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Dung beetles and nutrient cycling in a dryland environment

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ABSTRACT

Insects are involved in the biogeochemical cycles of multiple elements and influence soil fertility. In particular, soil insects and the functions that they support can affect the response of terrestrial ecosystems to environmental changes. We experimentally studied the role of dung beetles as recyclers of cow dung in drylands of the Central Monte in mid-western Argentina; and we extrapolated these results to ecosystem impact in a grazing field, considering the dung beetle's abundance in summer. We conducted experiments with four species of dung beetles (*Sulcophanaeus imperator*, *Eucranium arachnoides*, *Digitonthophagus gazella* and *Malagoniella puncticollis*), and quantified their abundance on the field. Dung beetles incorporated nitrogen, ammonium, and phosphorous to the soil, but this activity varied substantially among species. The highest quantity of organic matter, nitrogen and phosphate was incorporated to the soil by *S. imperator*, one of the larger beetle studied. While the per capita effect of *S. imperator* is superior to other species studied, the impact on the ecosystem of the invasive *D. gazella* might be superior due to their major abundance in grazing fields. Our results highlight the importance of considering both components, per capita effect and abundance, to estimate with more reliability the relative importance of dung beetle species. Given that the effect of dung beetles on nutrient cycling is variable among species, and their abundance is variable in space, it is important to conserve beetle diversity in order to maximize their beneficial impacts on soils. Therefore, dung beetle effect on soil might be crucial in drylands to mitigate the nitrogen losses caused by grazing.

1. Introduction

Insects contribute substantially to ecosystem services such as pathogen control, pollination, soil nutrient regulation, and cultural heritage as well as to disservices including, pests, diseases, and allergenic and toxic organisms (Noriega et al., 2018). Even though the number of studies about the ecosystem services provided by insects has been increasing during the last decade, more experimental approaches are necessary to assess the services provided by different species (Noriega et al., 2018). For example, diversity and abundance of herbivorous insects were assumed to be key drivers of many ecosystem services (Soliveres et al., 2016), and an experimental study (Belovsky and Slade, 2018) showed a plausible mechanism through which grasshoppers may affect nitrogen availability: by preferentially altering the abundance of faster versus slowing decomposing plants.

Dung beetles are one of the best studied groups of decomposers (Noriega et al., 2018) as they contribute to many ecological processes and/or services, including nutrient cycling, ecosystem productivity, bioturbation, primary and secondary seed dispersal, plant growth, control of flies and parasites, and litter decomposition (Nichols et al., 2008; Tixier et al., 2015; Manning et al., 2016). Their importance stems from their dung relocation behavior, which consists in taking a piece of dung from a dung pad and burying it. Dung relocation behavior is associated with nesting behavior: dung beetles bury the dung to use it as a food source and a nesting substrate (nest balls). Female dung beetles lay their eggs within the nest balls, where they develop in moderate temperature and moisture conditions (Hanski and Cambefort, 1991).

Through their dung relocation and burrowing activities dung

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Table 1
Description of species used in the experiments.

Species	Dung relocation behavior	Body size (mm)	Native/invasive
Digitonthophagus gazella (Fabricius, 1781)	Tunneler	10 to 13	Invasive
Sulcophanaeus imperator (Chevrolat, 1844)	Tunneler	23 to 28	Native
Eucranium arachnoides (Ocampo, 2010)	Lifter	18.4 to 30.4	Native
Malagoniella (*Megathopomina*) *puncticollis* (Blanchard, 1846)	Roller	10 to 13	Native

beetles have the potential to influence soil physical and chemical properties. Dung relocation and nest ball construction facilitate the activation of microorganisms in manure involved in the nitrogen cycle (Breymeyer et al., 1975; Kazuhira et al., 1991). They also connect the breakdown processes of dung occurring above- and below-ground, contributing to the homogenization of microbial communities (Slade et al., 2016). Nest ball production inhibits ammonia volatilization, improving soil fertility by facilitating nitrogen absorption by plants (Huerta et al., 2013), encourages manure moisture loss, promotes proliferation of aerobic bacteria, and promotes nitrification in the buried dung as well as in the leftovers that remain at the soil surface (Kazuhira et al., 1991). In addition, by making burrow tunnels, dung beetles also help to reduce soil compaction and increase soil aeration (Manning et al., 2016), facilitating nitrogen mineralization (Bertone et al., 2006). Compacted soils occur frequently in rangelands with heavy livestock loads and have reduced pore volume, inhibiting degradation of lignin from animal manure (Breland and Hansen, 1996). While several experimental studies have assessed dung removal efficiency by dung beetles (Andresen, 2003; Larsen et al., 2005; Slade et al., 2007; Rosenlew and Roslin, 2008; O'hea et al., 2010; Giraldo et al., 2011; Beynon et al., 2012; Nervo et al., 2014; Tixier et al., 2015), other studies have assessed the impact of such removal on chemical properties of soils performed by several beetles (Kazuhira et al., 1991; Bertone et al., 2006; Miranda et al., 2000; Yamada et al., 2007; Nervo et al., 2017; Shahabuddin et al., 2017). However, to the best of our knowledge no studies have assessed the individual species effect on different chemical properties of the soil, as we have done here. Then, per species or functional group approximation would be more beneficial to understanding how is the role of dung beetles in nutrient cycling.

In many rangelands in dryland ecosystems, dung accumulation from domestic mammals has become a severe problem (Schowalter, 2016). Grazer dung accumulates near corrals and water sources due to the grazers' defecation patterns. Therefore, in these areas, soil disruption and vegetation removal caused by grazing increase nitrogen losses to the subsoil and the atmosphere, with a net reduction of total nitrogen and organic matter in the soils (Meglioli et al., 2014). Dung beetles, as well as termites, perform an important ecological function incorporating livestock dung to the soil and promoting pasture regeneration (Schowalter, 2016).

In this study, we assess the role of dung beetles on nutrient incorporation from cow dung to soils in dry rangelands. We hypothesize that dung burial by dung beetles increases the nutrient concentration in the soil profile, by incorporating dung from the surface into the soil and by building burrow galleries that facilitate lixiviation. To test this hypothesis, we experimentally assessed nutrient incorporation into the soil at two different depths by four dung beetle species from the Monte desert of Argentina. We also estimated the ecosystem impact of different dung beetle species on organic matter incorporation to the soil by combining our data on effects of individual beetles on nutrient cycling in pots with beetle abundance in grazing fields. Our study is the first to evaluate the importance of three native and one invasive dung beetle species in preventing nutrient losses at soil chemical and ecosystem levels in a dryland, where livestock raising is the main type of land use.

2. Methods

2.1. Study species

Dung beetles can be classified in four main functional groups according to their dung removal behavior in the ecosystem of study: dwellers, which feed without burying the dung or if they bury it they do it immediately below; tunnelers, which bury dung without transporting it under the dung pat; lifters, which transport dung without forming a dung ball, catching the dung with the foretibiae and running forward using middle and hind legs; and rollers, which transport dung by shaping it into a ball, which they roll (Halffter and Matthews, 1966; Ocampo and Hawks, 2006; Davis and Scholtz, 2001). We selected four dung beetle species for our experimental study: *Digitonthophagus gazella*, (Fabricius, 1781), *Sulcophanaeus imperator* (Chevrolat, 1844) *Malagoniella* (Megathopomina) *puncticollis* (Blanchard, 1846), and *Eucranium arachnoides* (Ocampo, 2010) (Table 1). We chose these species based on their abundance and the representativeness of functional groups, so as to have an idea of the impact of the dung beetle community as a whole. Dweller beetles (Scarabaeidae: Aphodiinae), another functional group, were also present in the study area, but were not included in this study because they use dung inside the dung pad or move it near the soil surface, and are thus unlikely to have a significant effect on soil nutrients (Milotić et al., 2017; Rosenlew and Roslin, 2008). Body size is also important to classify dung beetle functionality, because body size is positively associated with dung burial (Slade et al., 2007; Nervo et al., 2014). Body lengths (an adequate proxy of body size; Shahabuddin and Tscharntke, 2005) of the study species are the following: *S. imperator*, 23–28 mm (Edmonds, 2000); *M.* (*Megathopomina*) *puncticollis*, 10–13 mm; *E. arachnoides*, 18–30 mm (Ocampo, 2010); and *D. gazella*, 10–13 mm (Montes de Oca and Halffter, 1998; Table 1).

2.2. Collection site of experimental materials

We collected beetles, soil and cow dung for experiments in cattle fields around The Man and Biosphere Reserve of Ñacuñán (340° 02′ S, 670° 58′ W), located in Mendoza Province, Argentina, in the Monte Biogeographic province. The climate of Ñacuñán is arid-semiarid with high seasonality, hot, humid summers and dry, cold winters; approximately 70% of the annual rainfall occurs between October and March (spring and summer; Marone et al., 2000; Abraham et al., 2009). The annual and inter-annual mean precipitation in the Central Monte is highly variable, from very dry (< 200 mm) to wet years (> 400 mm) (Estrella et al., 2001). In this study, we manually watered the experimental pots (see details below) to simulate a year with low rainfall, because it constitutes the most common extreme situation (Estrella et al., 2001), and nutrient incorporation to the soil by abiotic processes is presumably lower, which would make the effect of beetles more relevant than in wet years. Extensive grazing is the most common anthropogenic activity in the Central Monte (Villagra et al., 2009) and dung beetles use cow dung to feed and reproduce in addition to dung from native vertebrates (Ocampo and Molano, 2011).

Table 2

Model results (GLS) selected to estimate the different nutrients that *E. arachnoides*, *S. imperator* and *D. gazella* incorporate to the soil at depth 1 (0–10 cm) and 2 (10–20 cm). The 'Coefficient' column indicates the variation of each nutrient of each dung beetle species assessed compared to control (pot without beetles), and *p* indicates whether this difference is statistically significant. Bold coefficients indicate a significant difference with control, while an asterisk indicates a marginally significant difference with control at a confidence level of 95%.

Response variable	Soil depth (cm)	Treatment	Coefficient	sd	Statistics of models		Sample size
					F	*p*	
Organic matter	0–10	*E. arachnoides*	0.55	0.48	6.89	0.0005	20
		S. imperator	**2.9**	0.7			38
		D. gazella	**0.75**	0.32			28
Organic matter	10–20	*E. arachnoides*	0.11	0.19	7.15	0.0004	18
		S. imperator	**2.6**	0.6			40
		D. gazella	1.42*	0.76			24
Total nitrogen	0–10	*E. arachnoides*	75.4	46.31	4.08	0.011	24
		S. imperator	**132.8**	38.77			38
		D. gazella	63.84	40.48			24
Total nitrogen	10–20	*E. arachnoides*	142.7*	75.61	7.26	0.0004	20
		S. imperator	**340.45**	76.93			36
		D. gazella	41.38	33.9			10
Nitrate-N	0–10	*E. arachnoides*	−10.2	8.6	1.19	0.31	12
		S. imperator	−0.34	7.54			12
		D. gazella	−11.5	8.26			14
Nitrate-N	10–20	*E. arachnoides*	−2.75	7.78	0.57	0.63	10
		S. imperator	−0.19	3.5			24
		D. gazella	4.6	4.5			12
Ammonium-N	0–10	*E. arachnoides*	1.53	1.52	1.96	0.13	12
		S. imperator	−1.48	1.2			18
		D. gazella	−1.39	1.26			14
Ammonium-N	10–20	*E. arachnoides*	**3.28**	0.75	10.5	0.0001	12
		S. imperator	0.57	1.14			22
		D. gazella	−0.5	0.86			10
Phosphate-P	0–10	*E. arachnoides*	**12.94**	5.93	4.64	0.006	12
		S. imperator	**14.97**	6.7			18
		D. gazella	**18.05**	5.82			14
Phosphate-P	10–20	*E. arachnoides*	6.12	4.99	7.24	0.0004	12
		S. imperator	**33.09**	7.13			20
		D. gazella	7.84	7.7			12

2.3. Experiments to quantify the nutrients incorporated by dung beetles to the soil

2.3.1. General experimental procedures

We conducted two experiments to describe the effectiveness of dung beetles at incorporating nutrients to the soil. Both experiments were carried out at the CONICET Scientific and Technological Centre of Mendoza, Argentina. We collected dung and soils in the surrounding of The Man and Biosphere Reserve of Ñacuñán, air dried the soils, and placed soil and cow dung in gardening pots. We estimated the weight of soil necessary to fill the volume of the pots and approximate a soil bulk density observed in the field in a previous study (1.35 g/cm^3; Asner et al., 2003), avoiding excessive soil compaction that could prevent beetle tunneler behavior. All pots were covered with a mesh to prevent beetles from escaping. The cow dung (150 g) was placed in the center of the pot. Each pot was manually watered with a volume of water equivalent to 42 mm of rainfall in total (i.e. a column of water 42 mm height over all the pot surface), split into five watering events: 1, 10, 15, 20 and 29 days after the beginning of the experiment. Water quantity simulated local rainfall in the aridity situation (i.e., the rainfall average calculated for dry years in February and March, n = 15) that characterizes the study area, where the water is the main limitation on biological activity (Nielsen and Ball, 2015). To study nutrient content in the soil, soil samples were extracted at the beginning of the experiment, when pots were constructed, at two depths in each pot: 0–10 cm and 10–20 cm. The soil was stored until analysis in plastic bags, then it was sieved to extract woody debris and homogenized.

After the experimental units were constructed, beetle specimens of the different species were collected in the field using pit fall traps without water, to catch them alive, and baited with cow dung. Then each beetle was transported in individual plastic boxes with humid soils to the experimental station, and placed in the pots.

At the end of the experiment (after 70 days), to determine final nutrient concentrations in the soil, two samples were extracted with a 50 ml conic propylene Falcon tubes at the two depths. Dung decomposition rate depends mainly on temperature and precipitation; thus, we ran the experiment for 70 days to simulate at least two months of the rainy season (summer). We analysed organic matter, total nitrogen, ammonium, nitrate, and phosphorus concentrations in the soil samples of the experiment with tunnelers and lifter. In the experiment with the rollers, we analysed only organic matter.

2.3.2. Experiment I: soil nutrients incorporated by tunnelers and lifters

We used 21 pots, each with one individual of *S. imperator* (native large tunneler), 11 pots, each with one individual of *E. arachnoides* (native large lifter, one beetle per pot), 15 pots each with a male and a female of *D. gazella* (invasive small tunneler, two beetles per pot), and 15 control pots, all of 25 cm diameter and 28 cm high, and 10.5 kg of soil. We used couples instead of single beetles for *D. gazella* because in a preliminary experiment we observed that one individual of this species removes dung only if there is another individual, female or male, in the pot (M.B. Maldonado, personal observation). In addition, a previous study (Miranda et al., 2000) on nutrient incorporation to the soil by dung beetles reported positive results when placing a couple of *D. gazella* per experimental unit.

2.3.3. Experiment II: nutrients incorporated by rollers

Because of the different dung relocation behavior of *M. puncticollis*, we designed a different experiment to assess its effectiveness in nutrient incorporation into the soil. To allow individuals to roll the dung ball, we constructed pots of 40 cm diameter, 23 cm height, with 45 kg of soil. For this experiment, we manually built the pots with metallic mesh in the shape of a cylinder and covered them with black plastic inside and with mosquito netting at the top to prevent dung beetles from escaping. We used 20 pots with one non sexed *M. puncticollis* beetle each, and 8 control pots.

2.4. Soil nutrient analysis

A first group of subsamples was extracted to determine ammonium and nitrate concentration of the soil (considered to represent available nitrogen), a second group was used to determine gravimetric soil moisture, and a third one to determine total nitrogen, organic matter and phosphorous. Subsamples for ammonium determination were extracted with 2N KCl solution (20 g of soil in 60 ml of 2 N K Cl), and frozen until analysis. Subsamples for nitrate determinations were extracted with a silver sulphate extraction solution. Both ions, nitrate and ammonium, were analysed by spectrophotometry, with cadmium reduction method for nitrate (with HACH kits) and the phenol-hypochlorite method for ammonium (Weatherburn, 1967) (Table 2).

The second group of subsamples was dried at 100 °C for gravimetric moisture determination. The third group of subsamples was dried at 60 °C for total nitrogen, organic matter and available phosphorous determinations (Table 2).

The organic matter content was determined by dry combustion (Davies, 1974), and total nitrogen content was determined by the Kjeldahl method (Pearcy et al., 1989). Although loss of the ignition method (dry combustion; Davies, 1974) could overestimate organic matter content in the soil in comparison with other methods, we considered it appropriate to process simultaneously a large number of samples and to avoid the production of toxic wastes associated with other methods (Wang et al., 2012). Available phosphate was determined in Olsen extraction (4 g of soil in 10 ml de 0.5 M $NaHCO_3$) and spectrophotometry after the reaction with ammonium molybdate (Okalebo et al., 1993). Spectrophotometric measurements were carried out with spectrophotometer HACH DR2800.

2.5. Statistical analysis

Generalized least squares (GLS) models were used for experiments (I and II) to compare the nutrient contribution of each dung beetle species with the control. We selected two models per nutrient analysed (organic matter, total nitrogen, ammonium, nitrate, and phosphorous), one for the surface soil (0–10 cm) and another for the deeper soil (10–20 cm). Analyses were carried out using R (R Development Core Team, 2015, version 3.2.2) with the nlme package and following the model selection protocol proposed in Zuur et al. (2009, chapter 4).

The models considered the treatment (levels for experiment I: Control, *S. imperator*, *E. arachnoides* and *D. gazella*; levels for experiment II: Control and *M. puncticollis*) as the explanatory variable, whose variance was corrected with *varIdent* when necessary due to differences in variances between the treatments. The effect of each dung beetle species was estimated using the control, which was represented by the intercept in all the models. The response variable was the difference between the nutrient concentrations determined at the moment of pot disassembly (time 1) and during the pot assemblage (time 0).

2.6. Ecosystem impact

To estimate the ecosystem impact of each species, we estimated dung beetle abundance and diversity in five grazing fields in 2015 and 2016. We placed pitfall traps in a cattle grazing gradient, from 10 to 2500 m from the watering point (10, 60, 110, 300, 500, 1000, 1500 y 2500 m). At each distance to the water point we placed three traps, separated by 20 m, covering an approximate area of action of 600 m^2. The traps were baited with cow dung during three months: January, February and March of 2015, because the greater abundance of dung beetles occurs in the summer season. The traps were active in the field for 48 h., twice per month, adding up to 1458 traps. The abundance was estimated for each plot of a grazing field (i.e. each distance to the watering point), and was calculated with the data of the five grazing fields, during the three months of sampling.

To calculate the ecosystem impact of each species on nutrient cycling, we multiplied the amount of organic matter incorporated to the soil by each individual in the pots (values predicted in GLS models per species in grams/beetle for both depths), by the average abundances (number of individuals per 600 m^2 plot) of each species collected during the three study months. Moreover, error propagations were calculated with an on line calculator (Laffers, 2005–2008).

3. Results

The dung beetle species differed in their role as recyclers in our experimental pots, with the strongest effect found for *S. imperator* (native large tunneler). The differences observed in nutrient concentrations (day 70–day 0) varied between 0 and 10% for organic matter, between −507.72 and 808.63 μg of total nitrogen per gram of soil (μg g^{-1}), between −35 and 73 μg N-NO_3^- g^{-1}, between −13 and 3.5 μg N-NH_4^+ g^{-1}, and between −24 and 109 μg P-PO_4^{-3} g^{-1}.

3.1. Experiment I: nutrients incorporated to the soil by S. imperator, E. arachnoides and D. gazella

D. gazella increased significantly organic matter and phosphorus at surface level but not at a greater depth (Fig. 1, Table 2). In turn, *E. arachnoides* increased ammonium at the greater depth and phosphorus at the surface level (Fig. 1, Table 2). Finally, *S. imperator* increased significantly organic matter, total nitrogen and phosphorus at both depths (Fig. 1, Table 2).

3.2. Experiment II: nutrients incorporated by M. puncticollis

M. puncticollis did not increase organic matter concentration (Table 3) in the soil. Given this result, we decided not to perform other chemical analyses.

3.3. Ecosystem impact

D. gazella was the most important dung beetle for the ecosystem because it incorporated 6 times as much organic matter as *S. imperator*, while other species had a negligible impact as recyclers. *D. gazella* incorporated 595.35 g of organic matter in total in eight 600 m^2 plots, equivalent to 0.12 g of organic matter per m^2 (Table 4). This result is mainly due to the greater abundance of *D. gazella* in the field, as individual (per capita) effect of this species is lower than *S. imperator*. Contrarily, *S. imperator*, which had the highest per capita contribution of organic matter to the soil in the pots, incorporates only 81.9 g of organic matter in the eight 600 m^2 plots (i.e., ca. 6 times less than *D. gazella*), because of its relatively low abundance. The ecosystem impacts of *E. arachnoides* and *M. puncticollis* are relatively low, in both cases because of their low abundances and, also in the case of *M. puncticollis*, because of its low per capita effect (Table 4). Moreover, the ecosystem impacts decrease slightly with the distance to the water point (Pearson correlation: $r = -0.24$, $p = 0.19$, df = 30; Fig. 2).

4. Discussion

Our results support the hypothesis that dung burial by dung beetles increases the nutrient concentration in the soil profile and provides information on how different species can incorporate nutrients to the soil of this arid environment. Specifically, three of the four studied dung beetle species increased nutrient concentrations in the soil, although the effects of the different species varied in terms of nutrient type and quantity, suggesting that different species may complementarily

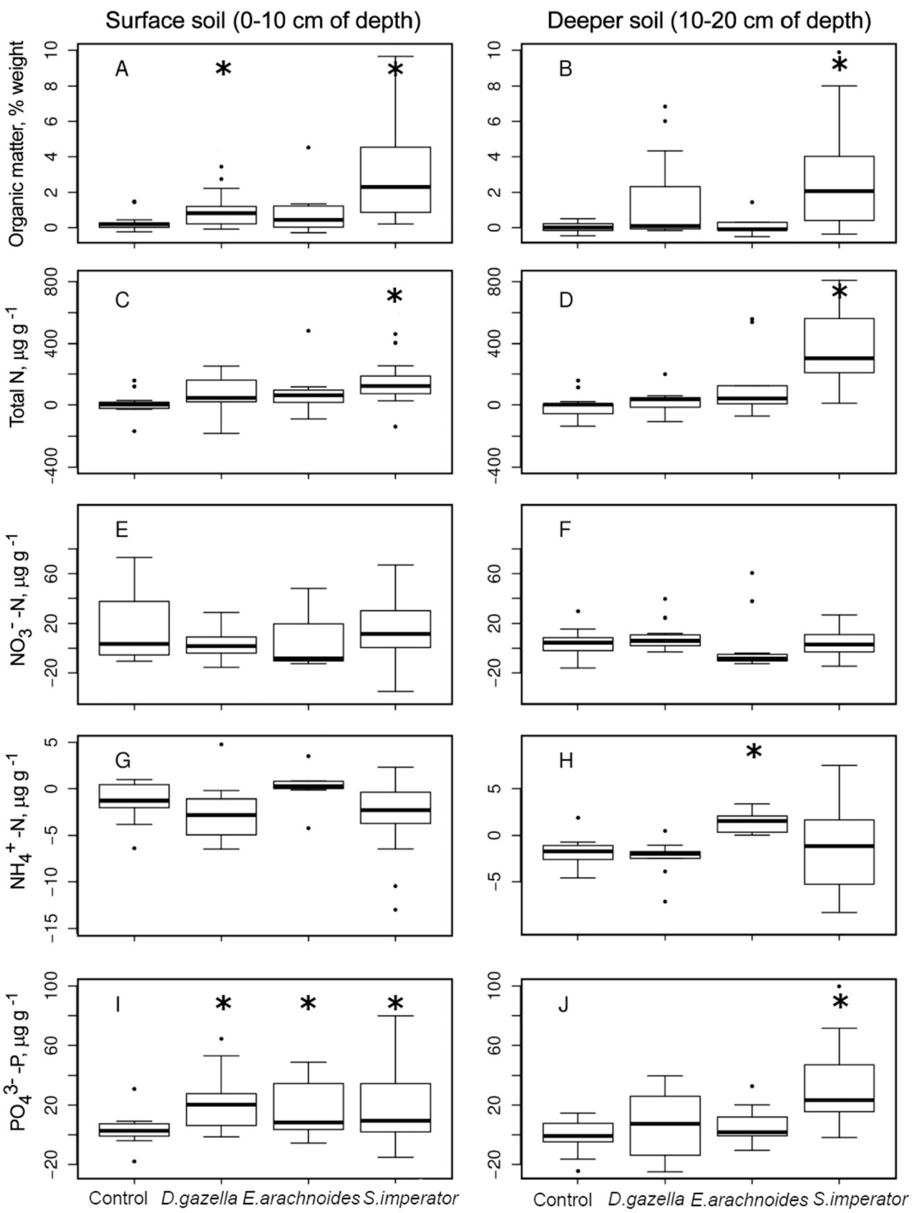

Fig. 1. Box-plots of beetle effect on nutrient incorporation (final-initial) into the soil. Box-plots on the left side show the effect on surface soils (0 to10 cm of depth). Box-plots on the right side show the effects on deeper soil (10 to 20 cm of depth). In all cases horizontal axes correspond to the treatments, from left to right listed in order of body size, from smaller to greater (although *E. arachnoides* and *S. imperator* has similar body size): Control (pots without beetles), *Digitonthophagus gazella*, *Eucranium arachnoides*, and *Sulcophanaeus imperator*. Top panels: (A and B) organic matter (% weight); middle panels C and D: total nitrogen (μg g^{-1}); E and F: Nitrate-N (μg g^{-1}); G and H: Ammonium-N (μg g^{-1}); I and J: Phosphate-P (μg g^{-1}). For each treatment, the middle line represents the median, the lower and upper box limits represent the first and third quartile in the data distribution, respectively, error bars indicate the point inside of 1.5 times the distance between the median and quartiles, and the circles represent the extreme values that exceed the error bars. Asterisks represent significant differences with the control ($p < 0.05$).

Table 3
Model values (GLS) selected to estimate the concentration of organic matter incorporated to soil at depth 1 (0–10 cm) and 2 (10–20 cm) by roller dung beetles. 'Coefficient' column indicates the variation of each nutrient of each dung beetle assessed respect to control (pot without beetles), and the *p* value indicates if this difference is statistically significant.

Treatment	Organic matter (0–10 cm)		Organic matter (10–20 cm)	
	Coefficients	Standard error	Coefficients	Standard error
M. puncticollis	0.48	0.3	0.17	0.21
	Model statistics F = 2.7	df = 1, *p* = 0.11	Model statistics F = 0.6	df = 1, *p* = 0.44

increase soil fertility and plant growth (Bang et al., 2005). Heterogeneity in soil nutrients, chemical form and vertical distribution, may induce plant diversity, similar to the ecological role reported for termites (Sileshi et al., 2010). Thus, plant and animal diversity may have a positive feedback towards higher diversity and productivity (Tilman et al., 1997; Soliveres et al., 2016). Furthermore, differences between beetle and control treatments indicate that cow dung deposition alone is not enough to incorporate nutrients to the soil. At the ecosystem level, the exotic beetle *D. gazella* is incorporating the highest quantity of organic matter to the soil compared with the other native species studied, because of the high abundance of this species in grazing fields. Our findings add to the evidence indicating that to estimate dung beetle species importance for an ecosystem more reliably we need to know both abundance and the per capita effect.

S. imperator contributed the most to nutrient cycling at the individual level compared to other species, increasing organic matter, total nitrogen and phosphorous concentrations into the soil at both depths analysed. These results could be explained by its behavior as a tunneler and its large body size. Dung beetles with tunneler behavior are good promoters of microbial activity and respiration in deeper layers of the soil (Menéndez et al., 2016; Haynes and Williams, 1993). Individuals of *S. imperator* also bury the dung in large pieces, disintegrating it first over the soil (M. B. Maldonado, pers. obs.), which prevents the formation of a dry crust, commonly formed over the dung pad, which may prevent rain from moistening dung and thus inhibit

Table 4
Estimation of ecosystem impact of dung beetles in a grazing field. The product of beetle abundance and organic matter incorporated per individual in the pots is detailed between parentheses. Abundance was estimated for each plot of a grazing field (i.e. each distance to water point). Individual effect was calculated adding organic matter incorporated at the two soil depths (0–10 and 10–20 cm depth) assessed. Propagated error are after the signs: ‘ ± ’.

Dung beetle abundance × grams of organic matter per species up to 20 cm depth (abundance ⁎ grams of organic matter per beetle)					
Distance to water point (meters)	*E. arachnoides*	*S. imperator*	*D. gazella*	*M. puncticollis*	Total organic matter incorporated in each plot (grams in 600 m^2)
10	3.24 ± 3.1	31.5 ± 17.4	122.85 ± 177.9	1.27 ± 0.8	158.86 ± 199.2
60	3.24 ± 3.2	12.6 ± 16.7	126.9 ± 196.5	2.54 ± 1.0	144.98 ± 217.4
110	1.08 ± 1.9	6.3 ± 16.5	98.55 ± 115.4	1.27 ± 0.8	107.2 ± 134.6
300	1.08 ± 1.8	6.3 ± 11.4	81 ± 110.9	2.54 ± 2.4	90.92 ± 126.5
500	1.08 ± 1.0	6.3 ± 3.8	62.1 ± 67.3	2.54 ± 2.1	72.02 ± 74.2
1000	1.08 ± 1.3	6.3 ± 14.1	44.55 ± 45.5	3.81 ± 4.8	55.74 ± 65.7
1500	1.08 ± 1.0	6.3 ± 3.5	28.35 ± 48.4	2.54 ± 5.2	38.27 ± 58.1
2500	1.08 ± 1.5	6.3 ± 7.0	31.05 ± 33.1	6.35 ± 8.5	44.78 ± 50.1
Total	12.96	81.9	595.35	22.86	712.77

microbial decomposition (Haynes and Williams, 1993). In addition, a larger body size implies that these beetles are consuming more dung than the smaller ones, even of the same functional group (Nervo et al., 2014). Given the high potential for dung burial of *S. imperator*, and their lower abundances in grazing fields, further population studies, as well as the effect of the invasive tunneler and the cow pest control on their abundance, are needed to design conservation strategies for this native beetle.

E. arachnoides individuals increased total nitrogen and phosphorous concentrations in the soil surface, and ammonium concentration at greater depths. This slighter effect compared to *S. imperator* effect could be explained by the burying behavior of *E. arachnoides*, as it relocates dung from the pad edges, causing a minor disintegration effect compared with tunnelers, even though their body size is relatively large (18–30 mm). This underground relocation of dung might explain the observed increased ammonium concentration in deeper layers of the soil sampled, a condition that might lead to increase nitrogen mineralization rates. This effect can be particularly relevant in arid lands, where nutrients standing above the dry soil surface are unavailable to plants, and are thus more likely to be lost by volatilization processes. Conversely if nutrients are in deeper, moister layers, they can be used by plants (Li et al., 2009) even up to one year later (Nervo et al., 2017) and independently of rains.

The exotic *D. gazella* individuals, in spite of being smaller than *S. imperator* and *E. arachnoides*, increased organic matter and phosphorous concentration, possibly because they crumble the dung pad, in the way described above for *S. imperator*. Other studies agree with our results (Rowarth et al., 1985; Haynes and Williams, 1993), reporting that phosphorous incorporation to the soil is enhanced by the physical breakdown of the dung. In the field, mechanical degradation is also produced by rains (Haynes and Williams, 1993), in addition to cow trampling, mainly on the trails (Campos et al., 2011). Therefore, mechanical degradation of dung by dung beetles could be more necessary during years with low rainfall, which are frequent in our study region.

The roller dung beetle *M. puncticollis* did not show a significant effect on soil organic matter, probably because this species transports only small dung pieces from the edges of the pad. The small quantities of transported dung are probably a direct result of the small body size of this species. In addition, transport of dung outside the dung pad may distribute nutrients in a larger area, preventing the detection of nutrient incorporation by our sampling method. In our study area there are other species that also belong to the roller functional group and are larger than *M. puncticollis*: *Megathopa villosa* (14.9–26 mm body length; Alfaro and Pizarro-Araya, 2008), and *Eudinopus dystiscoides* (30 mm; Invertebrate collection of IADIZA). *M. villosa* and *E. dysticoides*, both roller species, may be more efficient than *M. puncticollis*, but they are unlikely to be as good as tunnelers, as reported by Doube (1990) for other guilds, in which the tunnelers are more efficient than roller species.

Dung beetle ecosystem impact could be particularly important in highly disturbed areas of rangelands, such as those around water sources. Chillo et al. (2017) reported that decomposition rates over the soil are lower in areas around water sources, where grazing intensity is higher, compared with more distant sites, because of changes in plant

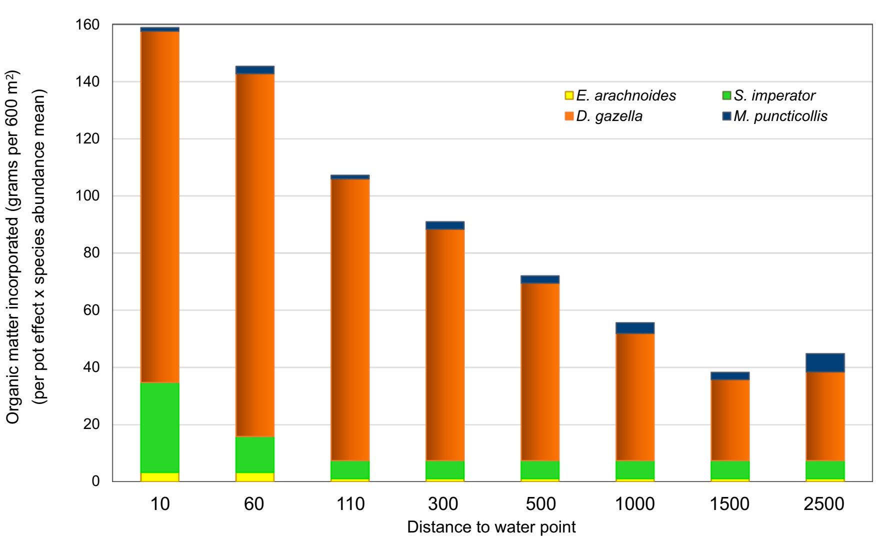

Fig. 2. Ecosystem impact of dung beetles. The estimation of organic matter incorporated (grams) per grazing field in three months of summer in each 600 m^2 plot. The impact was calculated by multiplying per capita effect of beetles in pots on organic matter incorporation by the average abundance (number of individuals/per 600 m^2 plot) of each species.

biomass and vegetation structure leading to decreased plant cover (Bisigato and Bertiller, 1997) and lower water infiltration (Yates et al., 2000). Other studies indicate that soil nitrogen and carbon are lower in the first 100 m around water points (Smet and Ward, 2006). In the present study, our estimates of nutrient incorporation in the ecosystem assumed no limitation by dung availability or environmental conditions, and a similar behavior in the pots as in the rangelands. We found that the dung beetle abundance and estimated nutrient incorporation, in particular of *D. gazella*, is higher in the first 300 m around the water point, contributing to mitigate the negative effect of grazing on decomposition rates, nitrogen and carbon concentration in the soil (Table 4, Fig. 2).

Finally, our results should be treated with caution since they arise from manipulative experiments and not directly from field measurements. Moreover, the experiments present some internal differences in design (pot size, one or a couple of beetles), because we considered differences in space and behavior requirements for each species. Future studies should address the impact of dung beetle directly in grazing fields, and the importance of native beetles on nutrient recycling using native animal dung in ungrazed fields.

5. Conclusions

The dung beetle species studied here appear to have an important, but differential role in nutrient cycling in our study system, and their relative importance also depends on the scale: microsite or ecosystem. Therefore, through their dung relocation and burrowing activities, they are likely to complementarily contribute to maintain soil fertility in this region. The strong ecosystem effect of *D. gazella* should stimulate additional studies about their use in restoration programs, albeit with caution, because of the potential for negative interactions between exotic and native dung beetles. The differential effect of beetle species on soil nutrients calls for conservation of the diversity of native beetles.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2019.03.035.

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