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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 ± 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