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# Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina

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**Abstract** The degradation and replacement of native ecosystems affects both their taxonomic and functional biodiversity. However, native species may find a gradient of habitat suitability in different land uses within a region. The aim of this study was to evaluate the effect of land use on the taxonomic and functional diversity of dung beetle assemblages in the southern Atlantic forest of Argentina. Dung beetles were sampled in both the native forest (control) and different land uses (Pine and Yerba mate plantations and cattle pastures) during the 2014 summer, using pitfall traps baited with human feces and rotten meat. Samplings were taken from 20 different sites, with five replicates of each land use and the native forest (100 pitfall traps in total). A total of 1699 beetles of 27 species were captured. *Canthon quinque maculatus*, *Canthon conformis* and *Dichotomius sericeus* were the most abundant species. Cattle pastures were the land use most negatively affected in their taxonomic and functional diversity, particularly large paracoprid dung beetles. Pine plantations maintained their taxonomic and functional diversity in relation to the native forest and Yerba mate plantations showed, in general, an intermediate situation. Microclimatic conditions (average temperature and humidity and maximum temperature) were correlated with functional diversity (the proportion of large paracoprid dung beetles decreased with increasing temperature) and are probably good predictors to explain the

observed patterns of functional diversity of dung beetles. The development of sustainable production systems that preserve the native biodiversity requires the conservation of key components from the ecological niche of native species, especially microclimatic conditions.

**Keywords** Fragmentation · Functional traits · Pastures · Richness · Subtropical forest · Tree plantations

## Introduction

The replacement, fragmentation and degradation of tropical and subtropical forests by intensive and semi-intensive land uses (e.g. cattle raising, tree plantations and agriculture) are the principal causes of biodiversity loss worldwide (Myers et al. 2000; Arellano et al. 2008; Sánchez-de-Jesús et al. 2015). To mitigate the negative effects of land use, sustainable production systems that preserve the native biodiversity, the ecosystem processes, productivity and ecological integrity of the system in the medium-long term should be developed (Gardner et al. 2009; Korasaki et al. 2012). Overall, land uses that maintain resources and conditions for native species through the maintenance of the structure and composition of the native vegetation and soils as well as of the microclimatic conditions are more suitable to preserve the native biodiversity than those that drastically modify the original resources and conditions (Fillooy et al. 2010; Zurita and Bellocq 2012; Filgueiras et al. 2015). However, more information on the ecological niche and habitat use of species (both in natural and anthropogenic environments) is required to increase our understanding of the sustainability of human land uses (Barlow et al. 2007; Waltert et al. 2011).

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Functional diversity, one of the most recent topics in ecology (Barragán et al. 2011), refers to the diversity of characters in the species that make up a community, which can affect ecosystem functioning (Tilman 2001; Casanoves et al. 2011). The anthropic disturbance of natural environments affects not only the taxonomic richness and composition of natural communities, but also the functional diversity, a fact that may have important consequences in the ecological processes mediated by the native species and ecosystem functioning (Nichols et al. 2007; Barragán et al. 2011).

Dung beetles (Coleoptera: Scarabaeinae) have an important role in ecosystem functioning; through the relocation of organic matter from the surface into the soil, dung beetles cause changes in the physical and chemical properties of soils and, consequently, are considered soil engineers (De Deyn and Van der Putten 2005; Nichols et al. 2008). This process of organic matter burial changes the porosity and pH of the soil and the water and nutrient availability for plants, decreases parasite incidence (particularly in cattle systems), and has an important role in secondary seed dispersal (Andresen 2002; Bardgett and Wardle 2010). However, dung beetles are particularly sensitive to anthropogenic habitat disturbance (Duraes et al. 2005; Nichols et al. 2007; Gardner et al. 2009; Rodrigues et al. 2013; Salomão and Iannuzzi 2015). Tropical and subtropical forest dung beetle species are usually unable to tolerate the conditions of open environments, and therefore cannot persist after the replacement of the native forest by crops and/or cattle systems (Spector and Ayzama 2003; Campos and Hernández 2015). The study of dung beetles through functional diversity is a good way to understand the effects of land uses on ecosystem processes. Some examples of this can be found in studies performed by Slade et al. (2007), who showed the consequences of functional changes (e.g. loss of large nocturnal tunnellers) on dung removal activity, or in those by Audino et al. (2014), who showed the role of habitat structure in land uses for native dung beetle diversity, and Manning et al. (2016), who suggested that the conservation of functional richness in dung beetle assemblages could be important to obtain multiple ecosystem services.

The aim of this study was to evaluate and compare the taxonomic and functional diversity of dung beetle assemblages in different land uses in the southern Atlantic forest of Argentina and to relate functional changes with changes in microclimatic conditions. We hypothesized that changes in microclimatic conditions associated with land uses (in relation to the native forest) would determine patterns of taxonomic and functional diversity. We expected that land uses reproducing the microclimatic conditions of the native forest would retain a higher taxonomic (richness and composition) and functional diversity of native dung beetles.

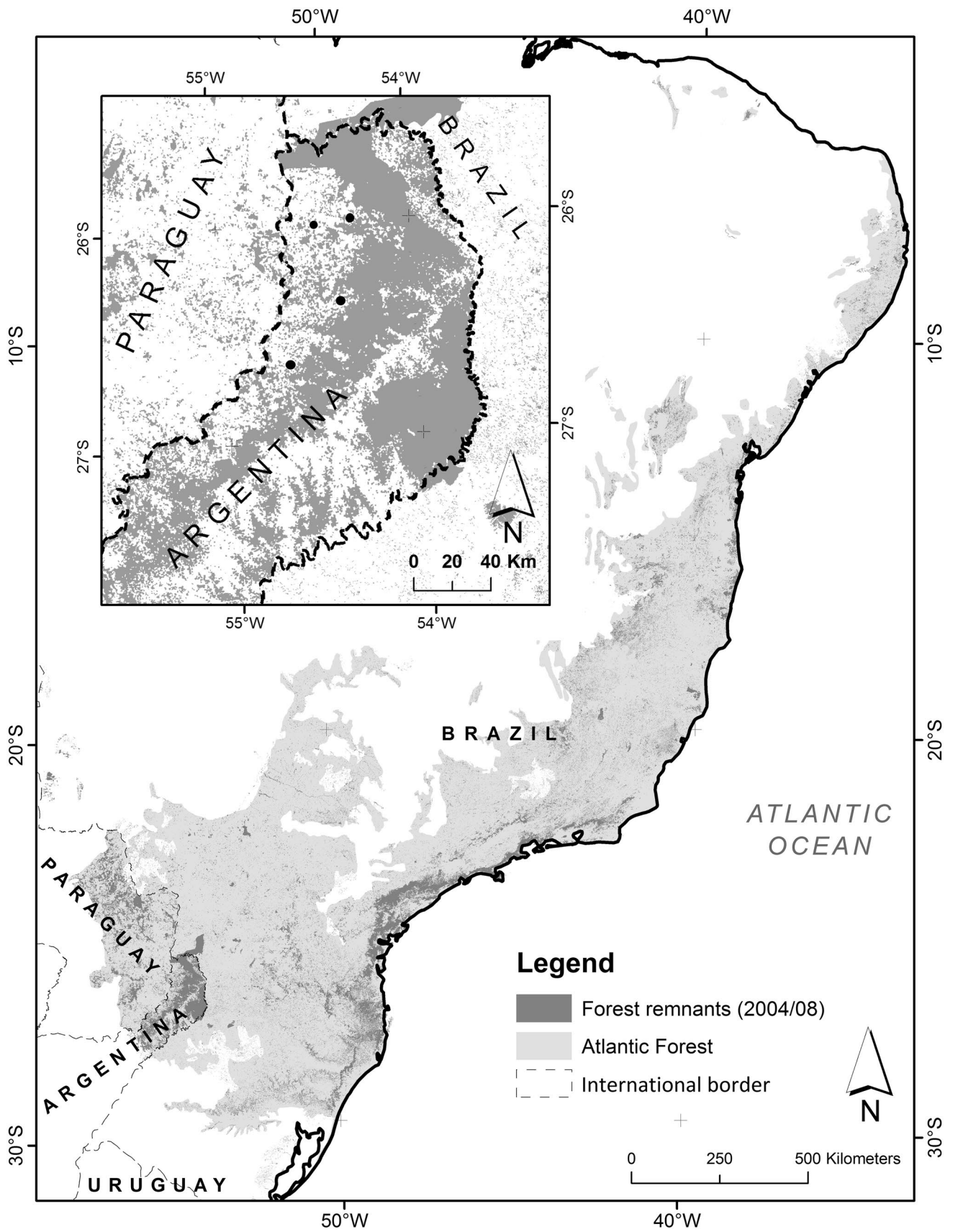
## Materials and methods

### Study area and sampling design

This study was performed in the southern Atlantic forest of Argentina (between 25°58'21"S, 54°17'22"W and 26°36'32"S, 54°41'43"W) (Fig. 1) in the summer (February–March) of 2014. The region is characterized by a warm climate with temperatures above 20°C, a cold season between June and August, and no dry season. The humidity is high most of the year, with an average annual rainfall of 2000 mm (Oliveira-Filho and Fontes 2000). Landscapes in the study area comprise large tracts of monoculture tree plantations (mainly *Pinus taeda*) and family farming (25–200 ha), characterized by a mixture of land uses performed at small-medium scale, including annual crops (corn and tobacco), cattle systems and perennial crops (mainly Yerba mate (*Ilex paraguariensis*) plantations) (Izquierdo et al. 2008; Zurita and Bellocq 2012). Both the native forest (which in the present study was used as the control) and the land uses are clustered in four locations: Esperanza Centro (26°0'20.73"S, 54°30'40.30"W), Gobernador Lanusse (25°58'53"S, 54°15'39"W), Santiago de Liniers (26°22'36"S, 54°23'14"W) and Montecarlo (26°34'00"S, 54°47'00"W), and the average distance between locations is 30 km (Fig. 1). All land uses and the native forest were represented in each location, reducing the potential influence of spatial autocorrelation within replicates of the same land use. Dung beetles were collected in the native forest and in three land uses: (1) Pine plantations (*Pinus taeda*) over 5 years old, (2) Yerba mate plantations, and (3) open pastures for cattle production. Sampling sites (land uses and native forest) varied between 4 and 17 ha in size (Appendix 1). Previous studies have shown that the microclimatic conditions and the structure and composition of the vegetation of the land uses selected differ from those of the native forest (Peyras et al. 2012; Zurita and Bellocq 2012). The land uses selected can be ordered along a gradient of canopy cover. Pine plantations are characterized by a high tree cover with trees 7–9 m in height, pastures are open areas with an almost absent tree layer, and Yerba mate plantations show an intermediate canopy cover, with trees with an average height of 1.70 m (Zurita and Bellocq 2012). Five replicates of each land use and five of the native forest were selected, separated by at least 1 km to assure their independence (20 sampling sites in total).

### Microclimatic conditions and dung beetle sampling

Automatic temperature and humidity sensors (HOBO Pro) were installed to record temperature and humidity at the ground level throughout the sampling period in three sites of each environment evaluated. The automatic sensors



**Fig. 1** Study area in the southern Atlantic forest of Argentina. *Black circles* represent sampling locations

recorded both temperature and humidity every 5 minutes for 16 days. From the temperature and humidity dataset, we calculated the average daily temperature in each sampling site and the maximum daily temperature. Average daily values were then averaged for the whole 16-day period to obtain a single value per sampling site.

In each sampling site (20 in total-five in the native forest and five in each land use), we installed five traps to capture dung beetles (25 traps per environment, 100 in total operated in two consecutive periods with human excrement and rotten meat). Within each replicate, traps were separated by 50 m, considered sub-samples and averaged for data analysis (Salomão and Iannuzzi 2015). Also, traps were separated by a minimum distance of 100 m from the nearest edge to reduce the influence of neighboring environments (Peyras et al. 2012). Traps consisted of a plastic container (12 cm in diameter and depth) filled with a 30% propylene glycol solution to avoid decomposition of individuals (Nichols et al. 2007). Human excrement and rotten meat were used to attract coprophagic and necrophagic dung beetle species respectively. Traps were operated for 16 consecutive days (eight with excrement and eight with rotten meat). 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 taxonomic keys (Vaz-de-Mello et al. 2011), comparison with a reference collection of the Instituto de Biología Subtropical (Puerto Iguazú, Misiones, Argentina) (SNDB-ID 1057) and consultation with specialists (Dr. Fernando Vaz-de-Mello and Dr. Jose Ramón Verdú).

### Taxonomic and functional diversity

To compare the taxonomic diversity between the land uses and the native forest (control), we estimated species richness and total abundance, we performed a non-metric multidimensional (NMDS) analysis (see “data analysis”) section, and decomposed betaSOR diversity (nestedness and turnover components). Species richness and abundance were estimated to demonstrate possible relationships with ecosystem functions. Among others, Larsen et al. (2005) and Yoshihara and Sato (2015) demonstrated a relationship between richness and ecosystem functions.

To describe functional diversity, we used two traits related to the process of organic matter burial: the food relocation pattern, which represents a proxy of the spatial distribution of organic matter in sites, and the body size, which indirectly determines the amount of organic matter buried by dung beetles (Barragán et al. 2011). For food relocation, we used the classification of Simmons & Ridsdill-Smith (2011) in three general patterns: (a) rollers (telecoprids), species that form balls of organic matter (dung or meat), and then roll and bury them to a variable

distance from the source; (b) tunnellers (paracoprids), species that create vertical or semi-horizontal tunnels below the mass of organic matter and put in it masses or balls of organic matter, and (c) dwellers (endocoprids), species that remain within the mass of organic matter. The body size was divided in two categories based on Barragán et al. (2011): (a) large beetles, 10 mm long or greater, and (b) small beetles, less than 10 mm long. To estimate the body size, we measured the body length of five individuals per species from the clypeus to the final abdomen with a manual Vernier caliper (0.05 mm accuracy).

To compare the functional diversity between the land uses and the native forest, we calculated (1) the proportional species richness and abundance for each category of food relocation pattern (telecoprid, paracoprid and endocoprid) and for each body size (large and small) and (2) multidimensional and multitrait indices that quantify the functional space occupied by each assemblage (Villéger et al. 2008; Casanoves et al. 2011). The indices used were: (1) functional richness (Fric: functional space occupied by species); (2) functional evenness (Feve: distribution of abundances); and (3) functional dispersion (Fdis: average distance between the center of the functional space of the species) (Villéger et al. 2008; Laliberté and Legendre 2010; Pla et al. 2012). Functional diversity indices were obtained using the FDiversity software (Casanoves et al. 2010).

### Data analysis

To compare the microclimatic conditions, and the taxonomic and functional diversity of dung beetles between the land uses and the native forest, we performed non-parametric Kruskal–Wallis and post-hoc comparisons (five replicates in four environments) (Di Rienzo et al. 2013; R Core Team 2016). Specifically, we compared: (1) the average temperature and humidity at ground level, (2) total abundance (number of beetles captured), (3) species richness, and (4) functional diversity indices (Fric, Feve, Fdis). To explore the dissimilarity in species composition between the native forest and the three land uses, we performed an NMDS analysis. The NMDS analysis was performed using the isoMDS function in the MASS package in R. Differences among groups in the NMDS analysis were tested using ANOSIM.

To examine the relationship between environmental conditions (maximum and average daily temperature and humidity) and the composition of functional groups (size and relocation pattern) and between the taxonomic and functional richness, we performed a Spearman's correlation test.

**Table 1** Number of captured individuals and richness of dung beetles in three land uses (Pine plantations, Yerba mate plantations, and cattle pastures) and in the native forest of the southern Atlantic forest of Argentina

	Forest	Pine	Yerba mate	Pasture
<i>Anomiopus germani</i>	2	0	5	1
<i>Canthidium aff. breve</i>	1	0	49	0
<i>Canthidium aff. trinodosum</i>	1	1	0	0
<i>Canthidium cavifrons</i>	3	3	1	0
<b><i>Canthidium dispar</i></b>	1	0	0	0
<b><i>Canthon lucidum</i></b>	0	0	3	0
<b><i>Canthon aff. paraguayanus</i></b>	0	0	0	1
<i>Canthon conformis</i>	42	16	392	16
<b><i>Canthon ornatus "thoracicus"</i></b>	0	0	25	0
<i>Canthon podagricus</i>	0	0	26	22
<i>Canthon quinquemaculatus</i>	240	69	48	15
<i>Canthon hystrio</i>	30	2	17	0
<i>Coprophanaeus cyanescens</i>	5	9	8	0
<i>Coprophanaeus saphirinus</i>	1	4	2	0
<i>Deltochilum komareki</i>	71	14	2	0
<b><i>Dichotomius depressicoli</i></b>	1	0	0	0
<i>Dichotomius mormon</i>	17	20	0	0
<i>Dichotomius sericeus</i>	178	65	7	53
<b><i>Digionthophagus gazella</i></b>	0	0	2	0
<i>Eurysternus aeneus</i>	0	0	7	1
<i>Eurysternus caribaeus</i>	64	58	0	0
<i>Eurysternus parallelus</i>	9	23	6	0
<b><i>Eutrichillum hirsutum</i></b>	0	0	0	8
<i>Ontherus azteca</i>	1	0	2	15
<i>Onthophagus tristis</i>	3	5	1	0
<b><i>Pseudocanthon sp.1</i></b>	0	0	1	0
<i>Uroxys dilaticollis</i>	1	2	1	0
Abundance	671	291	605	132
Richness (S)	19	14	20	9

Species captured in only one environment type are shown in bold

## Results

### Taxonomic diversity and microclimatic conditions

We collected a total of 1699 individuals belonging to 27 species. *Canthon conformis* (n=466), *C. quinquemaculatus* (n=421) and *Dichotomius sericeus* (n=303) were the most abundant species and were present both in all land uses and in the native forest (Table 1). From the total species captured, 20 were collected in the Yerba mate plantations (four exclusive species), 19 in the native forest (two exclusive species), 14 in the pine plantations and 9 in the pastures (two exclusive species) (Table 1). Median richness and abundance differed between the land uses and the native forest. Pastures showed a lower number of species and abundance than the Yerba mate plantations and the native forest, while tree plantations represented an intermediate situation (Table 2).

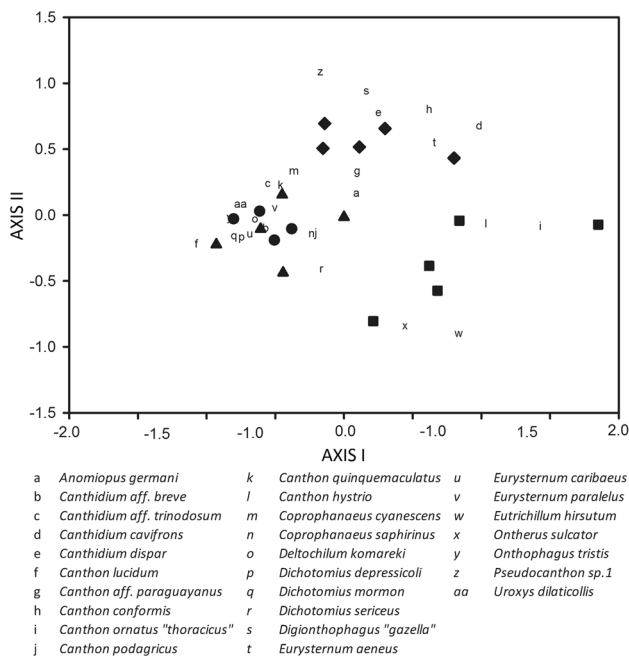
Both average temperature and humidity differed between the land uses and the native forest; pastures had the highest average temperature compared to the native forest, while Yerba mate plantations had the lowest average humidity; tree plantations showed environmental conditions similar to those of the native forest (Table 2).

The NMDS analysis showed three distinctive groups based on the composition of species: the Pine plantations and the native forest formed a single group, while the Yerba mate plantations and pastures formed separate groups (ANOSIM, R=0.69, p<0.01) (Fig. 2). Each habitat was associated with a particular group of species (Fig. 2). The partitioning of beta diversity between the native forest and the land uses showed that changes in the community composition of pine plantations followed a nested pattern (both habitats share species), while differences between the native forest and cattle pastures were mainly due to a replacement of species (Table 3). Yerba mate plantations

**Table 2** Kruskal–Wallis test for environmental conditions and taxonomic and functional diversity of dung beetles in three land uses (Pine plantations, Yerba mate plantations, and cattle pastures) and in the native forest of the southern Atlantic forest of Argentina

Land uses	Forest	Pine	Yerba mate	Pasture	H	P
Temperature average (°C)						
Medians	22 a,b	21.7 a	23.7 b	24.1 b	9.0	0.02
Humidity average (%)						
Medians	97.1 a,b	98.8 a	84.9 b	87.4 b	8.7	0.03
Abundance						
Medians	93 b	75 a,b	99 b	16 a	10.1	0.02
Richness						
Medians	9 b	9 b	10 b	5 a	10.7	<0.01
Functional indices						
Fric	7.0 a,b	8.4 c	7.6 b,c	1.4 a	16.8	<0.01
Feve	0.3 b,c	0.3 c	0.2 a,b	0.2 a		
Fdis	1.5 b,c	2.0 c	0.7 a	1.2 a,b		

H K-W H-statistic, P significance; different letters indicate significant differences in post-hoc comparisons, Fric functional richness, Feve functional evenness, Fdis functional dispersion



**Fig. 2** Non-metric multidimensional (NMDS) analysis of dung beetle assemblages in three land uses and in the native forest in the southern Atlantic forest of Argentina. closed triangle forest, closed circle Pine plantations, closed diamond Yerba mate plantations, closed square pastures

**Table 3** Species replacement ( $\beta_{SIM}$ ) and nestedness ( $\beta_{SNE}$ ) (*sensu* Baselga 2010) for dissimilarity values ( $\beta_{SOR}$ ) of dung beetle assemblages between the native forest and different land uses (Pine plantations, Yerba mate plantations, and cattle pastures) and within land uses in the southern Atlantic forest of Argentina

	$\beta_{SIM}$	$\beta_{SNE}$	$\beta_{SOR}$
Native forest—pine plantations	0	15	15
Native forest—yerba mate plantations	26	2	28
Native forest—cattle pastures	44	20	64
Pine plantations—yerba mate plantations	21	14	35
Pine plantations—cattle pastures	66	7	73
Yerba mate plantations—cattle pastures	22	30	51

represented an intermediate situation with both native forest species and open-habitat species.

**Functional diversity**

Pastures showed different patterns between proportional richness and proportional abundance (Fig. 3). Regarding

richness, pastures showed a higher proportion of telecoprids and a lower proportion of paracoprids than the native forest, while Yerba mate plantations presented an intermediate situation in the proportion of both groups. Regarding abundance, pastures and yerba mate crops showed a higher proportion of telecoprids than the native forest, whereas Pine plantations showed an intermediate situation. The proportion of endocoprids showed no differences between the land uses and the native forest. In relation to body size, the native forest and Pine plantations showed a higher abundance and similar richness of large beetles compared to pastures and Yerba mate plantations (Fig. 3).

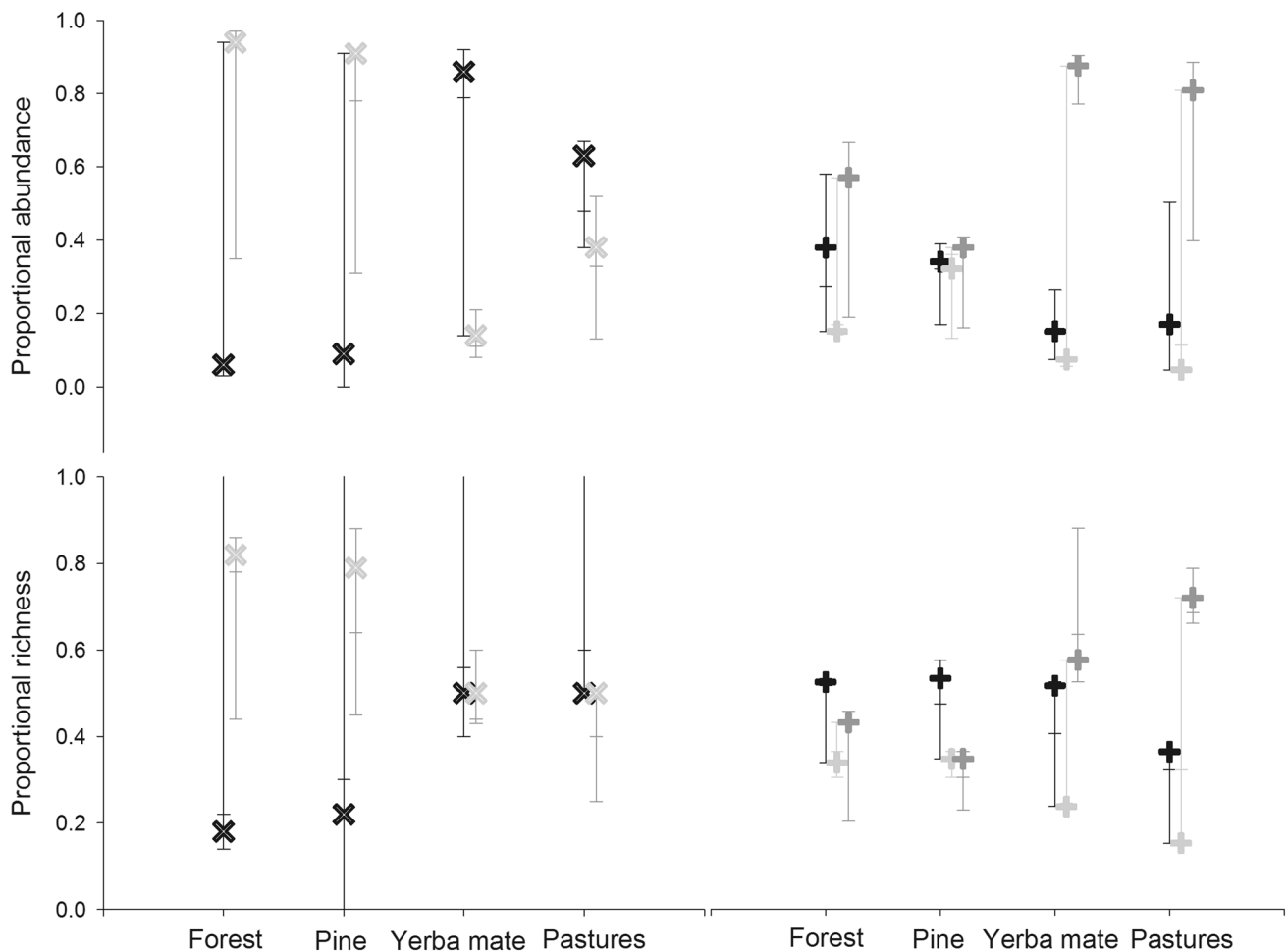
The functional diversity indices showed differences between land uses and the native forest (Table 2). Functional richness showed the lowest value in pastures compared to the native forest, while functional evenness was lower in both pastures and Yerba mate plantations than in the native forest and tree plantations. Finally, functional dispersion differed only between the Yerba mate and the pine plantations (Table 2).

The Spearman's correlation test showed that the microclimatic conditions influenced the proportional richness and abundance of functional groups (Table 4). In general, the proportional richness and abundance of small beetles increased with temperature and decreased with humidity, whereas those of large species showed the opposite pattern. The proportional abundance of paracoprids and endocoprids decreased with temperature and increased with humidity, whereas that of telecoprids showed the opposite pattern (it increased with temperature and decreased with humidity) (Table 4).

**Discussion**

Similar to that observed in previous studies in tropical and subtropical regions (Nichols et al. 2007; Peyras et al. 2012; Rodrigues et al. 2013), in the present study, carried out in the southern Atlantic forest of Argentina, the replacement of the native forest modified the taxonomic and functional diversity of dung beetle communities. However, the magnitude of the taxonomic and functional changes in relation to the native forest differed between land uses, creating a gradient of response associated with the conservation of microclimatic conditions, from the most contrasting environments with the highest temperature and lowest humidity (open pastures) to the most similar ones (tree plantations with similar temperature and humidity); Yerba mate plantations represented an intermediate situation. Similar results have been previously found in the study area with birds (Zurita et al. 2012) and in other previous studies with dung beetles (Scheffler 2005; Neita and Escobar 2012; Audino et al. 2014; Gómez-Cifuentes et al. 2015). All evidences





**Fig. 3** Proportional abundance (*upper figures*) and richness (*lower figures*) by body size (*left figures*) and relocation pattern (*right figures*) of dung beetle assemblages in three land uses (Pine plantations, Yerba mate plantations, and cattle pastures) and in the native forest

in the southern Atlantic forest of Argentina. *Black plus* paracoprids, *light gray plus* endocoprids, *dark gray plus* Telecoprids, *black times* small beetles, *gray times* large beetles

support the hypothesis that land uses that preserve, at least partially, key components of the ecological niche of species (microclimatic conditions for dung beetles, vertical complexity for birds, etc.) are more suitable for native species.

In agreement with previous results (Giraldo et al. 2011; Audino et al. 2014; Menegaz et al. 2015), despite the high abundance of resources (cow dung) in cattle pastures, both the taxonomic and functional diversities of dung beetles were strongly reduced in relation to those of the native forest and the other land uses. This result could be explained by the frequent use in this environment of antiparasitic agents (mainly ivermectin) and the extreme environmental conditions (high temperature and low humidity). In general, forest tropical dung beetles show low thermal tolerance (Lumaret et al. 1993; Moreira et al. 2009). In our study, the higher temperature and lower humidity in pastures were associated with changes in dung beetle diversity, particularly functional changes. Consequently, changes in

beta diversity between the native forest and pastures were mainly explained by a replacement of species as a consequence of changes in microclimatic conditions. On the other hand, the similar environmental conditions of the pine plantations and the native forest could explain the high taxonomic and functional similarity between both environments in our study (Peyras et al. 2012) and in other tropical regions (Nichols et al. 2007). In this type of land use, the dung beetle assemblage was a sub-set of the forest assemblage (nested pattern). The high dung beetle taxonomic diversity found in the Yerba mate plantations was an unexpected result, given the high structural simplification and the high ground temperature in this environment compared to the native forest. However, the combination of open sites between lines of trees and shaded areas below trees allows the coexistence of open-area species (*Canthon podagricus* and *Digitonthophagus gazella*) and native forest species (*Coprophanæus cyanescens*, *Deltochilum komareki*, etc.),

**Table 4** Correlations between environmental variables and the proportional abundance and richness of functional traits of dung beetles in the southern Atlantic forest of Argentina

	Small	Large	Paracoprids	Endocoprids	Telecoprids
	R	R	R	R	R
$T_{max}$					
Richness	0.78**	-0.78**	-0.37*	-0.44*	0.6*
Abundance	0.82**	-0.82**	-0.63*	-0.57*	0.6*
$T_{ave}$					
Richness	0.69**	-0.69**	-0.38*	-0.36*	0.62*
Abundance	0.80**	-0.08**	-0.46*	-0.68*	0.49*
$H_{ave}$					
Richness	-0.73**	0.73**	0.73**	0.25*	-0.84**
Abundance	-0.87**	0.87**	0.68*	0.64*	-0.67*

$T_{max}$  maximum temperature,  $T_{ave}$  average temperature,  $H_{ave}$  average humidity,  $R$  Spearman's correlations test

\* $P < 0.05$ , \*\* $P < 0.01$

and this could explain the unexpected richness of this land use. Moreover, native species probably use Yerba mate trees as a microclimatic refuge. Thus, differences in species composition (beta diversity) between the native forest and the Yerba mate plantations were a mix between native species (nested pattern) and a replacement of species.

The absence of paracoprid species in open land uses could be associated with the higher soil temperature and lower humidity and soil compaction in these environments, which lead to a rapid dung desiccation and obstruct the manipulation and burial of the resource in the same site (typical of paracoprid species). On the other hand, telecoprid dung beetles have the ability to transfer the food ball to a more suitable site for burial and could, in consequence, be able to persist in open environments (Halffter et al. 1992; Nervo et al. 2014; Campos and Hernández 2015). The dominance of small dung beetle species in pastures could be related to their thermal tolerance and burial ability; in general, small species show higher thermal and lower humidity tolerance (lower area/volume ratio) and a greater burial ability in compacted soils than large species (Verdú et al. 2006; Larsen et al. 2008; Almeida and Louzada 2009; Moreira et al. 2009; Barragán et al. 2011). At the ecosystem level, these differences in the functional composition and abundance of dung beetles may imply a very different horizontal and vertical relocation of organic matter into the soil between land uses; small telecoprid species from open environments probably relocate dung in a larger area than large paracoprid species from the native forest and tree plantations.

Previous studies have shown that different components of functional diversity may be affected by human disturbances (Mouillot et al. 2013; Audino et al. 2014). In our study, functional richness and dispersion showed differences between the land uses and the native forest, while functional evenness remained similar. This emphasizes the importance of using more than one functional measure to determine the effect of land uses on functional diversity (Barragán et al. 2011). According to Batalha et al. (2010), a community with higher functional diversity tends to perform ecosystem processes more efficiently. In our study, the pine plantations maintained higher functional diversity and, consequently, the ecological processes performed by dung beetles (organic matter burial) are potentially more efficient than in the Yerba mate plantations and pastures. The low functional dispersion and the high functional richness observed in the Yerba mate plantations are probably a consequence of the low temporal stability in this land use caused by the constant disturbance caused by the pruning of trees.

The replacement of the complex and heterogeneous native forest by extremely simplified monoculture land uses (Pine and Yerba mate plantations, cattle systems, etc.) have clear and different effects on the taxonomic and functional structure of dung beetle assemblages. In our study, dung beetle abundance was reduced by more than 50 and 30% in species richness in pine plantations, but the functional diversity was similar to that of the native forest. On the other hand, pastures showed a decrease of more than 80% in abundance and more than 50% in species richness, and a drastic decrease in functional diversity. Species loss was not a random process; large and paracoprid species were more affected than small and telecoprid species due to thermal restrictions and soil compaction (Larsen et al. 2005; Gardner et al. 2009; Shahabuddin et al. 2010). The loss of ecological processes mediated by dung beetles probably affects the productivity of land uses in the medium and long term (Braga et al. 2012). Consequently, a better understanding of the mechanism that determines the use of anthropic environments by dung beetles is crucial to the development of ecological and economically sustainable production systems.

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## Appendix 1

See Table 5.

Site	Location	Latitude	Longitude	Area (ha)
Forest	Gobernador Lanusse	25°59'34.47"S	54°18'5.37"W	16
Forest	Esperanza Centro	25°59'28.10"S	54°30'19.25"W	10
Forest	Esperanza Centro	26°1'8.56"S	54°30'42.93"W	13
Forest	Santiago de Liniers	26°21'37.83"S	54°23'24.19"W	10
Forest	Monte-carlo	26°36'56.93"S	54°41'43.40"W	5
Pine	Esperanza Centro	25°59'49.77"S	54°30'18.63"W	17
Pine	Gobernador Lanusse	25°58'30.07"S	54°17'58.32"W	10
Pine	Eldorado	26°25'14.25"S	54°36'51.85"W	4
Pine	Santiago de Liniers	26°20'38.65"S	54°21'26.72"W	8
Yerba mate	Gobernador Lanusse	25°59'30.13"S	54°18'19.53"W	6
Yerba mate	Esperanza Centro	25°59'36.39"S	54°30'19.20"W	4
Yerba mate	Santiago de Liniers	26°21'44.26"S	54°23'33.46"W	5
Yerba mate	Monte-carlo	26°36'27.46"S	54°41'46.19"W	6
Yerba mate	Esperanza Centro	25°59'26.50"S	54°29'31.61"W	6
Pasture	Gobernador Lanusse	25°59'39.34"S	54°18'19.64"W	17
Pasture	Gobernador Lanusse	25°58'16.55"S	54°17'24.26"W	10
Pasture	Esperanza Centro	26°0'31.89"S	54°30'24.50"W	9
Pasture	Santiago de Liniers	26°20'37.29"S	54°21'35.58"W	4
Pasture	Monte-carlo	26°36'46.00"S	54°41'24.81"W	5

## References

- Almeida SSP, Louzada JNC (2009) Estrutura da comunidade de Scarabaeinae (Scarabaeidae: Coleoptera) em fitofisionomias do Cerrado e sua importância para a conservação. *Neotrop Entomol* 38:32–43
- Andresen E (2002) Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecol Entomol* 27:257–270
- Arellano L, León-Cortés J, Halfiter 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
- Audino L, Louzada J, Comita L (2014) Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? *Biol Conserv* 169:248–257
- Bardgett R, Wardle D (2010) Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change. Oxford series in ecology and evolution. Oxford university press, Oxford, p 301
- Barlow J, Gardner TA, Araujo IS et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc Natl Acad Sci USA* 104:18555–18560
- Barragán F, Moreno CE, Escobar F, Halfiter G, Navarrete D (2011) Negative impacts of human land use on dung beetle functional diversity. *PLoS One* 6:e17976
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecol Biogeogr* 19(1):134–143
- Batalha MA, Cianciaruso MV and Motta-Junior JC (2010) Consequences of simulated loss of open cerrado areas to bird functional diversity. *Nat Conservação* 8:34–40
- Braga RF, Korasaki V, Audino LD, Louzada J (2012) Are dung beetles driving dung-fly abundance in traditional agriculture areas in Amazon? *Ecosystems* 15:1173–1181
- Campos R, Hernández M (2015) Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. *Ecol Indic* 49:216–227
- Casanoves F, Pla L, Di Rienzo JA, Díaz S (2010) FDiversity: a software package for the integrated analysis of functional diversity. *Methods Ecol Evol* 2:233–237
- Casanoves F, Pla L, Di Rienzo JA (2011) Valoración y análisis de la diversidad funcional y su relación con los servicios ecosistémicos, 1, 384. CATIE, Turrialba
- De Deyn G, Van Der Putten W (2005) Linking aboveground and belowground diversity. *Trends Ecol Evol* 20:625–633
- Di Rienzo JA, Casanoves F, Balzarini MG, Gonzalez L, Tablada M, Robledo CW (2013) InfoStat versión 2013. Grupo InfoStat, FCA. Universidad Nacional de Córdoba, Córdoba. doi:10.1111/j.2041-210X.2010.00082.x
- Duraes R, Marins W, Vaz-De-Mello F (2005) Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brazil. *Neotrop Entomol* 34:721–731
- Filgueiras B, Tabarelli M, Leal I, Vaz-De-Mello F, Iannuzzi L (2015) Dung beetle persistence in human-modified landscapes: combining indicator species with anthropogenic land uses and fragmentation-related effects. *Ecol Indic* 55:65–73
- Filloy J, Zurita GA, Corbelli J, Bellocc MI (2010) On the similarity among bird communities: testing the influence of distance and land use. *Acta Oecol* 36:333–338
- Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, Sodhi NS (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecol Lett* 12:512–582
- Giraldo C, Escobar F, Chara J, Calle Z (2011) The adoption of silvopastoral systems promotes the recovery of ecological

- processes regulated by dung beetles in the Colombian Andes. *Insect Conserv Divers* 4:115–122
- Gómez-Cifuentes A, Gimenez V, Munevar A, Zurita GA (2015) Estructura y composición de las comunidades de escarabajos estercoleros (Scarabaeidae: Scarabaeinae) en diferentes sistemas ganaderos del bosque Atlántico de Argentina. *Entomol Mex* 2:588–594
- Halffter G, Favila E, Halffter V (1992) A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomol Mex* 84:131–156
- Izquierdo AE, De Angelo CD, Aide TM (2008) Thirty years of human demography and land-use change in the Atlantic Forest of Misiones, Argentina: an evaluation of the forest transition model. *Ecol Soc* 13:3
- Korasaki V, Lopes J, Brown GG, Louzada J (2012) Using dung beetles to evaluate the effects of urbanization on Atlantic forest biodiversity. *Insect Sci* 20:343–406
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305
- Larsen TH, Williams NM, Kremer C (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol Lett* 8:538–547
- Larsen TH, Lopera A, Forsyth A (2008) Understanding trait-dependent community disassembly: dung beetles, density functions and forest fragmentation. *Conserv Biol* 22:1288–1298
- Lumaret JP, Galante E, Lumbreras C, Mena J, Bertrand M, Bernal JL, Cooper JF, Kadiri N, Crowe D (1993) Field effects of ivermectin residues on dung beetles. *J Appl Ecol* 30:428–436
- Manning P, Slade E, Beynon S, Owen L (2016) Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. *Agric Ecosyst Environ* 218:87–94
- Menegaz P, Arellano L, Medina MIM, Lopez S (2015) Response of the copro-necrophagous beetle (Coleoptera: Scarabaeinae) assemblage to a range of soil characteristics and livestock management in a tropical landscape. *J Insect Conserv* 19:947–960
- Moreira FMS, Nobrega RSA, Jesus EC, Ferreira DF, Perez DV (2009) Differentiation in the fertility of inceptisols as related to use in the upper Solimoes river region, western Amazon. *Sci Total Environ* 408:349–355
- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends Ecol Evol* 28:167–177
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent YJ (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Neita JC, Escobar F (2012) The potential value of agroforestry to dung beetle diversity in the wet tropical forests of the Pacific lowlands of Colombia. *Agrofor Syst* 85:121–131
- Nervo B, Tocco C, Caprio E, Palestini C, Rolando A (2014) The effects of body mass on dung removal efficiency in dung beetles. *PLoS One* 9:e107699
- Nichols E, Larsen T, Spector S, Davis AL, Escobar F, Favila M, Vulinac YK (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biol Conserv* 137:1–19
- Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME, Network TSR (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol Conserv* 141:1461–1474
- Oliveira-Filho AT, Fontes LAM (2000) Patterns of floristic differentiation among Atlantic forests in Southeastern Brazil and the influence of climate. *Biotropica* 32:793–810
- Peyras M, Vespa N, Bellocq M, Zurita G (2012) Quantifying edge effects: the role of habitat contrast and species specialization. *J Insect Conserv* 17:807–820
- Pla L, Casanoves F, Di Rienzo J (2012) Quantifying functional diversity. *Springer briefs in environmental science*, Springer, Dordrecht, 2191–5555
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Rodrigues M, Uchoa M, Ide S (2013) Dung beetles (Coleoptera: Scarabaeoidea) in three landscapes in Mato Grosso do Sul, Brazil. *Braz J Biol* 73:211–200
- Salomão R, Iannuzzi L (2015) Dung beetle (Coleoptera, Scarabaeidae) assemblage of a highly fragmented landscape of Atlantic forest: from small to the largest fragments of northeastern Brazilian region. *Rev Bras Entomol* 59:126–131
- Sánchez-de-Jesús H, Arroyo-Rodríguez V, Andresen E, Escobar F (2015) Forest Loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. *Landsc Ecol* 31:843–854
- Scheffler PY (2005) Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *J Trop Ecol* 21:9–19
- Shahabuddin, Hidayat P, Manuwoto S, Noerdjito WA, Tschardt T, Schulze CH (2010) Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. *J Trop Ecol* 26:53–65
- Simmons L, Ridsdill-Smith J (2011) Ecology and evolution of dung beetles. Blackwell Publishing Ltd, Hoboken
- Slade E, Mann D, Villanueva J, Lewis O (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *J Anim Ecol* 76:1094–1104
- Spector S, Ayzama S (2003) Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian neotropical forest-savanna ecotone. *Biotropica* 35:394–404
- Tilman D (2001) Functional diversity. *Encyclopedia Biodivers* 3(1):109–120
- Vaz-De-Mello FZ, Edmonds WD, Ocampo FC, Schoolmeesters P (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* 73:1–73
- Verdú JR, Arellano L, Numa C (2006) Thermoregulation in endothermic dung beetles (Coleoptera: Scarabaeidae): effect of body size and ecophysiological constraints in flight. *J Insect Physiol* 52:854–860
- Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301
- Waltert M, Bobo KS, Kaupa S, Montoya ML, Nsanyi MS, Fermon H (2011) Assessing conservation values: biodiversity and endemism in tropical land use systems. *PLoS One*. doi:10.1371/journal.pone.0016238
- Yoshihara Y, Sato S (2015) The relationship between dung beetle species richness and ecosystem functioning. *Appl Soil Ecol* 88:21–25
- Zurita GA, Bellocq MI (2012) Bird assemblages in anthropogenic habitats: identifying a suitability gradient for native species in the Atlantic forest. *Biotropica* 44:412–419