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ORIGINAL PAPER

Response of the copro-necrophagous beetle (Coleoptera: Scarabaeinae) assemblage to a range of soil characteristics and livestock management in a tropical landscape

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Abstract Understanding changes in copro-necrophagous beetle diversity related to characteristics of habitat and soil associated with livestock management systems can provide a tool for the conservation of edaphic fauna and improved use of natural resources. We evaluated changes in species diversity and assemblage structure in copro-necrophagous beetles under different livestock management systems in an anthropized tropical dry forest landscape in Mexico. We used a standard sampling protocol to capture copro-necrophagous beetles in three livestock management systems: silvopastoral systems with *Guazuma ulmifolia* Lam. (SPS) associated with grasses, treeless pastures (monocultures) and managed tree fallows of tropical dry forest with livestock. We characterized the habitat structure, management practices and physico-chemical parameters of the soil in each system. We recorded a total of 1423 specimens belonging to 15 species. The results show a greater beetle species richness in the SPS with *G. ulmifolia,* which declines with reduced site complexity and soil quality and increased management practice intensity. There was a positive relationship between beetle species abundance and the soil physico-chemical characteristics such as moisture and nutrient content, as well as with the density of plants. A negative effect of management practices (use of insecticides, anti-parasite treatments and burning) was observed on beetle abundance; when the analyzed variables were related to each individual species, only four species responded to differences in levels of nitrogen and magnesium, as well as to the management practice and density of plants. Systems where perennial woody plants (trees and/or shrubs) interact with traditional components (animals and herbaceous forage plants) under integrated management can provide favorable conditions for the maintenance of a relatively high diversity of beetle species as well as a refuge for species with different habitat requirements.

Keywords Scarabaeinae · Species diversity · Silvopastoral systems · *Guazuma ulmifolia* · Tropical dry forest · Pasture · Livestock management

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Introduction

Agricultural and livestock activities have generated high rates of deforestation in tropical forests, causing simplification and fragmentation of the landscape (Foley et al. 2005; Gibson et al. 2011). Extensive livestock management systems and fragmented areas promote species loss and can cause changes in ecological processes of importance to the function of ecosystems (Giller and O'Donovan 2002; Kremen 2005; Giraldo et al. 2011). Transformation of areas for food production and the use of inputs such as fertilizers and pesticides can generate important changes in soil quality (Vitousek et al. 1997; Smill 2000; Goldewijk and Ramankutty 2004), causing the loss of fertility through acidification, mobilization of toxic elements, immobilization of nutrients, mineralization and rapid reduction of organic material (Schjonning et al. 2004). These processes cause environmental damage and negative changes to some ecological functions (e.g. nutrient cycling, soil erosion) (Constanza et al. 1997) that can translate into a loss of ecosystem services (Krebs et al. 1999; Tilman et al. 2001). However, alternative management options such as silvopastoral systems (SPS) are more compatible with biodiversity conservation (McNeely and Schroth 2006; Bhagwat et al. 2008) and rational resource use (Huxley 1983). In silvopastoral systems, perennial woody plants (trees and/or shrubs) interact with the herbaceous forage plants and livestock under an integrated management system (Torres 1983) that allows diversification of production and integration of livestock, forest and crops (Abdo et al. 2008; Bhagwat et al. 2008; Giraldo et al. 2011). This can enhance the social, economic and environmental benefits for land users at all levels (Huxley 1983; Abdo et al. 2008). Silvopastoral systems generate mosaics of vegetation that provide refuge for certain species and increase connectivity between patches of vegetation, establishing biological corridors between the different habitats that comprise the landscape (Neita and Escobar 2012).

Copro-necrophagous beetles (Coleoptera, Scarabaeinae) are useful indicators in biodiversity analysis, particularly in the tropics (Favila and Halffter 1997; McGeoch et al. 2002; Nichols et al. 2007). Many studies have shown that these organisms are strongly affected by environmental disturbances, such as fragmentation of the tropical rainforest and land use intensification, modifying both the composition and diversity of the species in their assemblages (e.g. Hernández and Vaz-de-Mello 2009; Barlow et al. 2010; Korasaki et al. 2012).

It is known that secondary vegetation and remnants of tropical dry forest favor the presence of copro-necrophagous beetle species of the forest habitat, as well as generalist species that can survive in anthropized landscapes (Halffter and Arellano 2002; Andresen 2008, Arellano et al. 2008b). Diversity of beetle species is relatively high in silvopastoral systems (Giraldo et al. 2011, Neita and Escobar 2012; Arellano et al. 2013; Damborsky et al. 2015) and beetles have been shown to increase the functions of ecosystems (dung elimination, soil turnover and seed dispersal (Giraldo et al. 2011) under these conditions. By incorporating organic material into the soil, beetles have the potential to improve the biomass yield of the pastures by changing the soil physico-chemical characteristics (Bornemissza and Williams 1970; Kalisz and Stone 1984). Recent studies highlight the fact that silvopastoral systems imply reduced production costs while mitigating soil erosion (e.g. through the cultivation of borojó (*Borojoa patinoi*), Neita and Escobar 2012).

We investigate changes in the species diversity and assemblage structure of copro-necrophagous beetles as a function of soil characteristics, vegetation structure and management type in an anthropized tropical dry forest landscape in central Veracruz, Mexico. The predictions of the study were: (1) the abundance, biomass and diversity of beetle species will diminish with reduced habitat structural complexity and soil quality and increased intensity of management practices, and (2) introduced species will be more dominant in systems with intensive management practices and low quality soils. Study of the diversity of organisms present under different livestock management systems in tropical dry forest sites contributes towards understanding the ecological processes that occur in these systems and provides a valuable tool for the conservation of edaphic fauna and improved use of natural resources.

Materials and methods

Study zone

The study was conducted in the municipality of Paso de Ovejas in Veracruz, Mexico (19°12′55″N; 96°31′33″W). The elevation of this zone ranges from 10 to 400 masl and the climate is classified as Aw″0 (w) (i′) g, the driest of the warm sub-humid climates, with summer rains (June–September) (Köppen modified by García 1973). Annual mean temperature ranges from 24 to 26 °C and precipitation is below 1000 mm per year (Bautista-Tolentino et al. 2011). The predominant soils in the region are molisols, vertisols, entisols and inseptisols: these are generally shallow, rocky and low in organic matter (López 2008).

The dominant vegetation in the area was tropical dry forest; however, secondary vegetation of this forest now predominates, featuring species such as *G. ulmifolia*, *Acacia pennatula* (Schltdl. & Cham.) Benth., *Acacia cochliacantha* Humb. & Bonpl. Willd; *Senna atomaria* (L.) H.S. Irwin & Barneby, *Diphysa carthagenensis* Jacq., *Caesalpinia cacalaco* Bonpl.; *Tabebuia chrysantha* Jacq. G. Nicholson, *Leucaena lanceolata* S. Watson, and *Gliricidia sepium* (Jacq.) Kunth ex Walp) (Leyva 2006). The main land uses are cultivation of sugar cane, cucurbit and maize, as well as dual-purpose (meat and dairy) cattle (Bautista-Tolentino et al. 2011).

The ranchers in the study area are small property owners, mostly *ejidatarios*, who practice extensive livestock production using management systems that have been established for less than 10 years. According to López (2000), the livestock management systems in the municipality of Paso de Ovejas comprise production units with low levels of technology (they do not use electric fences, irrigation, tractors, fodder cutters, etc.) and where feeding is based on grazing pastures. This is an essential practice in many parts of the tropics, which are represented to a large extent by native plant species of limited forage value and are, in general, managed inappropriately.

Some sites had been cultivated or grazed and subsequently abandoned. This fact has permitted the establishment of the species that were present in the soil seed bank. These sites [managed tree fallows (MTF)] present three to four strata of vegetation since the ranchers retain trees and shrubs deemed useful for productive activity (e.g. *G. ulmifolia, Vachellia pennatula, Leucaena sp*., etc.). Uncultivated plant species that grow among the crops, sometimes considered to be weeds, are maintained along with forest trees, especially those of some utility to the ranchers. The remaining herbaceous plants and some shrubs are cut and the cleared space provides an area where the livestock can rest and feed. There is a subsequent fallow period (where the plot is completely unused) to allow regeneration of the site, while animal dung is incorporated into the soil as a fertilizer.

Guazuma ulmifolia is a tree native to the tropical regions of Latin America (CATIE 2006) that is considered multipurpose because of the wide variety of products and services it provides to agriculture, livestock production (CATIE 2006), and the medical and cosmetic industries (Manríquez-Mendoza et al. 2011). In the study area, it has been implemented in agro- and silvopastoral systems as a source of forage (foliage and fruits) associated with tropical grasses (Manríquez-Mendoza et al. 2011).

Characterization and selection of sites

We selected eight sites, located at between 174 and 279 masl: two fragments of secondary vegetation of tropical dry forest (managed tree fallows); two treeless pastures (TLP) and four silvopastoral systems featuring *G. ulmifolia* (Malvales: Sterculiaceae) associated with grasses (SSP). We characterized the sites and sampled a plot of 10,000 m^2 in each site. The key variables for site characterization were habitat structure, soil physico-chemical characteristics and livestock management intensity. The variables for description of the habitat structure in all sites were tree and shrub density and canopy cover. We measured the latter variable with a spherical densiometer (Forestry Suppliers Spherical Crown Densiometer, Concave Model C) at five randomly chosen points within three 100 m^2 quadrats located in each site. In the managed tree fallows (MTF), we also measured litter depth and tree diameter at breast height (DBH). We measured the density of trees and shrubs by census in quadrats of 10 $\times$ 10 m.

We classified the intensity of each livestock management system as low, medium or high, according to the presence and quantity of trees and shrubs and criteria of burning, pesticide use and antiparasitic treatment use. The general characteristics of each of the sampling sites are described in Table 1.

In the context of this study, we considered a soil of good quality (see SSSA 1997) to be one in which the physico-chemical parameters (NOM 021-SEMARNAT 2000) and visual appearance (allowing differentiation of the soil layer structural qualities) are maintained within the limits necessary to sustain biological productivity, maintain environmental quality and promote plant and animal health (Karlen et al. 1997) and biodiversity (Margesin and Schinner 2005; Pansu and Gautheyrou 2006). In each of the eight plots with livestock management, we took six soil samples (250 g) at the same points where the traps baited with cattle dung were placed. These samples were subsequently mixed and the soil homogenized. We then took a subsample of 500 g for each plot, which was used for the soil quality analysis (Table 2). We analyzed the following soil parameters in the samples collected from each site (NOM-021-RECNAT-2000): pH, Ca (cmol/Kg), Mg (cmol/Kg), available P (mg/Kg) (Bray-Kurtz test), K (cmol/kg) and texture (Bouyocus method). Total nitrogen and organic carbon contents were analyzed with a CN analyzer (TruSpec, LECO) and moisture content was obtained using Gardner (1986), as well as the real and apparent density per cylinder (Blake and Hartge 1986).

Dung beetle sampling

During August–September 2014 (rainy season), we sampled the eight selected sites. In order to capture coprophagous dung beetles, we set six pitfall traps in each site baited with 1.5 kg of cow dung (from animals not previously treated with chemical wormers), in two lines (50 m apart) with three traps each. Each trap was at a distance of 25 m from the other. We protected the pitfall traps from the rain with a fiberglass mesh structure. Also, to catch necrophagous beetles, we installed ten pitfall traps, each one baited with 60 g of fish. We quantified and identified all specimens found in study sites. A reference collection was deposited in the Red de Ecoetología of the Instituto de Ecología, A.C.

Statistical analysis

Inventory integrity

We evaluated the integrity of the dung beetles species inventory in each sampling site using two methods: (1) the non-parametric richness estimator Chao1 (Chao 1984); and (2) calculation of sample coverage, which is a measure of the inventory integrity that gives the proportion of the total

Table 1 General characteristics of each of the sampling sites in the municipality of Paso de Ovejas, Veracruz, Mexico

	Managed tree fallows		Treeless pastures		SPS of *Guazuma ulmifolia*			
	I	II	I	II	G_{700}	G_{900}	G_{1500}	G_{4000}
Total area of the sites (ha)	1	1	4.5	2.5	4	1.5	30	1
Number of cows per area	9	1	1	7	5	2	30	1
Trees per m^2	1.30	1.80	0	0	0.07	0.09	0.15	0.40
Litter depth (cm)	3.5	4.1	–	–	–	–	–	–
DBH (cm)	28.1 ± 15.75	30.2 ± 17.15	–	–	–	–	–	–
Canopy cover %	51.2 ± 14.17	62.4 ± 20.90	–	–	–	–	–	–
Livestock management practices	P	P	B, CH, P	B, CH, P	B, CH, P	CF, CH, P	B, CH, P	CF, CH
Intensity of management type	Low	Low	High	High	Medium	Medium	Medium	Medium

SPS = silvopastoral systems (silvopastoral systems of *Guazuma ulmifolia*: G_{750} = 750 plants/ha, G_{900} = 900 plants/ha, G_{1500} = 1500 plants/ha and G_{4000} = 4000 plants/ha). Livestock management practices = Chemical herbicides (CH), chemical fertilizers (CF), burning practiced (B), antiparasitic treatment use (once per year) (P)

Table 2 Parameters analyzed in the soils of the sampling sites in the municipality of Paso de Ovejas, Veracruz, Mexico

Parameter	Managed tree fallows		Treeless pasture		SPS of *Guazuma ulmifolia*			
	I	II	I	II	G_{700}	G_{900}	G_{1500}	G_{4000}
pH	6.10	5.70	6.20	5.60	6.10	6.30	6.00	6.00
Clay (%)	49.44	45.44	67.44	49.44	77.44	67.44	51.44	49.44
Sand (%)	30.20	38.2	18.2	28.2	8.2	12.2	26.2	32.2
Silt (%)	20.36	16.36	14.36	22.36	22.36	20.36	22.36	18.36
Texture	Clay	Clay	Clay	Clay	Clay	Clay	Clay	Clay
Moisture content (%)	20.58	28.68	43.02	25.74	57.44	39.07	47.61	30.89
P (mg/kg)	5.80	24.80	3.40	9.30	6.60	3.10	4.50	5.70
K (cmol/kg)	0.75	1.44	0.32	0.73	1.03	0.56	0.54	0.48
Ca (cmol/kg)	17.50	11.71	20.1	10.71	11.82	18.64	21.1	10.8
N (%)	0.35	0.20	0.20	0.16	0.28	0.20	0.38	0.12
Mg (cmol/kg)	9.25	6.08	12.58	5.32	13.29	13.67	8.87	6.65
Organic matter (%)	7.95	2.86	3.66	2.63	5.69	4.53	9.10	2.19
Organic carbon (%)	4.61	1.66	2.12	1.52	1.19	2.63	5.28	1.27
C:N ratio	13.00	8.00	11.00	10.00	12.00	13.00	14.00	10.00

SPS silvopastoral systems (abbreviation is found in Table 1)

number of beetles in a community that belong to each species represented in the sample. Sample coverage is based on the total number of beetles recorded and on the number of less abundant beetles, especially singletons ($f1$) and doubletons ($f2$) (Chao and Jost 2012), in order to construct and compare richness using species rarefaction curves based on the samples (Gotelli and Colwell 2001).

Analysis of abundance and biomass

We obtained dry weight per species by drying 10 individuals of each species at 45 °C for 48 h in an oven (Ríos Rocha and EC-33). For species with an abundance of less than 10 individuals, we weighed all of the captured individuals. We calculated the total biomass of beetles captured in each trap per site by multiplying the abundance of each species in a trap by the mean dry weight for that species and summing the resulting values. We compared the total abundance and biomass values of captured beetles among sites and, since the data did not present a normal distribution, we performed Kruskal–Wallis and Dunn contrast tests with the program BioEstat® (Ayres et al. 2007). We transformed biomass data using $\sqrt{x} + 1$ in order to reduce heteroscedasticity.

Dominance-diversity

We used dominance-diversity graphs (in log10) to explore the relationships between the abundance and biomass of species in the studied sites.

True diversity

We used the method proposed by Jost (2006) to compare beetle species diversity in each sampling site and habitat. This recognizes "true diversity" through the equivalent number of species. Specifically, it measures the diversity that would exist in a community made up of *i* equally common species.

Assemblage structure

We used contingency (X^2) tables to analyze changes in the proportions of species belonging to each group of the beetle's assemblage for each livestock management system. In order to study the feeding habits and size of the species, we used the classification of Halffter and Arellano (2002) and Arellano et al. (2005). We used the program CLAM (Chazdon et al. 2011) to classify species according to habitat preferences. A "supermajority" specialization limit (k = 0.67) with $P = 0.005$ was employed. This is suitable for the classification of species for which the sample size is small. Classification of the daily activity of the species (nocturnal, diurnal, and crepuscular) was based on information available in the literature (Hanski and Cambefort 1991; Montes de Oca and Halffter 1995; Morón 2003).

Response of the beetle assemblage to environmental characteristics

We evaluated the hypothesis of dependence between the abundance of dung beetles and the key variables used in this study with an analysis of covariance model (ANCOVA), with the number of individuals caught in each livestock system as the response variable and soil parameters, habitat structure and management intensity as a covariates. A significance level (α) of 5 % was established. We used stepwise analysis of regression to evaluate the relationship between the abundance of species captured in the sampling sites and the key variables of habitat structure, soil parameters and management. This was conducted with the program BioEstat® (Ayres et al. 2007).

Results

We recorded a total of 1423 beetle specimens, belonging to 10 genera and 15 species (Table 3). The number of species decreased by 50 % from systems with a more complex habitat structure to those of simpler structure.

Inventory integrity

Our analysis of the integrity of the inventory among the livestock management systems showed that the number of individuals presented wide variation, with no clear distinction between habitat types (see Table 3); however, coverage in all of the sites was close to 100 %. In the MTF I, almost 100 % coverage was obtained along with an abundance four times higher than that of MTF II (Fig. 1a). In the SPS, the plot with most individuals was G_{4000} (n values Fig. 1b) and there was a sampling efficiency of 100 % from the values estimated in the SPS with *G. ulmifolia*. However, the SPS that presented most species presented a richness that was similar to that of the MTF (13 species). In the TLP, richness was clearly lower (Fig. 1c). Most of the species were shared between the SPS and the MTF, apart from *Coprophanaeus corythus* (Harold, 1863), which was only present in two of the SPS sites. The TLP did not present exclusive species; they shared all of their species with other systems.

Analysis of abundance and biomass

Beetle abundance differed significantly among livestock management systems (Kruskal–Wallis, H = 9.12, df = 2; $P = 0.01$); the SPS had higher abundances compared to the TLP (Dunn, 11.66, $P < 0.005$) (Fig. 2). In terms of total abundance, the SPS and the MTF presented similar values, while the TLP presented fewer individuals (Table 3). MTF I presented a higher number of individuals than MTF II. In terms of the SPS, the highest abundance was observed in G_{4000}, which presented almost threefold higher values than the other SPS plots.

The total biomass observed in the sampled systems reduced almost threefold in magnitude from the MTF (2.7 ± 0.99 g and 0.9 ± 0.35 g, each site) to the TLP (0.7 ± 0.41 g and 0.6 ± 0.37 g, each site) (Table 3). We did not observe significant differences in biomass among sites of each type of livestock management system (Kruskal–Wallis, H = 7.15, df = 2; $P = 0.08$), but biomass was significantly higher in MTF I (31.0 g) than in SPS G_{700} (4.70 g) (Kruskal–Wallis, H = 18.07, df = 7; $P = 0.01$; Dunn, 40.23, $P < 0.005$). In MTF I, total biomass was more than two times higher than in MTF II. In the two TLP sites, abundance and total biomass were similar, only differing by 16 individuals and 1.65 g of biomass (Tables 3, 4).

True diversity

Analyzing the studied landscape as a whole, values of alpha diversity of order 0 (Table 5) represented 80 % of the gamma diversity of order 0. The mean richness in each

Table 3 Copro-necrophagous beetles (Coleoptera: Scarabaeinae) in livestock management systems in the municipality of Paso de Ovejas, Veracruz (Mexico), describing the ecological characteristics of the species

	Species	PS	SIZE	PA	AD	GF	HP	MTF		TP		SPS of *G. ulmifolia*			
								I N	II N	I N	II N	G_{700} N	G_{900} N	G_{1500} N	G_{4000} N
1	*Canthidium pseudopucticolle* Solis and Kohlmann, 2004	2.9	P	N	D	E	G	57	6	0	0	0	0	32	7
2	*Canthon cyanellus* LeConte, 1859	43.3	P	N	D	E	E	302	55	0	0	0	8	21	93
3	*Canthon indigaceus chiapas* Robinson, 1948	85.7	P	G	D	E	R	3	1	0	1	1	0	0	0
5	*Deltochilum scabriusculum* Bates, 1887	519	G	G	N	E	R	1	8	1	0	0	1	2	0
6	*Copris incertus* Say, 1835	116	M	C	N	T	R	7	2	1	0	1	0	0	2
7	*Copris lugubris* Boheman, 1858	177	M	C	N	T	G	63	8	8	7	1	1	2	15
8	*Dichotomius amplicollis* Harold, 1869	287	G	C	N	T	R	4	8	0	0	0	0	1	0
9	*Dichotomius colonicus* Say, 1835	666	G	C	N	T	R	2	0	0	0	0	1	3	2
10	*Digitonthophagus gazella* (Fabricius, 1787)	49.0	M	C	C	T	E	12	4	135	120	84	65	8	140
11	*Euoniticellus intermedius* Reiche, 1849	51.9	P	C	D	T	E	5	1	11	13	4	5	16	6
12	*Onthophagus hoepfneri* Harold, 1869	4.5	P	C	N	T	R	2	0	0	0	0	3	1	0
13	*Onthophagus landolti* Harold, 1880	5.3	P	C	N	T	G	15	5	0	0	0	0	6	2
14	*Coprophanaeus corythus* (Harold, 1863)	480	G	N	N	T	R	0	0	0	0	0	0	3	3
15	*Phanaeus scutifer* Bates, 1887	295	G	C	D	T	R	1	0	2	1	0	0	1	0
	Total							476	103	158	142	91	85	98	270

MDW: mean dry weight (mg). Functional groups: size (S: small, M: medium, L: large). FP: Feeding preferences (C: coprophagous, G: generalist, N: necrophagous). DA: daily activity (N: nocturnal; D: diurnal; C: crepuscular). FD: food relocation (T = tunnelers; R: rollers). HP: habitat preferences (G: generalist; S: specialist; R: less abundant). N: number of individuals. Managed tree fallows (MTF). Treeless mature (TP). Silvopastoral systems (SPS) of *Guazuma ulmifolia*: G_{750}, G_{900}, G_{1500} y G_{4000}

site was 12 species and total richness was 15 species. The beta diversity of orders 0, 1 and 2 were 1.29, 1.47 and 1.59, respectively. This indicates that, in these sites, there were more differences between the abundant species, in this case *Canthon cyanellus* Le Conte, 1859 and *Digitonthophagus gazella* (Fabricius, 1787).

When individual profiles per sampling site were evaluated (Fig. 2a), we found lower beetle diversity in the treeless pastures. The alpha diversity of order 1 was similar among MTF sites, while species richness (alpha diversity of order 0) was greater in MTF I. Among the silvopastoral systems, G_{750} presented the least pronounced alpha slope. In the SPS, where there was a greater density of plants per area, a more pronounced slope and thus lower equitability was observed (Fig. 3a). Given the relative abundance ($q = 2$, Fig. 3a), the SPS with lower densities of plants (G_{750}, G_{900} and G_{1500}) presented a similar trend to that observed in the treeless pastures, although the MTF had a more pronounced slope. A total of 93.3 % of species were shared between the MTF and the SPS and 46.6 % of species were shared between these systems and the TLP. True beta diversity of order 0 was highest in SPS (${}_0D\beta = 1.71$), given the higher heterogeneity of these sites. The beta diversity of order 1 was 1.45, while that of order 2 was 1.38.

In terms of diversity of order 1, the SPS G_{4000} presented the highest value (${}_1D\gamma = 7.09$), followed by MTF II (${}_1D\gamma = 5.37$), while the lowest value was observed in G_{750} (${}_1D\gamma = 1.43$) (Fig. 3b).

In the MTF, the highest number of equivalent species was obtained in MTF II with ${}_2D\gamma = 3.19$. In the silvopastoral systems, this was found in G4000 (${}_2D\gamma = 5.18$), which was similar to that of the treeless pastures (TLP I, ${}_2D\gamma = 1.33$; TLP II, ${}_2D\gamma = 1.41$). According to the profile of true beta diversity, values were similar among the studied sites (Table 5). Comparing the true beta diversity profile among livestock management systems (Fig. 3c), it can be seen that the system that shares most species among sites is that of the mature tree fallows (${}_0D\beta = 1.12$), in the case of medium abundance and dominant species. The treeless pastures shared the lowest number of species among the sites but shared the same abundant species (*D. gazella*) (${}_1D\beta = 1.0$, ${}_2D\beta = 1.0$).

Dominance-diversity

Digitonthophagus gazella (Fabricius, 1787) and *Canthon cyanellus* Le Conte, 1859 were the most abundant species. The former was distributed in all of the livestock management systems, while the latter was absent from the treeless pastures (Fig. 4a). Two species dominated the managed tree fallows: *C. cyanellus* and *Copris lugubris* Boheman, 1858. Together, these represented 73.9 % of the

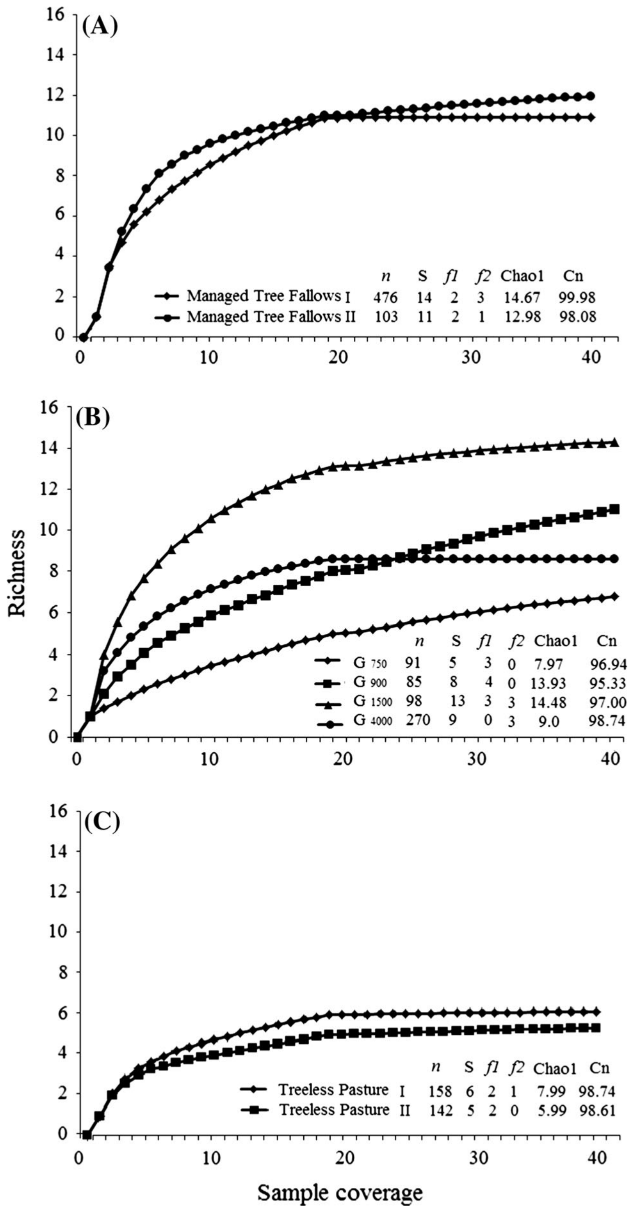

Fig. 1 Rarefaction curves based on beetle species richness in livestock management systems in the municipality of Paso de Ovejas, Veracruz (Mexico). **a** Managed tree fallows, **b** silvopastoral systems of *G. ulmifolia* and **c** treeless pastures. *n* number of beetles, *S* species richness, *f1* number of singletons, *f2*, number of doubletons, *Chao1* richness estimator, *Cn* sample coverage

total abundance. In MTF I, *Canthidium pseudopuncticolle* Solis & Kohlmann, 2004 also dominated, and was the third most dominant species in this site (12 %). In the SPS and TLP, the dominant species was *D. gazella,* representing 54.7 and 84.7 %, respectively, except in SPS G_{1500} where *C. pseudopuncticolle* (32.6 %) and *C. cyanellus* (21.4 %) dominated (Fig. 4a).

In terms of biomass, *C. cyanellus* and *D. scabriusculum* dominated in the managed tree fallows (Fig. 4b). However, based on biomass, *D. gazella* only dominated in G_{750} and G_{900}. *Dichotomius colonicus* Say, 1835 (22.0 %) and *C. corythus* (16.0 %) dominated in the SPS of G_{1500}, while *C. cyanellus* (55.3 %) and *D. gazella* (40.6 %) dominated in G_{4000} (Fig. 4b). In the treeless pastures, *D. gazella* dominated in terms of both abundance and biomass.

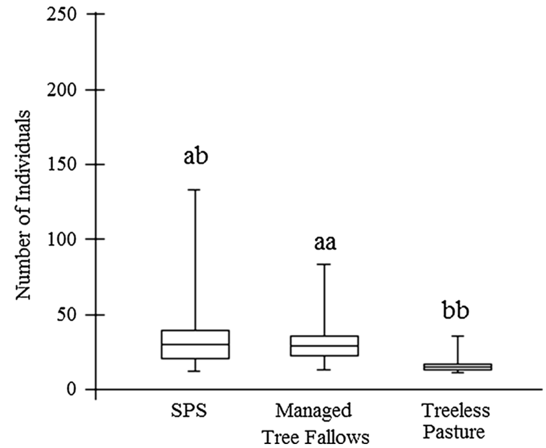

Fig. 2 Variation in the abundance of copro-necrophagous beetle species (median ± SD) in treeless pastures, silvopastoral systems and managed tree fallows of the tropical dry forest in the municipality of Paso de Ovejas, Veracruz (Mexico)

Assemblage structure

In terms of food relocation, we found 10 species of tunnelers and five rollers. No dweller species were recorded. Abundance of tunnelers and rollers was dependent on the type of livestock management system ($X^2 = 506.36$; df = 2; $P < 0.0001$), with the MTF (n = 438) and SPS (n = 476) presenting a greater abundance of rollers, but a greater abundance of tunnelers (n = 298) found in the treeless pastures.

Species abundance, according to daily activity, was dependent on the type of system ($X^2 = 305.37$; df = 2; $P < 0.0001$). There were more species of nocturnal beetles in the studied systems, but a greater abundance of diurnal species and only one species that presented crepuscular activity (*D. gazella*). In the managed tree fallows, there were more diurnal species than in the SPS of *G. ulmifolia* and the treeless pastures.

In terms of food preferences, we found a significant relationship between species abundance and type of livestock management system ($X^2 = 514.33$; df = 2; $P < 0.0001$). There was a greater abundance of coprophagous species in all of the studied systems, apart from the MTF, which presented more necrophagous species. In the MTF, there was only one specialist necrophagous species: *C. cyanellus* (6.8 %), while two specialist coprophagous species were presented in the SPS: *D. gazella* and *Euoniticellus intermedius* Reiche, 1849 (13.3 %). Three species (20.0 %) were classified as food generalists (*C. pseudopucticolle*, *Copris lugubris* Boheman,

Table 4 Biomass total (mg) the copro-necrophagous beetles (Coleoptera: Scarabaeinae) in livestock management systems in the municipality of Paso de Ovejas, Veracruz (Mexico)

	Species	MTF		TP		SPS of *Guazuma ulmifolia*			
		I	II	I	II	G_{700}	G_{900}	G_{1500}	G_{4000}
1	*Canthidium pseudopucticolle* Solis and Kohlmann, 2004	165.3	17.4	0.0	0.0	0.0	0.0	92.8	20.3
2	*Canthon cyanellus* LeConte, 1859	13,096.6	2381.5	0.0	0.0	0.0	346.4	909.3	4026.9
3	*Canthon indigaceus chiapas* Robinson, 1948	257.1	85.7	0.0	85.7	85.7	0.0	0.0	0.0
5	*Deltochilum scabriusculum* Bates, 1887	518.8	4150.4	518.8	0.0	0.0	518.8	1037.6	0.0
6	*Copris incertus* Say, 1835	115.6	231.2	115.6	0.0	115.6	0.0	0.0	231.2
7	*Copris lugubris* Boheman, 1858	11,119.5	141.2	1412.0	1235.5	176.5	176.5	353	2647.5
8	*Dichotomius amplicollis* Harold, 1869	1148.0	2296.0	0.0	0.0	0.0	0.0	287	0.0
9	*Dichotomius colonicus* Say, 1835	1332.0	0.0	0.0	0.0	0.0	666.0	1998	1332
10	*Euoniticellus intermedius* Reiche, 1849	259.5	51.9	570.9	674.7	207.6	259.5	830.4	311.4
11	*Digitonthophagus gazella* (Fabricius, 1787)	588.0	196.0	6615.0	5880	4116	3185.0	392	6860
12	*Onthophagus hoepfneri* Harold, 1869	10.6	0.0	0.0	0.0	0.0	13.5	5.3	0.0
13	*Onthophagus landolti* Harold, 1880	735.0	22.5	0.0	0.0	0.0	0.0	27	9
14	*Coprophanaeus corythus* (Harold, 1863)	0.0	0.0	0.0	0.0	0.0	0.0	1440.6	1440.6
15	*Phanaeus scutifer* Bates, 1887	294.7	0.0	589.4	294.7	0.0	0.0	294.7	0.0
	Total	31,003.9	14,302.6	9821.7	8170.6	4701.4	5857.3	9050.9	16,878.9

Managed tree fallows (MTF). Treeless mature (TP). Silvopastoral systems (SPS) of *Guazuma ulmifolia*: G_{750}, G_{900}, G_{1500} y G_{4000} (abbreviation is found in Table 1)

Table 5 Values of alpha ($^{q}D\alpha$,) gamma ($^{q}D\gamma$) and beta ($^{q}D\beta$) true diversity for different orders (q = 0, 1, 2), considering gamma diversity as the landscape, alpha diversity as the livestock management systems and beta diversity as the number of effective communities in the municipality of Paso de Ovejas in Veracruz, Mexico

Environment/sampling unit (SU)	Diversity	q = 0	q = 1	q = 2
Landscape/SU = 3	$^{q}D\alpha$	11.67	3.16	2.00
	$^{q}D\gamma$	15	4.65	3.17
	$^{q}D\beta$	1.25	1.47	1.59
Managed tree fallows/SU = 2	qDα	12.5	3.42	2.66
	qDγ	14	4.72	2.72
	qDβ	1.12	1.07	1.02
SPS of *G. ulmifolia*/SU = 4	qDα	8.75	3.17	1.96
	qDγ	15	4.40	2.17
	qDβ	1.71	1.44	1.38
Treeless pasture/SU = 2	qDα	5.5	1.79	1.37
	qDγ	7	1.81	1.37
	qDβ	1.27	1.01	1.00

Landscape, habitat type and (within habitat type) the number of sites sampled, were considered

1858 and *Onthophagus landoti* Harold, 1880) and 60 % of the sample comprised species that were less abundant in these livestock management systems (Table 3). In the MTF, four species were considered habitat specialists: *C. pseudopucticolle*, *C. cyanellus, D. amplicollis* and *O. landoti*, while in the TLP there were only two: *D. gazella* and *E. intermedius*.

Response of the beetle assemblage to environmental characteristics

A preliminary model analysis of covariance (ANCOVA) revealed a significant interaction between the abundance of dung beetles and covariates: soil parameters ($F = 4.58$, $GL = 13, P = 0.001$) and management intensity ($F = 4.19$, $GL = 6$, $P = 0.03$); and a non-significant interaction with habitat structure ($F = 0.096$, $GL = 5$, $P = 0.96$).

A significant relationship was also observed between the abundance of beetle species and the soil moisture, available phosphorous and potassium content ($R^2 = 0.94$, $F = 9.78$, $P = 0.03$); however, according to the analysis, the level of phosphorous was the most important predictor of total abundance (88 % of the determination). The other variables (pH, clay, sand and silt, levels of micronutrients (Mg, Ca), total nitrogen, organic matter and C:N ratio) did not show a significant relationship with beetle abundance ($R^2 = 0.35$, $F = 0.18$, $P = 0.90$), with organic matter responsible for only 4.39 %.

Similarly, habitat structure and shrub density did not significantly affect the abundance of the assemblage ($R^2 = 0.03$, $F = 0.0005$, $P = 0.94$). There were significant differences with respect to the negative effect of the use of insecticides on beetle abundance, application of chemical wormers and burning ($R^2 = 0.98$, $F = 37.40$, $P = 0.004$). There was a lower abundance of beetles in the site in which these practices were carried out.

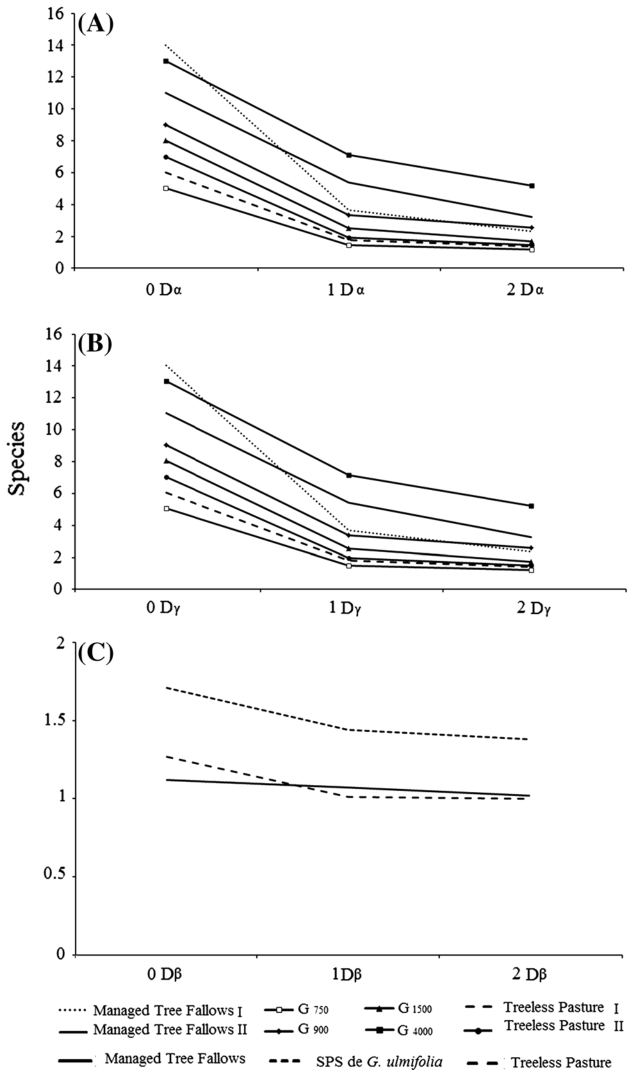

Fig. 3 Profiles of Alpha ($^{q}D\alpha$,) and gamma ($^{q}D\gamma$) true diversity for different orders (q = 0, 1, 2) in livestock management systems in the municipality of Paso de Ovejas, Veracruz (Mexico): **a** alpha diversity for the sampling sites; **b** gamma diversity for the sampling sites; **c** beta diversity for the livestock management systems

When each key variable was analyzed per species, few beetle species (only *Deltochilum scabriusculum* Bates, 1887 and *Dichotomius amplicollis* Harold, 1869) presented a significant relationship with the soil chemical characteristics in the studied livestock management systems. *Deltochilum scabriusculum* responded negatively to the low levels of nitrogen and magnesium in the soil of the studied sites where this species were most abundant (MTF II and SPS G_{1500}) ($R^2 = 0.98$, $F = 14.72$, $P = 0.006$). *Dichotomius amplicollis* only presented a negative relationship with levels of total nitrogen ($R^2 = 0.85$, $F = 26.47$, $P = 0.04$). No physical variable of the studied soils presented a significant relationship with any particular species.

Dichotomius amplicollis ($R^2 = 0.96$, $F = 159.84$, $P = 0.0001$) and *D. lobipes* ($R^2 = 0.93$, $F = 80.57$, $P = 0.0003$) presented a positive relationship with plant density in the studied systems (93–96 %), while presenting no relationship with habitat complexity. However, these species did respond positively in the sites where management intensity was low (*D. amplicollis*, $R^2 = 0.60$, $F = 9.04$ $P = 0.02$; *D. lobipes*, $R^2 = 0.56$, $F = 7.94$, $P = 0.03$). *Digitonthophagus gazella* presented a significant relationship with medium intensive management systems ($R^2 = 0.61$, $F = 9.39$, $P = 0.02$). The only species that responded positively to the management practices (use of agrochemicals and burning) were *D. amplicollis* ($R^2 = 0.94$, $F = 14.60$, $P = 0.009$) and *D. lobipes* ($R^2 = 0.96$, $F = 35.28$, $P = 0.002$); sites in which these management practices did not occur presented a greater abundance of these beetle species.

Discussion

Changes in land use for livestock management and the reduction in areas of forests because of human activity can generate negative changes in the richness and composition of dung beetle species and in the structure of their assemblage (Tscharntke et al. 2005; Barlow et al. 2010; Gardner et al. 2008; Lopes et al. 2011). These changes are reflected in our results since we found the abundance and diversity of beetle species diminished in line with reduced complexity of habitat structure and soil quality and with increasing intensity of management practices.

As in many other studies of dung beetles (Halffter et al. 2007; Navarrete and Halffter 2008; Korasaki et al. 2013; Favila 2014), we found low abundance and richness of species in the treeless pastures while in the SPS of *G. ulmifolia*, there was a richness and abundance similar to that of the managed tree fallows, which feature greater structural complexity.

Silvopastoral (Giraldo et al. 2011) and agroforestry systems (Neita and Escobar 2012) can buffer the adverse effects of rapid expansion of open areas and the consequent reduction of tropical dry forest area generated by technically conventional systems (Arellano et al. 2013). These types of productive management maintain biodiversity in the environment and may even increase it considering that the trees and shrubs create a microhabitat for diverse organisms (Beer et al. 2004).

It was observed that SPS represent a habitat type that, according to the density of *G. ulmifolia* plants, presents similarities in terms of the diversity of beetle species with the MTF (higher quantities of plants per hectare) and with the pastures (few shrubs per hectare).

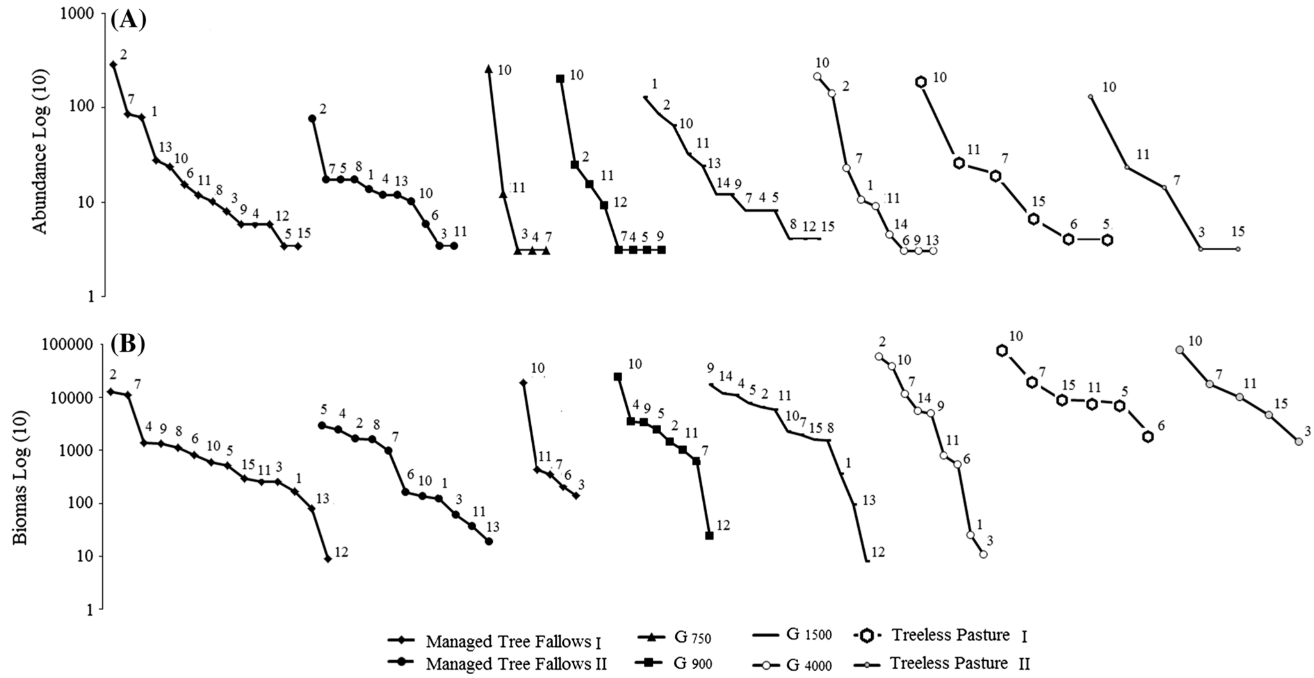

Fig. 4 Dominance-diversity relationships between the copro-necrophagous beetle species in treeless pastures, silvopastoral systems and managed tree fallows of tropical dry forest in the municipality of Paso de Ovejas, Veracruz (Mexico): **a** dominance-abundance in the sampling sites; **b** dominance-biomass in the sampling sites. The numbers that represent the species are those presented in Table 3

In terms of the managed tree fallows, richness and abundance of the beetles was high, possibly because the resources available in these sites are kept viable for longer periods due to the humidity maintained by the density of plants and also the type of management practiced (low intensity). Areas with a greater density of plants (e.g. fragments of Neotropical forests (Costa et al. 2013) present favorable conditions for an increased abundance of beetles, since vegetation cover is an important variable in their distribution (Halffter and Arellano 2002). In terms of the habitat structure evaluated, it was observed that *D. amplicolis,* a species with preference for dry and humid tropical forest habitat (Morón 2003), shows a strong relationship with low management intensity and plant density in the studied systems. The same relationship was recorded for *D. lobipes*.

In this study, few changes were found in species composition among the eight sampling sites, a finding that was reflected in the low number of equivalent communities. There was greater variability among sampling sites than within the types of livestock management systems, due to the effects of the density of shrubs and the management practices adopted. The proportion of species shared as a function of their patterns of abundance and richness differed in each system; however, high similarity was observed between the SPS and managed tree fallows of tropical dry forest.

Canthon cyanellus was the most abundant species in the MTF, where there are more trees present. According to the studies of Halffter and Arellano (2002) and Arellano et al. (2008a), this species is more abundant in fragments of tropical dry forests than in pastures, which is corroborated by our results. This species appears to be a specialist of the secondary vegetation of tropical dry forest or of the edge zones of tropical evergreen forests (Halffter et al. 1992; Favila and Halffter 1997).

The high abundance recorded for *C. cyanellus* can also be attributed to the fact that its highest emergence in the field is presented during the rainy season (May to September) (Halffter et al. 1983). In other tropical dry forests, it presents two peaks of abundance per rainy season (Arellano et al. 2008a), since individuals are in reproductive diapause during the dry season (Martínez and Montes de Oca 1994).

On the other hand, the structure of populations and assemblages of dung beetles is strongly influenced by high reproductive competition (Simmons and Ridsdill-Smith 2011) on rare and ephemeral food resources (Halffter and Matthews 1966; Hanski and Cambefort 1991). The abundant occurrences of *C. cyanellus* during the rainy season may be related to factors affecting reproductive success: age of first reproduction of females of mating frequency, quality and consistency of supply of a particular resource (Favila 2001).

Digitonthophagus gazella and *E. intermedius* were preferentially found in the treeless pastures. This supports the prediction of this study that there would be a greater dominance of introduced species in systems with intensive management practices and low quality soils. *Digitonthophagus gazella* and *E. intermedius* are introduced Indo-African species associated with a certain degree of environmental disturbance (Lobo 1996; Montes de Oca and Halffter 1998). They are typical of open areas and present opportunist strategies of occupation with a higher rate of reproduction and dispersion (Rougon and Rougon 1980; Cambefort 1984). Principally, *D. gazella* was introduced in many countries to help with the management of populations of dung diptera that are harmful to livestock (Fincher et al. 1983; Bianchin et al. 1992; Kohlmann 1994; Maes et al. 1997; Noriega et al. 2006; Vidaurre et al. 2008). These species can impact upon the native populations of beetles through competition for resource (dung) and habitat, a process that could be happening in the present study zone. However, experiments exploring the reproductive success of these species are required in order to confirm this.

In our livestock studied system, we recorded the food resource supply per hectare and observed that the highest quantity was found in the SPS with *G. ulmifolia* (203 dung pats/ha), management system that presents more cows (30 animals/ha), lower frequency of slashing and a variety of grass that grows to a height of more than 1.5 m (*Andropogon gayanus*). In this SPS, there was high species richness (13 species) as well as a high biomass of dung beetles. Two edge species and one exotic species (*C. pseudopucticolle*, *C. cyanellus* and *E. intermedius*) dominated in this system (in terms of abundance); however, in terms of biomass, the dominant species were *D. colonicus* (associated with disturbed environments) and *C. corythus* (an edge species). According to Tshikae et al. (2013), when differences in the availability of dung affect population size or eliminate the specialist beetles, an important alteration occurs in the composition and richness of the assemblage.

A greater abundance of tunneler beetle species of nocturnal and coprophagous habits was recorded. Studies conducted in tropical forests have demonstrated this same pattern (Escobar 2004; Arellano et al. 2005; Louzada et al. 2010; Barragán et al. 2014). These species can perform their ecological functions and contribute to the provision of ecosystem services, especially in relation to nutrient cycling given the improved soil structure and fertility that the beetles promote (Calafiori 1979), the disintegration and decomposition of organic material (Nichols et al. 2007; 2008) and the construction of tunnels that contribute to greater edaphic aeration (Bang et al. 2005).

Regarding soil quality variations, the measured levels of available phosphorus, potassium and nitrogen showed that soil quality was lower in the treeless pastures, where the lowest richness of beetles was found. *Deltochilum scabriusculum* responded negatively to the low levels of nitrogen and magnesium in the soil. *Dichotomius amplicollis* presented a negative relationship with levels of total nitrogen.

According to the ranchers in the sampling sites, the areas dedicated to extensive livestock management and others recently converted into SPS had been previously used for many years to cultivate maize, where apparently high quantities of chemical fertilizers and pesticides had been applied. This may have caused deterioration of the soil quality. Low values of organic carbon (mean, 2.5 % ± 1.56) were reported in the livestock management systems evaluated. When the supply of organic matter in the soil is low and processes of erosion, oxidation and lixiviation take place (through the production of maize using conventional technological packages), there is a loss of organic carbon, which may be the result of historical management practices utilized at the site.

Beetle abundance responded mainly to phosphorous, which was the nutrient that presented highest concentrations in the sampling sites. This can be attributed to the management history of the areas. The livestock production system with the highest concentration of available phosphorous was that of managed tree fallows; which had previously been used as maize fields. Such variation may be a product of the quantity of litter on the soil surface, which causes changes in the content and storage of carbon and could affect of the dynamic of the organic matter and the organic carbon, which facilitates the metabolic activity of the microorganisms responsible for processes of mineralization (Skjemstad et al. 1999).

There was a negative response in relation to the abundance of species in the studied sites and the management practices (use of agrochemicals, chemical wormers and burning). Studies show that the use of herbicides and ivermectin affects the structure of the community and reproductive activity of the beetles in pastures (Martínez et al. 2001; Lumaret and Martinez 2005; Martínez and Cruz 2009).

Livestock management systems that preserve trees as part of livestock management, e.g., the tree fallows of dry tropical forest and silvopastoral systems of *G. ulmifolia,* provide favorable conditions for the maintenance of landscape connectivity and diversity of species (i.e., good soil quality, low or medium intensity of management, high canopy cover, high quantities of leaf litter, etc.) and habitat conditions that are suitable for the persistence of a variety of species. Ranchers may decide to use conventional cattle production techniques with low plant diversity and high dependence on chemical fertilizers and herbicides. However, such a transformation would be likely to cause a dramatic change in the abundance of species within the landscape, with the local extinction of those species favored by landscape heterogeneity and landscape-scale extinctions in the longer term. In contrast, silvopastoral systems allow for a high diversity of beetles while maintaining profitable economic activity (livestock production). As we have stated, *Guazuma ulmifolia* is considered a multipurpose tree because of the wide variety of products and services it can provide to agriculture, livestock production, cattle fodder and the medical and cosmetic industries. These trees can reduce peak daytime temperatures near the soil surface and modify soil physical and chemical conditions, increasing fertility and moisture retention. Knowledge of the relationship between wildlife management practices and land use contribute to the effective management of ecosystems and therefore to the conservation of species diversity.

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