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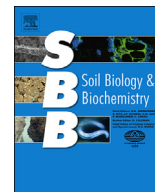*Instituto de Ciencias de la Tierra y Ambientales de La Pampa*

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Burrowing herbivores alter soil carbon and nitrogen dynamics in a semi-arid ecosystem, Argentina

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ABSTRACT

Activities of burrowing herbivores, including movement of soil and litter and deposition of waste material, can alter the distribution of labile carbon (C) and nitrogen (N) in soil, affecting spatial patterning of nutrient dynamics in ecosystems where they are abundant. Their role in ecosystem processes in surface soil has been studied extensively, but effects of burrowing species on processes in subsurface soil remain poorly known. We investigated the effects of burrowing and grazing by plains vizcachas (*Lagostomus maximus*, Chinchilidae), a large colonial burrowing rodent native to South America, on the distribution and dynamics of C and N in soil of a semi-arid scrub ecosystem in central Argentina. *In situ* N mineralization (N_{min}), potential N_{min} and CO_2 emissions were measured in surface soil (0—10 cm) and soil at the mean depth of burrows (65 ± 10 cm; mean $\pm$ 1 SD) in five colonial burrow systems and adjacent grazed and ungrazed zones. Decomposition and N dynamics of vizcacha feces on the soil surface and in burrow soil was assessed using litterbags. Total C and N in soil in burrows were 1.6 and 5.5 times greater than in undisturbed soil at similar depths, and similar to amounts in surface soil. Inorganic N, particularly NO_3^-, was consistently highest in burrows, intermediate in surface soil on burrow systems, and relatively low in all other zones. Despite high C and N content in all burrows, *in situ* net N_{min} was highly variable in burrow soil. Feces decomposed and released N more rapidly in burrow soil. Laboratory incubations indicated that soil moisture limited N_{min} under conditions that typically characterize burrow microclimate, and that rates increased dramatically at soil moisture contents >25% field capacity, which likely occurs during pulsed rainfall events. Thus, the high and seasonally stable NO_3^- content in burrow soil likely originated from the accumulation of pulsed mineralization events over time. Burrowing and waste deposition by vizcachas produced "resource islands" at the landscape scale. At a measured density of 0.3 burrow systems per hectare, colonial burrow soil contained an amount of inorganic N equal to 21% and 30% of plant-available N in surface soil and subsurface soil, respectively, in an area that represented only 0.35% of the landscape. Our study indicates that burrowing and deposition of waste results in a highly active subsurface layer in which C and N dynamics function much like surface soil when soil moisture is not limiting.

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1. Introduction

Labile carbon (C) and nitrogen (N) in soil organic matter drive microbial activity and N mineralization (N_{min}), largely determining plant-available N in semi-arid ecosystems (Mazzarino et al., 1998; Carrera et al., 2009; Yahdjian et al., 2014). Spatial distribution of soil organic matter is regulated by geomorphic features at large scales and by biotic factors at local scales, while temporal heterogeneity in microbial activity and N_{min} are strongly influenced by pulsed rainfall events (Austin et al., 2004; Yahdjian and Sala, 2010; Reichmann et al., 2013). Plant — soil feedbacks are well understood in shrub-dominated semi-arid ecosystems and can result in patches of C and nutrient-rich soil around woody vegetation embedded in a matrix of soil depleted in C and nutrients (Schlesinger et al., 1996; Mazzarino et al., 1998; Cross and Schlesinger, 1999; Eldridge et al., 2011; Sankey et al., 2012). Activities of animals also redistribute and

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concentrate labile C and N in soil, and this can occur at spatial and temporal scales that differ from geologic and plant-driven processes that typically control C and nutrient distribution in soil (Jobbágy and Jackson, 2001; Wagner et al., 2004; Wagner and Jones, 2006; Villarreal et al., 2008; Whitford et al., 2008; Eldridge et al., 2011).

Semi-fossorial, herbivorous mammals are a taxonomically diverse group in semi-arid shrub and grassland systems worldwide (Davidson et al., 2012; Fleming et al., 2014). These species forage on vegetation aboveground, but construct burrows and spend much of their time belowground. They have the potential to modify ecosystem processes horizontally across the landscape through grazing, and vertically in the soil profile by activities associated with burrowing. Their belowground activities, including burrowing, nest building, and waste deposition, may be particularly important because these activities potentially alter nutrient availability for deeply rooted vegetation and conserve nutrients that could otherwise be lost through disturbances such as fire, or erosion by wind or overland flow (Villarreal et al., 2008; Hierro et al., 2011; Monger et al., 2015; Bonachela et al., 2015). However, understanding of the role of mammals in belowground nutrient dynamics is limited because their impacts largely have been investigated for surface soil, and, with few exceptions studies of belowground effects of these species have focused on nutrient pools in soil rather than C and N dynamics. Thus key processes for understanding ecosystem-level impacts of herbivorous, burrowing mammals are largely unknown.

Processes by which herbivorous semi-fossorial species affect soil C and N dynamics include bioturbation, the movement of soil and litter, and deposition of waste material belowground (Cortinas and Seastedt, 1996; Whitford and Kay, 1999; Sherrod and Seastedt, 2001; Eldridge and Koen, 2008; Villarreal et al., 2008; Yurkewycz et al., 2014). Animal activity concentrated around burrow entrances may result in high rates of waste deposition at the soil surface, and burial of litter and waste material by soil ejected from burrows can stimulate decomposition and nutrient release (Ayarbe and Kieft, 2000; Canals et al., 2003; Kerley et al., 2004; Hewins et al., 2013; Yurkewycz et al., 2014). In contrast, mixing of surface and subsurface soil can dilute labile C and N content, and thus slows N turnover in surface soil. Similarly, belowground activities of burrowing species could accelerate or decelerate N cycling. Many burrowing herbivores forage aboveground and deposit waste material belowground in burrows, transferring and concentrating C, N and other nutrients from surface to subsurface locations, potentially increasing N turnover belowground (Whitford and Kay, 1999; Villarreal et al., 2008). In contrast, lower soil moisture and cooler temperatures deeper in the soil profile could reduce N turnover compared to cycling rates at the soil surface. The sum of positive and negative outcomes of these processes, coupled with the spatial distribution and dynamics of burrowing herbivore populations, determine their importance in C and N cycling at the ecosystem scale.

To understand how burrowing herbivores affect C and N dynamics in soil, we examined the activities of one of the world's largest semi-fossorial rodents (plains vizcacha, *Lagostomus maximus*, Chinchillidae, adult males 5–9 kg, adult females 3–5 kg; Plate S1), which is native to grasslands and semi-arid regions of central and southern South America. We predicted that: 1) waste deposition belowground in colonial burrows increases labile C and N in soil, leading to greater rates of microbial activity and net N_{min} compared to undisturbed subsurface soil, 2) multiple effects of vizcachas on surface soil on colonial burrow systems could either increase or decrease net N_{min}, depending on the whether increases in labile C and N from waste deposition compensate for decreases in C and N resulting from bioturbation and intense grazing, and 3)

intense grazing by vizcachas and their net effect on litter in locations surrounding burrows decreases labile C and N, resulting in reduced net N_{min} in surface soil. To quantify effects of bioturbation and waste deposition on C and N dynamics in subsurface soil, we measured C and N pools and *in situ* net N_{min} in colonial burrow systems and compared values to belowground locations that were not altered by vizcachas. Similarly, to assess combined effects of grazing, waste deposition and bioturbation on surface soil of burrow systems, we compared C and N pools and *in situ* net N_{min} on burrow systems to locations only subjected to grazing by vizcachas and those with no vizcacha activity. To further understand how activities of vizcachas interact with environmental factors affecting soil C and N dynamics, we evaluated interactive effects of soil moisture and temperature on microbial activity and net N_{min} in soil from colonial burrows and adjacent grazed and ungrazed locations in the laboratory. Given the high inter-annual variability in rainfall in our study site, these experiments provided insight into potential effects of vizcachas on nutrient dynamics over a broader range of environmental conditions than was captured during our field study. Using previously reported long term census data of vizcacha colonies in semi-arid scrub of central Argentina, we then estimated landscape-level effects of vizcachas on plant-available N in subsurface soil.

2. Methods

2.1. Site description

Research was conducted at Los Valles (39°11′S, 63°42′W), an approximately 10,000-ha livestock ranch located on the Colorado River, 50 km E of La Adela, La Pampa Province, Argentina. Annual mean air temperature is 15.2 °C, and mean air temperatures for July and January are 7.6 °C and 23.2 °C, respectively. Mean annual precipitation at La Adela is 459 ± 163 mm (mean ± 1 SD; 1970–2010), with a decrease in precipitation during the winter months. The landscape is composed of low angle slopes and large flat valleys, and includes eroded calcareous marine deposits of the Rio Negro formation. Soils are predominately entisols of alluvial origin and are sandy loams. Soil horizons are poorly differentiated. Vegetation is dominated by shrubs, primarily *Larrea divaricata* Cav., *Prosopis flexuosa* DC., *Condalia microphylla* Cav., *Geoffroea decorticans* Gillies ex Hook. & Arn. Burkart, and *Prosopidastrum globosum* Gillies ex Hook. & Arn. Burkart. Understory vegetation consists of perennial bunchgrasses (e.g., *Nassella* spp. and *Piptochaetium napostense* Speg.), subshrubs (e.g., *Ancantholipia seriphioides* A. Gray, *Cassia aphylla* Maslin), and herbs (e.g., *Baccharis* spp., *Sphaeralcea crispa* Baker). Los Valles ranch is lightly to moderately grazed by cattle.

2.2. Vizcachas, vegetation, and litter

Plains vizcachas are herbivorous rodents native to Pampas grasslands and adjoining semi-arid ecosystems in Argentina, Bolivia, and Paraguay (Plate S1). Vizcachas are highly social, and matrilineal groups occupy the same large communal burrow system (~5–20 m in diameter with 10–50 burrows) for long periods of time (years to decades; Branch, 1993; Branch et al., 1994, 1996). Vizcachas are keystone species and ecosystem engineers (Machicote et al., 2004; Hierro et al., 2011), and produce impacts in three spatially defined zones. First, within burrow systems (approximately 0.5–1 m below the soil surface), bioturbation and deposition of waste results in higher total C, N, phosphorus and inorganic N content in soil (Villarreal et al., 2008). Second, feces and urine are deposited on colonial burrow systems, intensive grazing nearly eliminates grasses and herbaceous vegetation, and

bioturbation redistributes subsurface soil onto the surface, including precipitated mineral deposits that subsequently re-weather (Villarreal et al., 2008). Third, in the zone surrounding burrows (~a radius of 30–60 m), grazing by vizcachas reduces herbaceous biomass and changes understory composition from grasses to annual and perennial herbs, resulting in a smaller quantity of higher quality litter compared to ungrazed zones (Branch et al., 1996; Villarreal et al., 2008). At another semi-arid site similar to our study site, and approximately 200 km to the NW (Lihue Calel National Park), fine litter mass in zones grazed intensely by vizcachas was approximately 40% lower than in ungrazed zones, but annual and perennial herbs had a higher N content than perennial grasses (33 and 25 vs. 15 mg N g tissue^{-1}, respectively; Villarreal et al., 2008). Perennial herbs decomposed more rapidly than grasses in litterbags (45 ± 3 vs. $62 \pm 4\%$ and 30 ± 2 vs. $52 \pm 5\%$ mass remaining after one and two years in the field, respectively; Clark et al., unpublished data). Reduction of herbaceous and fine litter biomass also reduces fire intensity in grazed zones surrounding burrows and on burrow systems, and promotes persistence of woody vegetation, increasing overall aboveground biomass and coarse woody debris (Hierro et al., 2011). These combined effects of vizcachas in and on burrows result in larger individuals of the dominant shrub, creosote bush, with higher N and P content in foliage on the burrow system compared to individuals in other zones (Villarreal et al., 2008; Hierro et al., 2011).

2.3. Soil carbon, nitrogen, and in situ net nitrogen mineralization

Soil sampling and *in situ* N_{min} measurements were conducted within 20-m by 20-m plots established at five active colonial burrow systems and their associated grazed and ungrazed zones. Grazed-only plots were established in a random direction immediately adjacent to the burrow systems, and ungrazed plots were located in a random direction and distance at 100 m–150 m from the burrow system. Plots represented concentric zones of decreasing effects of vizcachas (e.g., burrowing + grazing, grazing only, and no grazing). Soil in each plot was sampled at three-month intervals; fall (April to June; southern hemisphere), winter (July to September), spring (October to December), and summer (January to March). Surface soil (0–10 cm depth) was sampled at nine random points in each plot. A bucket auger was then used to core to a depth of approximately 100 cm at each point on the burrow systems. If an active burrow was encountered at any depth (typically at 40–90 cm depth from the surface), a subsurface soil sample corresponding to a depth of 0–10 cm on the floor of the burrow was collected. If an active burrow was not encountered, an approximately 10-cm thick subsurface soil sample was collected at the equivalent depth of the mean depth of burrows sampled in that colonial burrow system. Samples from the three closest locations at each depth were pooled to produce three surface and three sub-surface samples for each burrow system. Surface samples from grazed-only and ungrazed plots were pooled similarly. Subsurface soil was sampled at the equivalent depth of sampled burrows at every third point in the grazed-only and ungrazed plots because variability in N and C was low (Villarreal et al., 2008), and these samples were not pooled. Thus, three pooled surface samples (0–10 cm depth) and three subsurface samples (ranging between 40 and 70 cm depth) were produced for each plot. All samples were sieved using a 2-mm mesh sieve to remove roots and coarse fragments in the field, and subsamples were stored in sealed plastic bags to measure gravimetric soil moisture content. Bulk density was sampled in all surface plots and on burrow floors. Bulk density and particle size of soil were similar among all zones (Table S1).

Soil cores (10 cm tall, 7-cm inner diameter) constructed of PVC tubing were used to estimate net N_{min} in surface and subsurface soil in each plot. Two resin rings (0.5 cm tall, 7-cm outer diameter), one containing Rexyn 101 cation exchange resin (16–50 mesh size, Fisher Scientific, Fair Lawn, New Jersey) and the other containing Ionac anion exchange resin (16–50 mesh size, J. T. Baker, Inc., Phillipsburg, New Jersey) were inserted in one end of each tube, and then approximately 100-g dry weight equivalent of soil was placed in the tube. A second set of resin rings was inserted above the soil sample. Within 24 h of soil collection, soil cores containing surface soil were buried with the tops 5 cm below the surface, and those containing subsurface soil were buried with tops approximately 5 cm below burrow floors, or buried at the mean depth of burrow floors. Soil cores remained in the field for three months and then were harvested. Initial and final water contents of soil in each tube was measured gravimetrically using sub-samples that were weighed, dried at 70 °C, and then weighed when dry. This process for preparing and installing soil cores was repeated each season to estimate annual N_{min}.

Ion exchange resin bags were used to estimate relative rates of N_{min} in surface soil in each plot. Resin bags were prepared using commercial nylon hose rinsed repeatedly in deionized water and were filled with 10.0 g of same cation or anion exchange resin used in the resin rings described above. Resin bags (n = 4 of each type) were placed at cardinal directions 50 cm from surface soil cores in each plot. Resin bags remained in the field for three months and were replaced by a new set every season.

2.4. Feces decomposition and nitrogen dynamics

Litterbags (10 cm by 15 cm, 1-mm mesh size) were used to estimate decomposition of vizcacha feces over a 3-year period in the field. Fresh feces were collected near burrow entrances and allowed to air dry for 2–3 weeks. Approximately 5-g dry weight equivalent was placed in each litterbag. Separate air-dried subsamples (n = 10) of vizcacha feces were weighed, dried at 70 °C, and weighed again to calculate initial mass, and then ground to estimate initial C and N content. Litterbags were placed on the surface or buried at the mean depth of burrows in three of the colonial burrow systems sampled for *in situ* N_{min} (n = 18 at each burrow system and depth). Litterbags were collected at 6, 12, and 36 months, and samples were dried at 70 °C, weighed to calculate final mass, and subsamples were ground for C and N analysis.

2.5. Soil respiration and net nitrogen mineralization in the laboratory

Nine additional soil samples were collected from random locations at 0–10 cm depth in each plot, and then pooled to produce a single sample for each of the three zones at each burrow system. For subsurface soil, nine soil samples were collected at the mean depth of burrows in each colonial burrow and pooled, and three samples were collected and pooled from each grazed-only and ungrazed plot. Samples were refrigerated at 4 °C until use (approximately five days). In the laboratory, 100-g dry weight equivalent from each sample was weighed into 125-ml poly-ethylene bottles. Soil samples were then incubated at 25 °C. Water content was adjusted weekly to field capacity (approximately 24.1 ± 0.3 g H_2O 100 g soil^{-1}) throughout the experiment by placing each bottle on a digital balance (0.1-g resolution) and adding the appropriate amount of distilled water. Following an initial two-week period to allow for disturbance effects and non-biological CO_2 release, soil respiration was measured at 2, 3, 4, 6, 8, 10, and 12 weeks. Bottles were sealed and purged with CO_2-free air, and then allowed to incubate for 10–60 min, depending on final CO_2 concentrations. Air in the headspace was sampled using 20-ml

nylon syringes. CO_2 concentrations in syringes were analyzed immediately using an infrared gas analyzer (IRGA; LiCor 6252, LiCor, Inc., Norman, Nebraska) calibrated with appropriate span gases that were traceable to primary CO_2 standards. We assumed that CO_2 emissions from soil approximated activity of microbial populations because visible roots were removed from soil during sieving before the *in situ* and laboratory experiments, and the period of non-biological release of CO_2 that typically occurs early in an experiment from calcareous soil and disturbance effects was excluded from analyses. Potential N_{min} at 25 °C and saturated soil moisture was estimated from 10-g equivalent dry weight sub-samples extracted at 0, 2, 4, 8 and 12 weeks from soil samples from each zone and depth from replicates that were used to measure soil respiration. A second set of 100-g dry weight equivalent soil samples from each zone and depth was used to explore relationships between soil water content and temperature on rates of net N_{min} in the laboratory. Moisture content of each sample was maintained gravimetrically at 25, 50, 75, or 100% field capacity, and samples were incubated at 15 or 25 °C for 12 weeks. A 10-g subsample from each bottle was extracted for analyses at the end of the experiment.

2.6. Analytical procedures

Total C and N content of soil and litterbags were measured using a CNS analyzer (Carlo Erba, Milan, Italy). Initial and final concentrations of NH_4^+ and NO_3^- in all soil samples were measured by extracting 10-g equivalent dry weight of soil in 100 ml of 2 M KCl for 24 h within 24 h of collection for most (>90%) of samples in the field, and immediately in the laboratory. Extracts were filtered using Gelman AE 0.45-μm pore size filters and a polypropylene syringe. Resin rings and bags were extracted in 100 ml of 0.2 M HCl (cation resins) or 0.1 M NaHCO3 (anion resins) for 24 h. Resin rings and bags that were prepared but not exposed to soil in the field were extracted and analyzed as blanks. Ammonium was analyzed using an indophenol colorimetric technique. Nitrate + nitrite were analyzed colorimetrically following NO_3^- reduction in a copper/cadmium column (Keeny and Nelson, 1982). Particle size was measured using the pipette method (USDA, 1992).

2.7. Statistical analyses

We used linear mixed models constructed with the lmer function from R package lme4 (Bates et al., 2015) to evaluate effects of vizcachas on C and N pools and dynamics in soil. Mean values of response variables from each zone and depth in each colony were used as replicates. Interaction terms were omitted from models if omission did not significantly decrease the log likelihood of the model. Comparisons among zones and depths were made with Tukey's tests that adjust P values for multiple comparisons using

the lsmeans package in R. Prior to analyses, data were transformed when necessary to meet statistical assumptions. We tested for significant differences in C and N content and annual *in situ* N_{min} rates in soil along the gradient of vizcacha activity across the three zones (burrow systems, adjacent grazed-only zones, and ungrazed zones) using mixed models with zone and depth (surface, subsurface) as fixed effects and colony site as a random effect. Mixed models were constructed for NH_4^+ N and NO_3^- N in resin bags with zone as the only fixed effect because resins bags were placed in surface soil only. We fit an exponential decay model [α + exp (β * time)] to C and N loss from feces in litterbags using SigmaPlot Version 10.0, and examined percent loss of C and N mass at 36 months with a mixed model that incorporated depth as a fixed effect and colony site as a random effect. To estimate cumulative net CO_2 emission from soil in the laboratory incubation experiment, we fit a non-linear equation [α + β * exp (γ * time)] to daily CO_2 emission rates to account for a rapidly mineralized labile C, and more slowly mineralized recalcitrant C. We tested for differences in cumulative amounts of CO_2 released by soil from each zone and depth with a mixed model. To examine differences in effects of soil moisture, temperature, and zone on net N_{min} in the laboratory experiment, we constructed mixed models for surface and sub-surface soil with zone, depth, temperature, and moisture content as fixed effects and colony site as a random effect.

3. Results

3.1. Soil carbon, nitrogen and in situ net nitrogen mineralization

Burrowing and waste deposition by vizcachas increased total C and N in burrow soil by 1.6 and 5.5 times, respectively, compared to levels in undisturbed subsurface soil (Table 1). Total C in burrow soil was equivalent to amounts in surface soil on burrows and did not differ significantly from total C in grazed-only and ungrazed zones. Total N content in burrow soil was similar to amounts in surface soil from all three zones. In contrast to their effects on burrow soil, activities of vizcachas had little effect on total C or N in soil at 0−10 cm depth. Activities of vizcachas had a strong effect on soil N_{inorg} content; annual mean values were highest in burrow soil, intermediate in surface soil on burrow systems, and relatively low in all other zones (Table 1). Surface soil on burrows had the highest proportion of NO_3^- N and undisturbed subsurface soil the lowest (Table 1).

Summed over the year, N_{inorg} in resin bags on burrow systems was 2.3 and 2.1 times greater than in resin bags on grazed-only and ungrazed zones, respectively (Table 2). Consistent with N_{inorg} in soil on burrow systems, annual NO_3^- N in resin bags on burrows was greater than in other zones, and comprised a greater proportion of N_{inorg} (50 ± 11%) compared to resin bags on grazed-only (32 ± 7%)

Table 1

Total carbon and nitrogen content, C:N ratios, initial ammonium N and nitrate N content, and annual *in situ* net N mineralization in surface soil (0−10 cm) and soil at the mean depth of burrows (65 ± 10 cm; mean ± 1 SD) in five colonial burrow systems and their associated grazed and ungrazed zones. Values are means ± 1 SE. Inorganic N values for each zone are averages of all four seasons sampled. Letters indicate significant differences of LSM comparisons in the best-fit linear mixed model with all pairs compared.

	Surface soil			Subsurface soil			Wald chi square[1]		
	Burrows	Grazed-only	Ungrazed	Burrows	Grazed-only	Ungrazed	Zone	Depth	Zone x depth
Carbon (g C kg^{-1})	6.6 ± 0.3[ab]	8.2 ± 1.0[ab]	10.2 ± 1.8[a]	6.5 ± 1.1[ab]	4.4 ± 0.7[b]	3.5 ± 0.8[b]	6.2[*]	24.6[***]	12.1[**]
Nitrogen (g N kg^{-1})	0.7 ± 0.1[a]	1.0 ± 0.1[a]	1.1 ± 0.1[a]	1.1 ± 0.1[a]	0.2 ± 0.1[b]	0.2 ± 0.0[b]	10.4[**]	46.3[***]	61.6[***]
C:N Ratio	9.6 ± 0.6[ab]	8.4 ± 0.5[ab]	9.0 ± 0.7[ab]	6.0 ± 0.9[a]	21.6 ± 2.1[d]	15.5 ± 3.4[bd]	0.4	7.4[**]	38.6[***]
NH_4^+ N (mg N kg^{-1})	3.3 ± 0.8[a]	1.4 ± 0.4[a]	2.2 ± 0.6[a]	43.2 ± 7.5[b]	1.4 ± 0.4[a]	1.3 ± 0.7[a]	268.9[***]	1.2	126.2[***]
NO_3^- N (mg N kg^{-1})	60.0 ± 17.5[a]	7.5 ± 3.9[d]	3.7 ± 0.5[c,d]	380.4 ± 35.4[b]	2.6 ± 0.3[c,d]	2.3 ± 0.3[c]	513.2[***]	3.5[*]	65.4[***]
N_{min} (mg N kg^{-1} yr^{-1})	38.9 ± 9.9[a]	27.6 ± 5.8[a]	22.9 ± 8.8[a]	−68.9 ± 35.5[b]	3.9 ± 1.9[a]	4.9 ± 2.2 [a]	0.6	0.7	12.1[**]
N_{min} (g N m^{-2} yr^{-1})[2]	5.1 ± 1.3	3.5 ± 0.7	2.9 ± 1.1	−8.3 ± 4.3	0.5 ± 0.2	0.6 ± 0.3			

[1]Degrees of freedom for Wald chi squares: Zone, 2; Depth, 1; Zone*Depth, 2; p values: * < 0.05, ** < 0.01, *** < 0.001.
[2]Calculated for a depth of 0−10 cm for surface soil and a 10-cm layer at the mean depth of colonial burrow systems.

Table 2
Ammonium and nitrate in resin bags (mean µg NH_4^+ N or NO_3^- N g $resin^{-1}$ ± 1 SE) buried at a depth of 5–10 cm for 3-month periods on burrows and in grazed-only and ungrazed zones. Values for annual NO_3^- N with different letters correspond to significant differences (P < 0.001) using LSM comparisons in the best-fit linear mixed model.

Zone	Autumn	Winter	Spring	Summer	Annual
NH_4^+ N					
Burrows	4.6 ± 1.3	9.1 ± 1.6	12.5 ± 4.0	21.5 ± 10.5	47.7 ± 13.6
Grazed-only	3.0 ± 0.7	3.0 ± 0.4	6.5 ± 1.7	15.2 ± 7.5	27.8 ± 8.5
Ungrazed	4.4 ± 0.5	10.2 ± 2.8	4.7 ± 0.9	13.9 ± 5.8	33.1 ± 4.8
NO_3^- N					
Burrows	2.2 ± 0.5	12.8 ± 5.2	7.4 ± 1.9	24.8 ± 10.5	47.2 ± 9.7[a]
Grazed-only	1.0 ± 0.2	1.8 ± 0.6	3.6 ± 0.7	7.0 ± 2.1	13.3 ± 2.9[b]
Ungrazed	1.2 ± 0.4	2.4 ± 0.1	2.9 ± 1.2	6.5 ± 2.5	13.1 ± 2.9[b]

Wald chi square tests: Annual sum NH_4^+ N, X^2_2 = 0.3, P > 0.1; Annual sum NO_3^- N, X^2_2 = 25.2, P < 0.001.

and ungrazed zones (28 ± 14%; Table 2). N_{inorg} in resin bags in all three zones was lowest in the relatively wet autumn months (April to June), and highest in summer (January to March), when air temperature was greatest and soil moisture was initially relatively low (Fig. 1, Table 2).

Seasonal *in situ* net N_{min} was highly variable in burrow soil, and annual net N immobilization occurred (Table 1, Fig. 2b). Both seasonal and annual *in situ* net N_{min} were low in undisturbed subsurface soil (Table 1, Fig. 2b). Activities of vizcachas had little effect on seasonal or annual *in situ* net N_{min} in surface soil; rates were not significantly different on burrow systems and in grazed-only and ungrazed zones (Table 1). With the exception of the dry summer months, *in situ* net N_{min} in surface soil on burrow systems was characterized by greater spatial variability than in grazed-only and ungrazed zones (Fig. 2a).
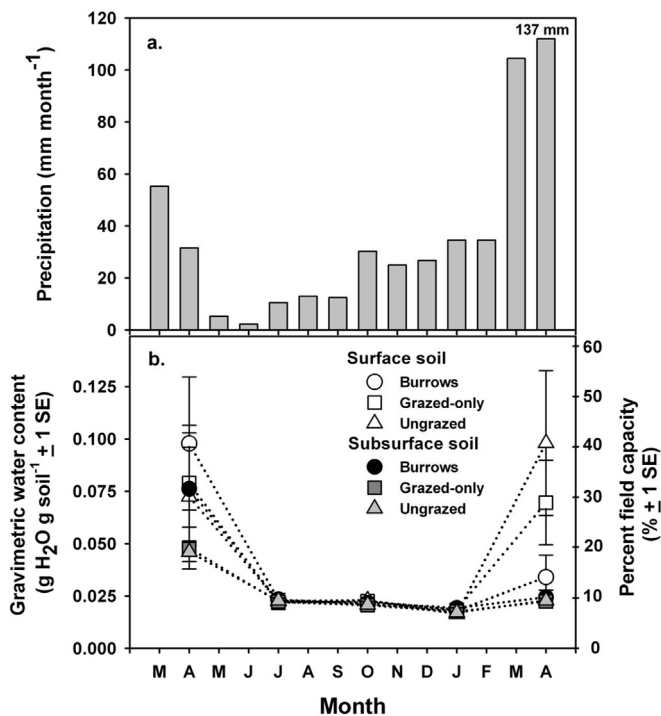
Fig. 1. a Monthly precipitation depth (mm $month^{-1}$) and 1b. soil moisture content expressed as gravimetric water content and percent field capacity ±1 SE in surface soil and at the mean depth of vizcacha burrow systems sampled in fall (April to June), winter (July to September), spring (October to December), and summer (January to March). Final soil moisture contents were sampled at the end of March.

3.2. Litter decomposition

Loss of C and N from feces was an exponential function of time, and was faster in buried litterbags compared to those on the soil surface (Fig. 3a,b, Table S2). By the third year, C and N mass in feces in buried litterbags was only approximately 61% and 54% of that in litterbags on the soil surface (Fig. 3a,b).

3.3. Soil respiration and potential nitrogen mineralization in the laboratory

In burrow soil, burrowing and waste deposition by vizcachas resulted in initial CO_2 emission rates that were 3.7 and 3.5 times greater than from undisturbed subsurface soil in grazed-only and ungrazed zones, and similar to those from surface soil from all three zones (Fig. 4a, Table S3). Activities of vizcachas had little effect on initial CO_2 emission rates from surface soil (Fig. 4a, Table S3). Estimated cumulative CO_2 emissions were similar from soil in burrows and surface soil, and significantly lower from undisturbed subsurface soil in grazed-only and ungrazed zones (Table S3).

Potential N_{min} was much greater in burrow soil than in undisturbed subsurface soil, and equivalent to rates in surface soil from grazed-only and ungrazed zones (Fig. 4b). These results were reflected in the strong interaction between zone and depth in the
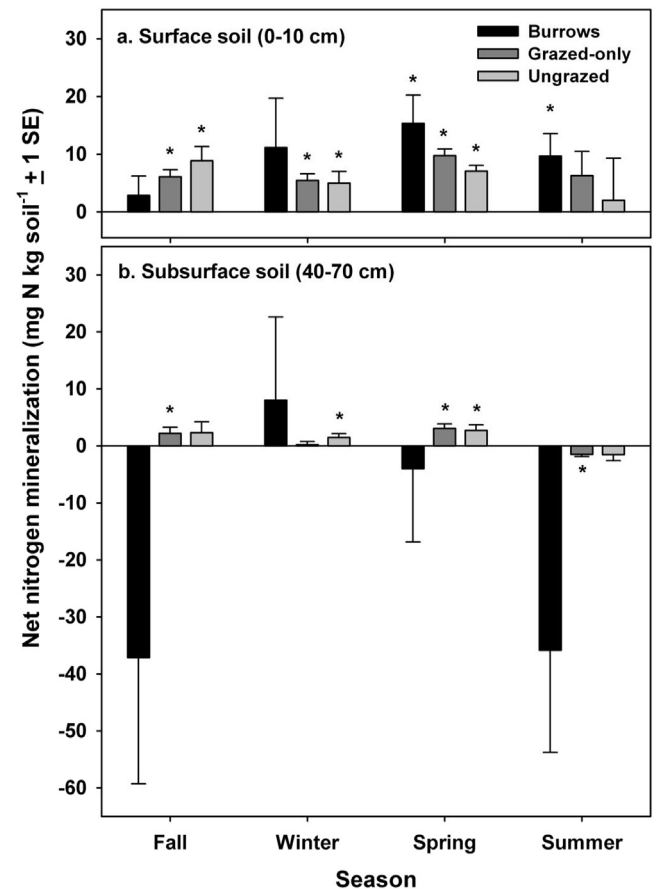
Fig. 2. Seasonal *in situ* net nitrogen mineralization (N_{min}) in (a) surface and (b) subsurface soil in five colonial burrow systems and associated grazed-only and ungrazed zones estimated using soil resin cores placed in the field over 12-week periods. Soil cores were placed in surface soil and at the mean depth of burrow floors (n = 5 burrow systems, values for each burrow system are the mean of three resin cores in each zone during each season). Seasonal values with an asterisk exceed ±2 SE, and indicate significant net nitrogen mineralization occurred.
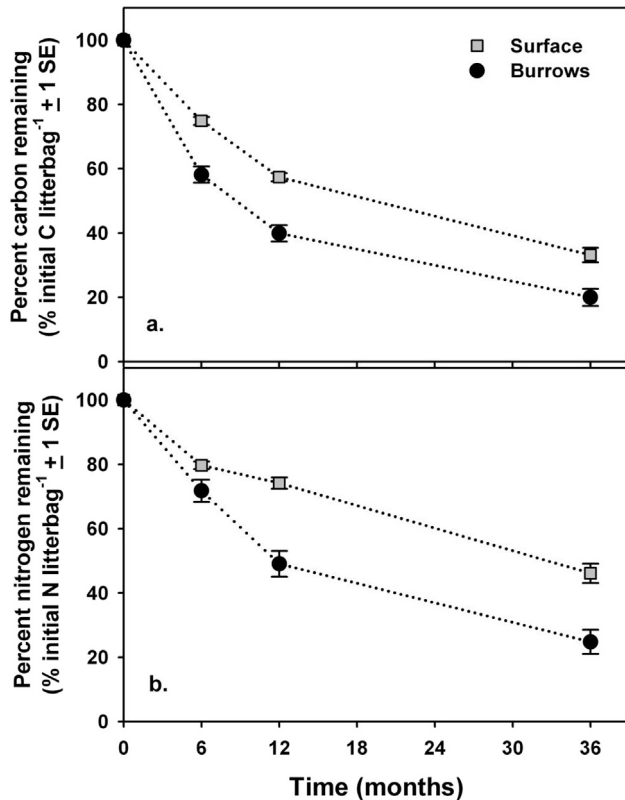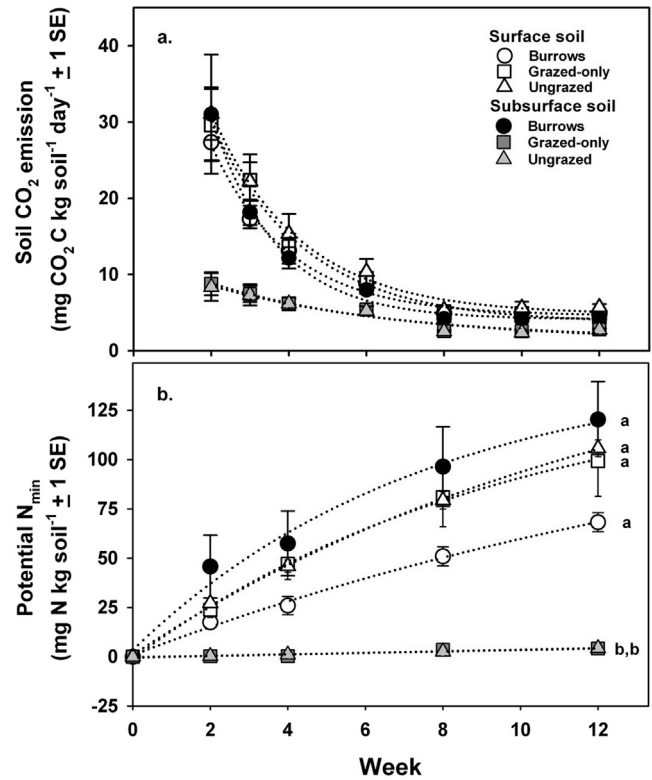
Fig. 3. (a) Percent carbon mass and (b) percent nitrogen mass remaining in feces litterbags on the soil surface and buried at the mean depth of burrows in colonial burrow systems. Values are means ± 1 SE.

Fig. 4. (a) Daily rates of soil CO_2 release (mg C kg soil^{-1} day^{-1}) in surface and subsurface soil from colonial burrows, grazed-only and ungrazed zones incubated at 100% field capactiy and 25 °C for 12 weeks, and (b) cumulative potential N_{min} in surface and subsurface soil from colonial burrows, grazed-only and ungrazed zones incubated at 100% field capacity and 25 °C for 12 weeks. In both graphs, the top set of lines includes data from all zones for surface soil and data from subsurface soil from burrows, and data from subsurface soil for grazed-only and ungrazed zones fall on the same line at the bottom of each graph.

mixed model (Zone, X^2_2 = 9.2, P < 0.01; Depth, X^2_1 = 13.8, P < 0.001; Zone*Depth, X^2_2 = 153.7, P < 0.001). Potential N_{min} in surface soil on burrow systems was lower than in surface soil from other zones during some weeks, but by the end of the experiment no significant differences were detected between surface soil on burrows and in other zones (Fig. 4b.; burrows vs. ungrazed zone, t = 2.88, P = 0.08; burrows vs. grazed zone, t = 2.24, P = 0.26). When samples from all zones and depths were considered together, cumulative potential N_{min} from week two to twelve was highly correlated with cumulative CO_2 emissions from soil (y = 0.138 x − 30.10, P < 0.001, r^2 = 0.72).

Soil temperature and moisture content strongly affected net N_{min} rates in burrow soil and all surface soil during laboratory incubations, and the interactions between these factors in the best-fit models were significant (Fig. 5, Table S4). Net N_{min} was much greater in burrow soil compared to rates in subsurface soil from grazed-only and ungrazed zones at both temperatures and all moisture levels above 25% field capacity (Fig. 5b). In surface soil from burrow systems, net N_{min} at 25 °C and 100% field capacity was significantly lower than in surface soil from grazed and ungrazed zones (Fig. 5a), and significantly lower than in ungrazed zones at 25 °C and 25% field capacity. No differences in N_{min} rates were detected among zones for surface soil at other soil moisture contents and temperatures. Variation in net N_{min} in surface soil in this experiment was lower than for N_{min} associated with measurement of CO_2 emissions and, as a result, patterns for surface soil that appeared as non-significant trends in the experiment measuring CO_2 emissions and N_{min} were significant in this experiment.

During these laboratory incubations, net N_{min} rates in burrow soil responded to temperature differently than those in surface soil. Net N_{min} in burrow soil was high at both 15 °C and 25 °C at all soil

moisture contents above 25% field capacity, averaging only 1.24 ± 0.27 times greater at 25 °C compared to rates at 15 °C (Fig. 5b). In contrast, net N_{min} in surface soil from all three zones was significantly higher at 25 °C as compared to 15 °C when soil moisture was above 25% field capacity, averaging 3.25 ± 0.35 times greater (Fig. 5a).

4. Discussion

The greatest effect of activities of vizcachas on soil C and N dynamics was in burrow systems, where burrowing and deposition of waste increased labile C and N, resulting in increased net N_{min} rates when soil moisture was not limiting, and producing the highest N_{inorg} content measured in any location. On the surface of burrows, activities of vizcachas had little effect on *in situ* net N_{min} compared to rates in surface soil in grazed-only and ungrazed zones, but did increase N_{inorg} content. Contrary to our prediction, intense grazing by vizcachas had no detectable effect on C and N dynamics in surface soil. Our study indicates that burrowing and deposition of waste result in a highly active subsurface layer in which C and N dynamics function much like surface soil when soil moisture is not limiting.

Deposition of labile C and N belowground by vizcachas occurs well below the depth of surface litter deposition and decomposition, major processes that contribute to N turnover in soil in semi-arid systems (Carrera et al., 2009; Reichmann et al., 2013). Vizcacha feces are a likely source of labile C and N for microbial populations in burrow soil, as indicated by higher rates of decomposition and N
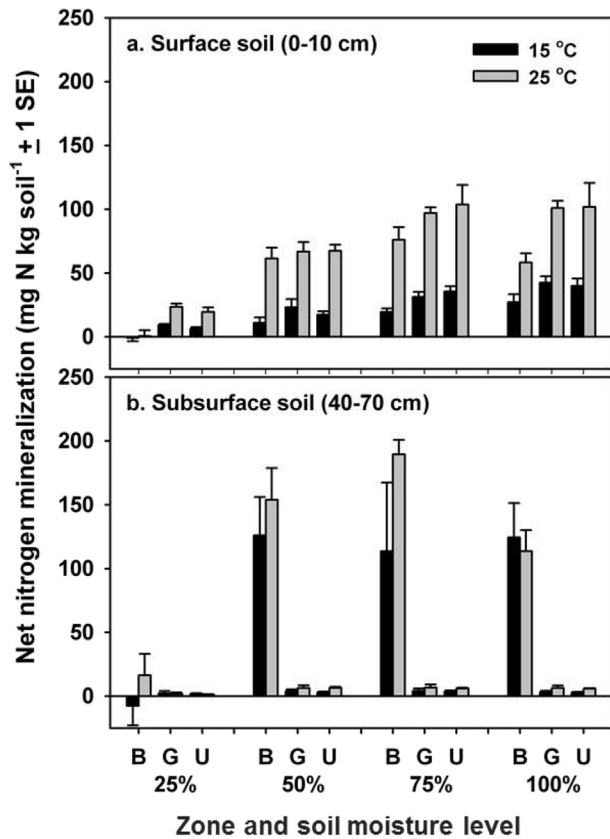
Fig. 5. Net N_{min} in (a) surface and (b) sub-surface soil from colonial burrows, grazed-only and ungrazed zones at 25, 50, 75, and 100% field capacity incubated at 15 °C or 25 °C for 12 weeks.

release from feces in buried litterbags compared to litterbags on the soil surface. However, despite high C and N content compared to undisturbed subsurface soil, *in situ* N_{min} was highly variable in burrow soil. Pulsed water supply strongly affects activity of microbial populations in soil, thus relationships between labile C and N supply and rates of N_{min} can be complex in semi-arid ecosystems (Mazzarino et al., 1998; Austin et al., 2004; Yahdjian and Sala, 2010; Cregger et al., 2014). Although the activity of vizcachas had little effect on bulk density or soil particle size, orientation and slope of individual burrows can affect hydrologic flow in and around burrows as noted for other burrowing rodents (Reichman and Seabloom, 2002). Soil moisture content was sampled at the beginning and end of four intensive seasonal field campaigns, and was above 25% field capacity in burrow soil only in autumn following a period of high rainfall. Although our periodic gravimetric measurements of soil moisture may not have adequately captured the wetting and drying dynamics of surface or subsurface soils, low soil moisture content likely occurred in burrow soil throughout most of the year and apparently had an overriding effect on *in situ* net N_{min} rates observed in soil in colonial burrows. Net N_{min} during laboratory incubations also was low under conditions that typically characterize burrow microclimate (e.g., 15 °C, 25% field capacity). Thus, the relatively high and seasonally stable NO_3^- concentrations in burrows likely originated from accumulation of pulsed mineralization events over time (e.g., Mazzarino et al., 1998; Austin et al., 2004; Yahdjian and Sala, 2010), rather than continuously high *in situ* rates of net N_{min}. Because potential evaporation exceeds precipitation in this semi-arid region (Paoloni et al., 2003), leaching losses are reduced and NO_3^- accumulation occurs in the absence of plant uptake or microbial immobilization

(Mazzarino et al., 1998; Walvoord et al., 2003; Reichmann et al., 2013).

Net N_{min} in soil from colonial burrows increased dramatically at soil moisture contents greater than 25% field capacity at both temperatures during laboratory incubations. In contrast to surface soil where net N_{min} was strongly affected by temperature, net N_{min} rates in burrow soil were similar at 15 °C and 25 °C during these laboratory incubations when soil moisture was not limiting. This somewhat surprising result could be due differences in microbial communities in surface soil and soil in burrows, or to other unmeasured abiotic or biotic variables.

Burrowing species alter properties of surface soil on burrow systems by bioturbation, grazing and deposition of waste (Whitford and Kay, 1999; Reichman and Seabloom, 2002; Villarreal et al., 2008). In the case of vizcachas, bioturbation and deposition of waste appear to be the primary mechanisms affecting N cycling on the burrow systems given the lack of effects of vizcachas on soil in intensely grazed zones without burrows. Bioturbation by vizcachas mixed large volumes of surface and subsurface soil and we observed a trend towards reduced total C and N on burrow systems, as has been noted for other burrowing species such as pocket gophers (e.g., *Thomomys* spp. and *Geomys* spp.) and prairie dogs (*Cynomys* spp., Cortinas and Seastedt, 1996; Reichman and Seabloom, 2002; Canals et al., 2003; Kerley et al., 2004).

Waste deposition by vizcachas resulted in elevated N_{inorg} in surface soil on and near burrows, also consistent with effects of pocket gophers (Canals et al., 2003; Kerley et al., 2004), kangaroo rats (e.g., *Dopodomys spectabilis*, Chew and Whitford, 1992; Whitford and Kay, 1999), and prairie dogs (Holland and Detling, 1990). Although we noted a non-significant trend in reduced total C and N because of bioturbation and the occurrence of reduced N_{min} in surface soil from burrow systems compared to soil from grazed-only and ungrazed zones during some laboratory incubations, *in situ* annual N_{min} was similar in surface soil in all three zones. A possible explanation for these observations is that total C and N on burrow systems is partially derived from waste material and thus is relatively high quality. This could simultaneously account for relatively high *in situ* net N_{min} rates observed in the field, and reduced cumulative N_{min} during laboratory incubations, because labile C and N were exhausted relatively rapidly at higher soil moisture contents and temperature in the laboratory.

Despite the large impact of vizcachas on herbaceous plant biomass and accumulated litter in the grazed zones surrounding burrows (Villarreal et al., 2008; Hierro et al., 2011), both *in situ* and laboratory incubations in our study indicated that net N_{min} rates in surface soil in grazed-only and ungrazed zones were similar, and thus intensive grazing by vizcachas had little effect on C and N dynamics in surface soil. A potential mechanism accounting for these observations is that the increase in quality of litter produced by the shift in plant composition with grazing from perennial grasses to annual and perennial forbs compensated for the reduction in litter quantity in grazed zones (Sirotnak and Huntley, 2000; Villarreal et al., 2008; Vaieretti et al., 2013). Our field data also indicate that activities of vizcachas did not promote erosion of organic matter pools or result in soil compaction, potential mechanisms that affect C and N dynamics in other heavily grazed ecosystems (e.g., Schrama et al., 2013), as we observed no differences in soil organic matter content, bulk density or particle size in surface soil in zones with and without vizcacha activity.

Nitrogen availability is an important factor controlling productivity of vegetation in semi-arid ecosystems (Lajtha and Whitford, 1989; Reichmann et al., 2013; Yahdjian et al., 2014). Other studies at our site and nearby sites provide information that links belowground activities of vizcachas with vegetation dynamics on burrow systems, and indicate that a portion of the mineralized N in burrow

soil is available to deeply rooted shrubs (Villarreal et al., 2008; Hierro et al., 2011). Vizcacha feces are relatively depleted in ^{15}N, and this signal was detected in foliage of *L. divaricata* growing on colonial burrows but not in foliage from other zones (Villarreal et al., 2008). In addition to higher foliar N content, individuals of *L. divaricata* growing on colonial burrows are larger, have greater leaf area, account for greater biomass, and likely are more productive than shrubs in ungrazed zones (Hierro, 1999; Hierro et al., 2011).

Vizcachas create a strong patterning of vegetation structure and litter mass across the landscape through herbivory and by altering fire dynamics (Branch et al., 1996; Villarreal et al., 2008; Hierro et al., 2011). Our research here indicates that bioturbation and waste deposition by vizcachas alter the distribution of C and N in soil, resulting in production of "resource islands" that differ in spatial distribution compared to resource-rich patches that typically occur beneath individual patches of woody vegetation in semi-arid ecosystems in Argentina (Mazzarino et al., 1998; Carrera et al., 2009). Survey data from our two sites (Lihue Calel and Los Valles) indicate that a single colonial burrow system covers an average of 116 m^2 ± 49 m^2, and the density of colonial burrow systems is 0.3 ± 0.05 systems ha^{-1} (mean ± 1 SE) when vizcacha populations are high (Branch et al., 1996; Villarreal et al., 2008). N$_{inorg}$ content in soil at the mean depth of burrows at Los Valles and Lihue Calel averaged 438 mg N$_{inorg}$ kg soil^{-1}, compared to 6 mg N$_{inorg}$ kg soil^{-1} in surface soil and 4 mg N$_{inorg}$ kg soil^{-1} in subsurface soil in grazed and ungrazed zones. Across a landscape with a density of 0.3 colonial burrows per hectare, we calculated that a 10-cm thick layer of soil at the mean depth of burrows contains an amount of plant-available N equivalent to approximately 21% and 30% of the plant available N in surface soil and subsurface soil (10-cm layers), respectively, in an area that represents only 0.35% of the landscape. This is very likely an underestimate of the actual N$_{inorg}$ pool size in burrow systems across the landscape, because a much greater volume of soil is enriched in C and N by waste deposition in colonial burrow systems, which can extend to ~100 cm depth in soil, as burrows are continuously reworked over the life of the colony (Villarreal et al., 2008).

Burrowing animals are widespread in arid and semiarid grasslands and shrublands worldwide (Kinlaw, 1999; Whitford and Kay, 1999; Davidson et al., 2012; Fleming et al., 2014), and vizcachas are just one example of ecosystem engineers that redistribute C, N and other nutrients in the soil profile. For many species, foraging above ground and concentrating labile C, N and other nutrients belowground likely results in production of resource-rich patches of various sizes and depths in the soil profile that persist on the landscape, while population numbers fluctuate through time or even become locally extinct, often as a direct result of human extirpation (Davidson et al., 2012). Because redistribution of C, N, and other nutrients affects resource availability for vegetation, animal activities can alter spatial patterning of competitive interactions, plant diversity and productivity, and produce ecological legacies that affect ecosystem functioning for years to decades (e.g., Villarreal et al., 2008; Hierro et al., 2011; Monger et al., 2015). Such ecological legacies potentially buffer semi-arid ecosystems from impacts of disturbance events such as fire or erosion by wind or overland flow. For example, redistribution and concentration of C and N in soil by vizcachas and other burrowing animals in fire-prone semi-arid ecosystems could conserve N which otherwise would be volatized during combustion processes in fires (Hierro et al., 2011). Given the broad taxonomic and geographic representation of burrowing species in ecosystems, our results demonstrate the importance of incorporating belowground activities of other burrowing species in studies of soil C and N distribution and dynamics if we aim to understand drivers of key ecosystem processes.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.08.027.

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Supplementary Tables:

Table S1. Bulk density and particle size in surface soil (0-10 cm) and soil at the mean depth of burrows (65 ± 10 cm; mean ± 1 SD) in five colonial burrow systems and the associated grazed and ungrazed zones.   Values are means ± 1 SE.

Depth/Zone	Bulk density	Particle size (%)		
	(g cm^{-3})	Sand	Silt	Clay
Surface soil (0-10 cm depth)				
Burrows	1.30 ± 0.07	75.5 ± 3.6	17.0 ± 2.4	7.5 ± 2.3
Grazed-only	1.25 ± 0.09	73.7 ± 5.8	17.5 ± 2.5	4.9 ± 1.7
Ungrazed	1.28 ± 0.09	77.4 ± 2.2	17.8 ± 3.7	5.4 ± 3.2
Subsurface soil (65 ± 10 cm depth)				
Burrows	1.20 ± 0.07	77.6 ± 1.6	17.5 ± 2.5	4.9 ± 1.7
Grazed-only	-----	76.1 ± 3.0	15.6 ± 2.4	8.3 ± 1.8
Ungrazed	-----	78.3 ± 3.4	15.9 ± 4.0	5.8 ± 2.4

Table S2. Mean parameter estimates for carbon and nitrogen loss from vizcacha feces in litterbags on the soil surface and buried at the mean depth of burrows and percent of initial C or N mass remaining after three years. Parameter estimates (means ± 1 SE) are based on the exponential decay model Mass remaining = α * exp (-β * time). Values for C or N with different letters are significantly different at $P < 0.05$ using LSM comparison in the best-fit mixed model at 36 months.

	Depth	α	β	F	P	r^2	% remaining at 36 months
Carbon	Surface	98.3 ± 1.1	0.040 ± 0.002	683.4	<0.001	0.94	33.2 ± 0.3[a]
	Burrows	97.4 ± 2.4	0.073 ± 0.005	434.4	<0.001	0.90	20.4 ± 3.4[b]
Nitrogen	Surface	97.4 ± 1.2	0.023 ± 0.001	256.2	<0.001	0.86	46.1 ± 2.3[a]
	Burrows	97.6 ± 5.3	0.049 ± 0.007	265.7	<0.001	0.84	24.9 ± 6.7[b]

Wald chi square tests for differences in decomposition with depth: Percent C mass remaining after 36 months - $X^2_1 = 14.9$, $P < 0.001$; Percent N mass remaining after 36 months, $X^2_1 = 12.8$, $P < 0.001$.

Table S3. Mean parameter estimates for net CO_2 emission (mg carbon kg soil^{-1} day^{-1}) from saturated soil incubated at 25 °C based on the exponential decay model $f_{CO2} = \alpha + \beta * \exp(-\gamma * time)$. Cumulative CO_2 release (mg C kg soil^{-1} ± 1 SE) over the 10-week experiment from each colonial burrow system and zone was calculated using parameter estimates. Percent total C emitted was calculated from cumulative CO_2 emissions and total C values in Table 1. Mean daily CO_2 emission rates are shown in Fig. 3a. Values for cumulative C emissions with different letters correspond to significant differences (P<0.05) detected using LSM comparisons in the best-fit linear mixed model.

Depth and Zone	α	β	γ	F	P	r^2	Cumulative C	% Total C
Surface soil (0-10 cm)								
Colonial burrows	4.60 ± 0.63	60.68 ± 7.20	0.071 ± 0.008	270.0	< 0.001	0.99	652.3 ± 45.4[a]	9.9 ± 0.7
Grazed zones	3.70 ± 0.96	60.54 ± 7.02	0.060 ± 0.008	214.4	< 0.001	0.99	708.8 ± 81.2[a]	8.6 ± 1.0
Ungrazed zones	4.77 ± 0.74	63.34 ± 6.08	0.062 ± 0.007	337.1	< 0.001	0.99	770.6 ± 70.9[a]	7.6 ± 0.7
Subsurface soil (40-70 cm)								
Colonial burrows	4.12 ± 0.55	87.81 ± 9.90	0.085 ± 0.008	392.5	< 0.001	0.99	621.8 ± 58.3[a]	9.6 ± 0.9
Grazed zones	1.54 ± 1.33	11.39 ± 1.52	0.032 ± 0.014	40.5	< 0.01	0.93	316.3 ± 29.5[b]	7.2 ± 0.7

| Ungrazed zones | 1.20 ± 1.59 | 10.90 ± 1.29 | 0.028 ± 0.014 | 39.1 | < 0.01 | 0.93 | 312.2 ± 35.4^{b} | 8.9 ± 1.0 |

Wald chi square tests: Zone, $X^2{}_2 = 2.1$, $P > 0.1$; Depth: $X^2{}_1 = 0.2$, $P > 0.1$; $X^2{}_2 = $ Zone*Depth <0.0001.

Table S4. Results of best-fit linear mixed model for net N_{min} in surface and subsurface soil from colonial burrows, grazed-only and ungrazed zones at 25, 50, 75, and 100 % field capacity incubated at 15 °C or 25 °C for 12 weeks in the laboratory.

Variable	Surface soil (0-10 cm depth)			Subsurface soil (65 ± 10 cm depth)		
	Wald chi square (X^2)	df	P	Wald chi square (X^2)	df	P
Zone	21.1	2	<0.001	4.8	1	<0.1
Temperature	9.5	1	<0.01	7.1	1	<0.001
Moisture	116.8	3	<0.001	152.9	3	<0.001
Zone*Moisture[1]	----	--	----	99.0	6	<0.001
Temp*Moisture	83.4	3	<0.001	20.2	3	<0.001
Zone*Temp*Moisture[1]	----	--	----	18.4	8	<0.05

[1]Interaction terms were omitted where this did not significantly decrease the log likelihood of the model.

Plate S1. A male vizcacha (*Lagostomus maximus*) emerging from one of the entrances of a colonial burrow system in a semi-arid scrub ecosystem, Lihue Calel National Park, La Pampa Province, Argentina.