diversity, evenness, and dominance were significantly higher in both forests than in OP. In Scarabaeidae, abundance was highest in UF, intermediate in PP, and lowest in OP, having significant differences between the native forests and the other two habitats. Species richness, diversity, and evenness were significantly higher in PP than in UF and OP. Dominance was significantly higher in UF than in OP and PP. Staphylinidae (except Oxytelinae) showed that all community parameters were significantly higher in UF and in PP than in OP. Coprophagous Oxytelinae showed that abundance was significantly higher in UF than in the other two habitats, and the one in PP was significantly higher than in OP. Species richness was significantly higher in both forests than in OP. Nevertheless, species richness had very low values in both forests and abundance in pastures was negligible; the absence of these species precluded the estimation of H′ and evenness.
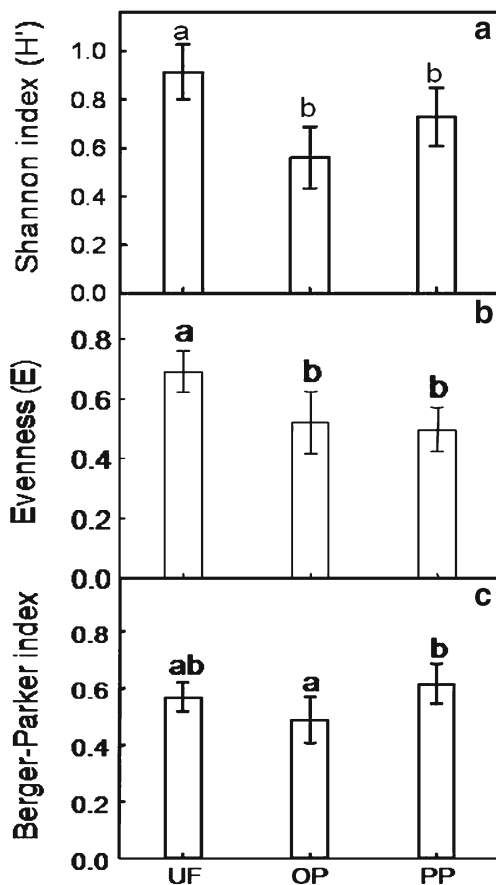

Fig 3 Mean (± SE) values of **a** Shannon index, **b** Pielou index (evenness), and **c** Berger-Parker index of coprophilous beetles in pitfall traps located in xeric upland forests (*UF*), open pastures (*OP*), and pine plantations (*PP*). *Different letters on bars* indicate significant differences between habitats.

The nMDS provided a well-defined ordination (stress=0.12) of coprophilous beetle assemblages, with five groups of taxa (Fig 5): (a) those that exclusively occurred or prevailed in OP: *Canthidium moestum* Harold, *Trichillum morelli* Verdú & Galante and *Philontus bonariensis* Bernhauer; (b) those prevailing in PP: *Ataenius* sp., *Cercyon* sp., *Anotylus* sp. 2, Paederinae, *Rugilus* sp., and *Philontus longicornis* Stephens; (c) taxa shared by OP and PP: *Ateuchus robustus* (Harold), *Onthophagus hirculus* Mannerheim, and *Ataenius platensis* Blanchard; (d) taxa shared by UF and PP: *Ataenius perforatus* Harold, *Uroxys terminalis* Waterhouse, *Rolla* sp., *Anotylus* sp. 1, *Aleochara* spp., and *Atheta* spp.; and (e) exclusive or prevailing taxa in UF: *Heterothops* sp., *Quedius* sp., and *Aphodius* sp.

Different habitats supported distinctly different coprophilous beetle assemblages (ANOSIM, Global R=0.55; P=0.001). Significant differences in species composition were found between all pairs of habitats (P=0.001 in all cases). The SIMPER procedure identified the coprophagous species *U. terminalis* and *A. perforatus* as typifying species of the coprophilous beetle communities in UF and PP (Table 3). However, these species also discriminated both communities because of their differential pattern of abundance between habitats (Table 4). *Uroxys terminalis* was more abundant in UF, while *A. perforatus* was more abundant in PP (Electronic Supplementary Material 1). Another

typifying species were the Staphylinidae species *Rolla* sp. (predator) in UF and *Anotylus* sp. 1 (coprophagous) in PP (Table 3). Both species also contributed to differentiate both forests (Table 4). Typifying species in OP differed from those of forests: *O. hirculus*, *A. robustus* (Scarabaeidae), and *A. platensis* (Aphodiidae) (Table 3). These species mainly discriminated between assemblages of pastures and both forests (Table 4).

Discussion

This study showed important spatio-temporal variations in coprophilous beetle assemblages inhabiting natural (xerophilous forests inhabited by a small and medium mammalian fauna) and anthropogenic (open pastures grazed by cattle and recent pine plantations used as refuge by cattle) habitats. Habitat type had a pronounced effect on coprophilous beetle assemblages' structure and composition. Each habitat was dominated by a small group of species.

Dung beetle assemblages in the three habitats were dominated by Aphodiidae (endocoprids) that feed on dung within the pad, and also by small paracoprids species of Scarabaeidae (<10 mm), which bury the dung in tunnels beneath the dung to form brood and feeding chambers. Species of these two functional groups remove the
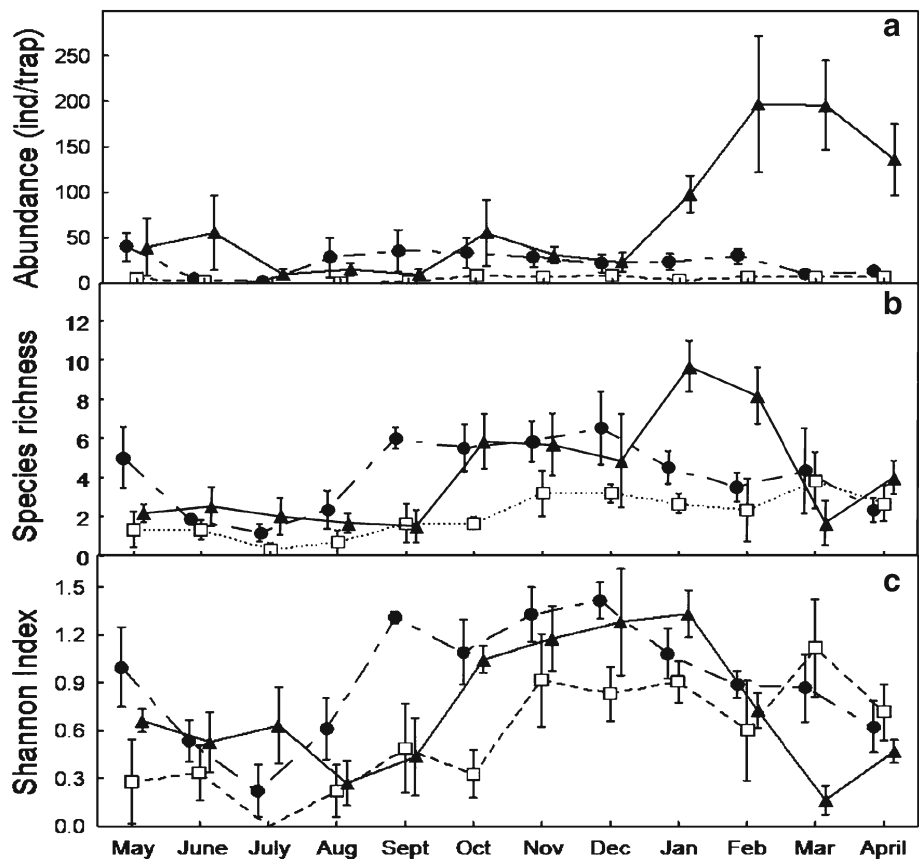

Fig 4 Monthly variations (mean±SE) in **a** abundance, **b** species richness, and **c** Shannon index of coprophilous beetles in pitfall traps located in xeric upland forests (*black circle*), open pastures (*white square*), and pine plantations (*black up-pointing triangle*).

Table 2 Mean (± SE) values abundance, richness, diversity, evenness, and dominance per trap of the most frequent beetle families in xeric upland forests (UF), open pastures (OP), and pine plantations (PP).

	UF	OP	PP	$F_{(2,210)}$
Aphodiidae				
Abundance (ind/trap)	7.6±1.35[a]	0.8±0.19[b]	44.2±6.39[c]	43.46[**]
Species richness	1.1±0.10[a]	0.4±0.07[b]	1.1±0.08[a]	21.64[**]
Shannon index	0.2±0.04[a]	0.03±0.02[b]	0.1±0.02[a]	9.70[**]
Evenness	0.3±0.05[a]	0.04±0.02[b]	0.1±0.03[a]	8.77[**]
Berger-Parker index	0.7±0.05[a]	0.4±0.06[b]	0.8±0.04[a]	21.41[**]
Scarabaeidae				
Abundance (ind/trap)	12.5±1.46[a]	2.6±0.47[b]	6.9±0.86[c]	28.85[**]
Species richness	0.7±0.03[a]	0.6±0.05[a]	0.9±0.05[b]	10.40[**]
Shannon index	0.1±0.02[a]	0.2±0.03[a]	0.3±0.05[b]	15.40[**]
Evenness	0.1±0.03[a]	0.2±0.05[a]	0.4±0.05[b]	12.49[**]
Berger-Parker index	0.9±0.04[a]	0.5±0.05[b]	0.7±0.04[b]	15.47[**]
Staphylinidae except Oxytelinae				
Abundance (ind/trap)	4.1±0.60[a]	0.6±0.14[b]	2.8±0.52[a]	23.75[**]
Species richness	1.4±0.14[a]	0.5±0.11[b]	1.2±0.14[a]	13.58[**]
Shannon index	0.3±0.05[a]	0.1±0.03[b]	0.3±0.05[a]	6.54[*]
Evenness	0.3±0.05[a]	0.1±0.04[b]	0.3±0.05[a]	7.53[**]
Berger-Parker index	0.6±0.05[a]	0.2±0.05[b]	0.5±0.05[a]	14.95[**]
Staphylinidae Oxytelinae				
Abundance (ind/trap)	1.5±0.41[a]	0.03±0.02[b]	0.5±0.14[c]	14.77[**]
Species richness	0.4±0.06[a]	0.03±0.02[b]	0.3±0.06[a]	11.70[**]
Shannon index	0	0	0.02±0.01	
Evenness	0	0	0.04±0.02	
Berger-Parker index	0.4±0.06	0.03±0.17	0.2±0.05	

Different superscripts (a, b, and c) indicate heterogeneous groups according to the results of Tukey test . The lack of individuals of Staphylinidae (Oxytelinae) in pastures precluded the application of ANOVA procedures for diversity indices.

*P<0.01; **P≤0.001.

dung slowly (Doube 1991). Large paracoprids or telecoprids species (Scarabaeidae), which remove the dung at a fast rate (Doube 1991), were absent, even though they were found in other studies and carried out in open pastures in Uruguay (Morelli *et al* 1997, 2002). These differences could be attributed to a limiting factor influencing the larger dung beetle species in the study area, which could be the little deep clay-slimy soil. Doube (1991) found that large rollers and tunnelers preferred deep
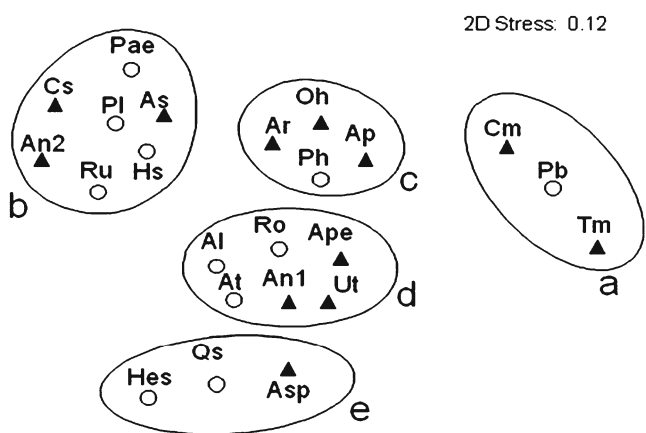

Fig 5 Non-metric multidimensional scaling of coprophilous beetle species based on the Bray–Curtis similarity index. Abbreviations correspond to taxa (see "ESM", Appendix 1). Clusters define: (*a*) taxa prevailing or exclusively in open pastures, (*b*) taxa prevailing in the pine plantations, (*c*) taxa shared by the pastures and pine plantations, (*d*) taxa shared by xeric upland forest and pine plantations and (*e*) exclusive or prevailing taxa in xeric upland forest. Symbols represent functional feeding guilds: (*black up-pointing triangle*) coprophagous; (*white circle*) predators.

Table 3 Similarity percentages of typifying (>10%) species in the average similarity (within-group), identified by the SIMPER procedure for the coprophilous beetle assemblages analyzed in Sierra de Minas, Uruguay.

Typifying species	UF	PP	OP
Ataenius perforatus	31.12	46.68	
Uroxys terminalis	40.15	25.08	
Rolla sp.	13.89		
Anotylus sp.1	11.20		
Hister sp.		18.53	
Onthophagus hirculus			33.09
Ateuchus robustus			23.90
Ataenius platensis			21.55
Average similarity	50.44	52.06	34.80

UF Xeric upland forests, *OP* open pastures, *PP* pine plantations.

Table 4 Similarity percentages of discriminating (>5%) species in the average dissimilarity (between-groups), identified by SIMPER procedure for the coprophilous beetle assemblages analyzed in Sierra de Minas, Uruguay.

Discriminating species	UF vs. PP	UF vs. OP	OP vs. PP
Uroxys terminalis	10.48	19.09	14.73
Ataenius perforatus	17.01	13.18	23.60
Rolla sp.	11.17	10.12	6.45
Anotylus sp. 1	10.19	6.58	9.54
Onthophagus hirculus	6.05	9.82	9.55
Aphodius sp.	6.34		
Ataenius platensis		7.51	7.43
Ateuchus robustus	9.45	8.09	9.22
Average dissimilarity	55.51	86.24	80.10

UF Xeric upland forests, *OP* open pastures, *PP* pine plantations.

sandy soils, while small beetles were not influenced by soil type. The dominance of small dung beetles usually causes a decreasing rate of dung degradation, and therefore ecosystems are negatively influenced by dung accumulation (Jankielsohn *et al* 2001). This fact was evident in small pine plantations and in pastures, where cattle are usually concentrated.

Aphodiidae coprophagous species were more abundant, with higher species richness, diversity, evenness, and dominance in both forests than in pastures. These results are consistent with other studies in north temperate regions in North America that reported that the majority of species are restricted to forests, specializing on deer, and small mammal dung (Hanski 1991). In contrast, in Europe, most species use the dung of domestic mammals in pastures (Hanski 1991). This difference may be attributed to the different histories of these regions since the last glaciation and earlier. Human impact on the landscape, with the attendant cattle, horses, and other domesticated mammals, has been significant in Europe for thousands of years (Hanski 1991). In South America, climatic changes within historical times have contributed to the extinction of many species of mammals, giving rise to the current fauna, which is relatively poor in large mammals (Gill 1991). Livestock represents an exotic fauna introduced by Europeans in Pampean region since 400 years. Since then, cattle predominate in pasture ecosystems and small and medium mammals are mainly restricted to woodland habitats. Therefore, the majority of Aphodiidae species has been unable to colonize the cattle dung in pastures because of their general eco-physiological adaptations to forest habitats (Hanski 1991), even though cattle dung in forests is readily colonized by native species (Hanski & Cambefort

1991). This could explain the high diversity of Aphodiidae found in pine plantations in this study. Nevertheless, more ecological studies of Aphodiidae assemblages should be needed in temperate regions of South America.

Xeric upland forests showed a poor Scarabaeidae dung beetle fauna. This assemblage was dominated by one species, *U. terminalis*, which is probably associated with native mammal feces and requires shadowed habitats. This species has been captured only in wooded habitats in Uruguay (González-Vainer *et al* 2005). On the other hand, the highest species richness, diversity, and evenness of coprophagous Scarabaeidae were found in pine plantations. Baited traps in these habitats attracted the typical species of native forests and the most generalist species of pastures. Pastures showed an intermediate diversity of Scarabaeidae, with common species that have been already captured in pastures of other Uruguayan regions (Morelli *et al* 1997, 2002).

Staphylinidae predators were more abundant and had higher species richness, diversity, and evenness in both forests than in pastures. Coprophagous Oxytelinae also showed higher species richness in forests than in pastures. These results reinforce the notion that open habitats are clearly not suitable for most Staphylinidae groups (Caballero *et al* 2009) and that rove beetles prefer complex habitats that provide shelter from predation and greater moisture levels for their prey items (mainly dipteran larva) (Greenberg & Thomas 1995, Lassau *et al* 2005, Ganho & Marinoni 2006).

The comparison between pastures with the adjoining small 15-year pine plantations performed in this study revealed that habitat alterations have caused a drastic change in species composition and in the structure of coprophilous beetle assemblages. The high number of beetle species in those pine plantations could be attributed to the invasion and colonization of native forest specialist species, attracted by the presence of cow dung. This result is consistent with other studies that have shown that pine plantations may support high native beetle species richness when they are close to native forests (Gunther & New 2003, Finch 2005, Ganho & Marinoni 2006). However, the effects of plantations with exotic conifers on the composition and structure of arthropod assemblages in Uruguay still need to be assessed.

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References

Achaval F, Clara M, Olmos A (2004) Mamíferos de la República Oriental del Uruguay. Imprimex, Montevideo, p 176

Arellano L, León Cortés JL, Halffter G (2008) Response of dung beetle assemblages to landscape structure in remnant natural and modified habitats in southern Mexico. Insect Conserv Divers 1:253–262

Baz A (1988) Selección de macrohábitat por algunas especies y análisis de una comunidad de escarabeidos coprófagos (Coleoptera) del Macizo de Ayllón (Sistema Central, España). Ann Soc Entomol Fr (N S) 24:203–210

Brousseau PM, Cloutier C, Hébert C (2010) Selected beetle assemblages captured in pitfall traps baited with deer dung or meat in balsam fir and sugar maple forests of Central Quebec. Environ Entomol 39:1151–1158

Caballero U, León-Cortés JL, Morón-Ríos A (2009) Response of rove beetles (Staphylinidae) to various habitat types and change in Southern Mexico. J Insect Conserv 13:67–75

Cabrera Walsh G, Cordo HA (1997) Coprophilous arthropod community from Argentina with species of potential use as biocontrol agents against pest flies. Environ Entomol 26:191–200

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Gorley RN (2001) PRIMER v5: user manual/tutorial. PRIMER-E, Plymouth, p 91

Colwell RK (2009) EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application: http://purl.oclc.org/estimates

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond 345:101–118

Davis ALV (1994) Habitat fragmentation in southern Africa and distributional response patterns in five specialist or generalist dung beetle families (Coleoptera). Afr J Ecol 32:192–207

Davis ALV (1996) Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). Pedobiologia 40:260–280

Desière M (1987) Ecologie des coléoptères coprophiles en prairies permanente pâturée. II. Les brigades de Coléoptères adultes coprophiles. Bull Ecol 18:13–21

Doube BM (1991) Dung beetles of southern Africa, p. 133–155. In: Hanski I, Cambefort Y (eds) Dung beetle ecology. Princeton University Press, Princeton, p 520

Durães R, Martins WP, Vaz de Mello FZ (2005) Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brasil. Neotrop Entomol 34:721–731

Evia G, Gudynas E (2000) Ecología del Paisaje en Uruguay. Montevideo, DINAMA y Junta de Andalucía, 173

Finch O (2005) Evaluation of mature conifer plantations as secondary habitat for epigeic forest arthropods (Coleoptera: Carabidae, Araneae). For Ecol Manag 204:21–34

Ganho NG, Marinoni RC (2006) A variabilidade espacial das famílias de Coleoptera (Insecta) entre fragmentos de floresta ombrófila Mista Montana (Bioma Araucária) e plantação de *Pinus elliottii* Engelmann, no Parque Ecológico Vivat Floresta, Tijucas do Sul, Paraná, Brasil. Rev Bras Zool 23:1159–1167

Gill B (1991) Dung beetles in tropical american forest, p. 211–229. In: Hanski I, Cambefort Y (eds) Dung beetle ecology. Princeton University Press, Princeton, p 520

González-Vainer P, Morelli E, Baruffaldi L (2005) First report of *Uroxys terminalis* Waterhouse, 1891 (Coleoptera: Scarabaeidae) in Uruguay, with brief descriptions of male and female. Elytron 19:37–42

Greenberg C, Thomas MC (1995) Effects of forest management practices on terrestrial coleopteran assemblages in sand pine scrub. Fla Entomol 78:271–285

Gunther MJ, New TR (2003) Exotic pine plantations in Victoria, Australia: a threat to epigaeic beetle (Coleoptera) assemblages? J Insect Conserv 7:73–84

Halffter G, Edmonds WD (1982) The nesting behaviour of dung beetles (Scarabaeinae): an ecological and evolutive approach. Instituto de Ecología AC, Mexico, p 176

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9, http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hanski I (1991) The dung insect community. In: Hanski I, Cambefort Y (eds) Dung beetles ecology. Princeton University Press, Princeton, pp 5–21, 520 pages

Hanski I, Cambefort Y (1991) Spatial processes. In: Hanski I, Cambefort Y (eds) Dung beetles ecology. Princeton University Press, Princeton, pp 283–304, 520 pages

Horgan FG (2008) Dung beetle assemblages in forests and pastures of El Salvador: a functional comparison. Biodivers Conserv 17:2961–2978

Jankielsohn A, Scholtz CH, Louw S (2001) Effect of habitat transformation on dung beetle assemblages: a comparison between a South African nature reserve and neighboring farms. Environ Entomol 30:474–483

Lassau SA, Hochuli D, Cassis G, Reid CA (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? Divers Distrib 11:73–82

Lobo JM (1992) Microsucesión de insectos en heces de vacuno: influencia de las condiciones ambientales y relación entre grupos tróficos. Graellsia 48:71–85

Lobo JM, Martín-Piera F, Veiga CM (1988) Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). I. Características determinantes de su capacidad de captura. Rev Écol Biol Sol 25:77–100

Magurran AE (1989) Diversidad ecológica y su medición. Ediciones Vedrà, Barcelona, p 200

Morelli E, González-Vainer P, Baz A (1997) Dung beetle (Coleoptera: Scarabaeidae) inhabiting bovine and ovine droppings in Uruguayan prairies. Coleopt Bull 51:197

Morelli E, González-Vainer P, Baz A (2002) Coprophagous beetles in Uruguayan prairies: abundance, diversity and seasonal ocurrence. Stud Neotropical Fauna Environ 37:53–57

Nichols E, Larsen T, Spector S, Davis AL, Escobar F, Favila M, Vulinec K (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biol Conserv 137:1–19

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Spector S, Ayzama S (2003) Rapid turnover and edge affects in dung beetle assemblages (Scarabaeidae) at a Bolivian neotropical forest-savanna ecotone. Biotropica 35:394–404

Stevenson B, Dindal D (1987) Functional ecology of coprophagous insects: a review. Pedobiologia 30:285–298

Veiga CM, Lobo JM, Martín-Piera F (1989) Las trampas pitfall con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). II: Análisis de efectividad. Rev Écol Biol Sol 26:91–109