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ALTERATION OF ECOSYSTEM STRUCTURE BY A BURROWING HERBIVORE, THE PLAINS VIZCACHA (*LAGOSTOMUS MAXIMUS*)

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Although the role of animals in altering ecosystem structure and dynamics has received increased attention in the last decade, large gaps in knowledge still exist, limiting our ability to incorporate animals into models of ecosystem dynamics. Our research on the plains vizcacha (*Lagostomus maximus*, family Chinchillidae), a colonial burrowing herbivore in grasslands and semiarid scrub of southern South America, addresses 3 of these gaps—belowground impacts of vertebrates on soils, net effects of multiple types of animal activities on ecosystem structure, and the scaling up of plot-level effects to the landscape. Our study demonstrated that grazing by vizcachas produced strong spatial patterns in composition, biomass, and nutrient pools in herbaceous vegetation. In burrows, total nitrogen (N), total phosphorus (P), and inorganic N were greater than in undisturbed soil at a similar depth. Burrow soil and foliage of shrubs growing on burrows were depleted in ^{15}N, reflecting the signature of vizcacha feces. Transport of caliche by vizcachas resulted in significantly greater P concentrations in surface soil on burrows. Indirect effects of vizcachas on shrubs, through alteration of soil nutrients, transport of caliche to the soil surface, and possibly altered fire regimes, resulted in greater biomass, foliar N and P content, and total N and P pools in shrubs. Net effects of vizcachas on ecosystem structure, above- and belowground, are spatially extensive, and likely persist much longer than the colonies of vizcachas that generated these effects. This study demonstrates that the largest impacts of herbivores on ecosystem structure can be through their effects on plants they do not consume and, in systems where biopedturbation is frequent, animal transport is among the key processes that determine vertical distribution of nutrients in the soil profile.

Key words: Argentina, ecosystem engineer, ecosystem structure, herbivory, *Lagostomus maximus*, nutrient cycling, rodent, semiarid scrub, soils, vizcacha

The extent to which an animal species alters ecosystem dynamics is determined largely by how its activities directly and indirectly modify amounts and distribution of vegetation, litter, soil organic matter, and plant-essential nutrients. Animals modify ecosystem attributes by a variety of processes, including foraging and deposition of waste (Eviner and Chapin 2005; Hobbs 1996), physical alteration of habitat (i.e., physical ecosystem engineering—Jones et al. 1994), and modification of the spatial distribution of abiotic and biotic materials (i.e., transport engineering—Reichman and Seabloom 2002; Wilby et al. 2001). For example, herbivores alter ecosystem structure directly through consumption of plant biomass and, indirectly, by shifting species composition of the plant community toward unpalatable or grazing-tolerant species (Augustine and McNaughton 1998; Kielland and Bryant 1998; Olofsson et al. 2001). Animal-induced changes in biomass and plant species composition can lead to changes in litter quantity and quality, soil nutrient pools, and resource availability to plants not consumed by herbivores (Sirotnak and Huntly 2000). By foraging out from a fixed location and returning with materials and depositing waste, many animals redistribute and concentrate organic matter and nutrients horizontally. Vertical transport of materials by animals (e.g., soil movement induced by burrowing, collection of nest material, caching of seeds, etc.)

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exposes these to different abiotic and biotic conditions (Sherrod and Seastedt 2001), potentially altering rates of decomposition and mineral weathering. In addition, spatial and temporal scales of animal activities often differ from those characterizing plant-driven processes (Ben-David et al. 2005; Frank and Groffman 1998) and may disrupt the strong controls over ecosystem processes that result from positive feedbacks between spatial distribution of plants and soil organic matter and nutrients (Aguiar and Sala 1998; Schlesinger et al. 1990).

Although the role of animals in altering ecosystem structure and dynamics has received increased attention in the last decade, large gaps in knowledge still exist. Our research on the plains vizcacha (*Lagostomus maximus*, family Chinchillidae), a colonial burrowing herbivore, addresses 3 of these gaps—belowground impacts of vertebrates on soils and secondary consequences of these impacts, net effects of multiple types of animal activities on ecosystem structure, and scaling up of plot-level effects to the landscape. First, although effects of animals on surface soil have been examined in numerous systems because aboveground litter inputs and fecal deposition often occur at or near the surface (e.g., Frank and Groffman 1998; García et al. 2002; Kielland and Bryant 1998), knowledge of belowground impacts of animals, particularly vertebrates, is limited. Because of their mobility, burrowing animals have the potential to redistribute and concentrate soil organic matter and nutrients within soil profiles rapidly compared to many plant-driven and geomorphic processes. Second, until recently research on the role of animals in ecosystems primarily has focused on trophic processes. With recent emphasis on ecosystem engineering, the range of animal impacts on ecosystems under study has expanded, but net effects of multiple types of activities of animals remain poorly known (Wilby et al. 2001). Third, although plot-level studies of animal impacts on ecosystem properties are increasingly common, these data must be linked with data on density and distribution of animals to evaluate impacts at the landscape scale. All 3 of these gaps limit our ability to fully incorporate animals into models of ecosystem dynamics.

The objective of this study was to determine effects of the plains vizcacha on ecosystem structure in semiarid scrub of central Argentina. The plains vizcacha is a key ecosystem engineer in the grasslands, savannas, and semiarid scrub from southern Paraguay and Bolivia to central Argentina (Boogert et al. 2006; Jackson et al. 1996). Like black-tailed prairie dogs (*Cynomys ludovicianus*) of North America, grazing activity of these rodents alters biomass and composition of herbaceous plant communities over large areas of the landscape, and their colonial burrow systems disturb large volumes of soil (Branch et al. 1996; Coppock et al. 1983; Detling 1998). We hypothesized that vizcachas increase soil organic matter and nutrient pools in subsurface soil by grazing herbaceous vegetation aboveground and redistributing carbon (C), nitrogen (N), and phosphorus (P) belowground, and that redistribution of nutrients affects the biomass and nutrient content of woody vegetation, which they do not consume. We investigated direct effects of herbivory by vizcachas on biomass and N and P pools in understory vegetation; indirect effects of vizcachas on the spatial distribution, biomass, and nutrient content of dominant woody vegetation; spatial redistribution of litter through herbivory and wood transport; and effects of burrowing and deposition of waste on C, N, and P pools in surface and subsurface soil. We then integrated these data with previously measured population densities (Branch et al. 1996) to estimate net effects of vizcachas on distribution of C, N, and P at the landscape level. Similar to prairie dogs, vizcachas have been exterminated over a large part of their range and extermination programs continue because they are considered a competitor with livestock for forage (Jackson et al. 1996). If our hypothesis is correct, loss of vizcachas could have widespread consequences for the structure and dynamics of semiarid ecosystems in southern South America.

Materials and Methods

Study area.—Research was conducted in Lihue Calel National Park (10,934 ha), located 250 km southwest of Santa Rosa, La Pampa Province, Argentina (38°00′S, 65°35′W). Mean annual air temperature is 15°C, and mean monthly temperatures for July and January are 7°C and 24°C, respectively (Lihue Calel National Park, in litt.). Annual precipitation is 495 ± 38 mm (mean ± 1 *SE*, 1984–2004). Topography consists primarily of low-angle slopes and plains. The soil is classified as a calcic aridisol and is a sandy loam. Soil horizons are poorly differentiated, but a discontinuous caliche layer occurs at depths ranging from 0.5 to 1.5 m.

Vegetation is dominated by shrubs, primarily creosote bush (*Larrea divaricata*), which comprises more than 90% of all individuals. Other shrubs include *L. cuneifolia*, *L. nitida*, *Condalia microphylla*, and *Prosopis flexuosa*. The understory consists of dwarf shrubs <50 cm in height (e.g., *Acantholippia seriphioides* and *Senna aphylla*), forbs (e.g., *Baccharis*, *Sphaeralcea crispa*, and *Glandularia parodii*), and perennial bunchgrasses (e.g., *Stipa*, *Poa*, and *Aristida*).

The plains vizcacha.—Plains vizcachas are large rodents (adult males 5–9 kg; adult females 3–5 kg) that live in colonies of approximately 10–30 individuals (Branch 1993a). Colony sites are used for multiple generations and consist of a burrow system ($\bar{X} = 150$ m^2 ± 9 *SE*) surrounded by a heavily grazed area. The open burrows connect to underground chambers that are up to 2 m in diameter and 0.5–2 m belowground (Jackson et al. 1996). Vizcachas forage aboveground at night, primarily on grasses and herbs (Branch et al. 1994b). Like black-tailed prairie dogs, they clip plants that they do not consume such as dwarf shrubs, presumably as a mechanism to reduce predation risk (Branch et al. 1994a; Weltzin et al. 1997). In our study area, density of burrow systems was 0.3 ± 0.05 systems/ha (mean ± *SE*—Branch et al. 1996). New colonies form in open areas where fire or other disturbance has reduced vegetation (Branch et al. 1994a, 1996).

Vegetation sampling.—Vegetation was sampled on burrow systems and along a single transect (20 × 90 m) at each of 4 colony sites (mean distance between sites ± *SE*, 3.4 ± 1.1 km). Transects were established in a random direction from burrow systems and extended from heavily grazed areas at the edge of burrows into the ungrazed matrix. No obvious gradients in

slope or soil factors such as composition or texture existed along the transects. Each transect was divided into three 30-m segments for sampling, representing a heavily grazed zone (0–30 m), a moderately grazed transition zone (>30–60 m), and a very lightly to ungrazed zone (>60–90 m), identified by absence of vizcacha feces and observations of foraging behavior (Branch 1993b).

Aboveground biomass of annual and perennial forbs, annual and perennial grasses, and dwarf shrubs was estimated at the time of peak standing biomass by destructive sampling of 24 plots (0.4 m^2) located randomly in each segment along each transect. Samples were separated by species into live and dead material, dried at 60°C for ≥48 h, and weighed. Aboveground biomass of shrubs was estimated in one 80-m^2 plot in the center of each burrow system and in a similar plot located randomly in each grazed, transition, and ungrazed zone along the transects. For each shrub, we measured diameter of the tallest stem at 10 cm above the soil surface, height of the tallest stem, and crown diameter. Aboveground biomass and live and dead mass of specific components (foliage, small stems ≤5 mm diameter, and large stems >5 mm diameter) were estimated for each shrub using allometric equations developed from destructive sampling of the same species near the site (Hierro et al. 2000). Shrubs are not browsed by vizcachas; therefore, the same equations were used for all zones. Mass of dead material from understory vegetation and shrubs was included in standing litter pools (see below).

Nitrogen and P pools in aboveground vegetation were estimated for all plants in each zone. *L. divaricata* was the only shrub species that occurred on all burrow systems and in all zones of the transects. At each colony, we collected samples of mature foliage from *L. divaricata* ($n = 3$ individuals) growing on the burrow system and in each zone along the transects at the time of peak biomass and analyzed these samples for N and P content. For all understory species, we collected 3–5 samples composed of aboveground tissues from 5 to 10 plants at the time of peak biomass to determine N and P content. Similar samples were taken of foliage, small stems, and large stems from all shrub species. With the exception of foliage of *L. divaricata*, samples were collected from areas that were not grazed by vizcachas. N and P pools in aboveground plant tissue were estimated by multiplying mean tissue concentration of each species by its respective biomass, and then summing values of all species in the group for each quadrat or plot.

Foliage samples of *L. divaricata*on the burrow system and in all zones of transects also were analyzed for natural abundance of $\delta^{15}N$ to determine whether shrubs have access to N pools derived from vizcacha feces in burrow soil. Where deposition of feces contributes to soil N, soil exhibits $\delta^{15}N$ contents that reflect those in feces (Ben-David et al. 1998; García et al. 2002). If plants obtain a significant portion of their N from this enriched soil, $\delta^{15}N$ content of foliage also should reflect this signature. We expected values of $\delta^{15}N$ in shrub foliage on burrow systems to differ from those in other zones because of deposition of N belowground by vizcachas.

Litter and soil sampling.—Litter and soil were sampled at 9 random points on 3 burrow systems and in each 30-m segment along the transects at the end of the growing season. Litter on the soil surface was collected within 0.25-m^2 quadrats at each sampling point and sorted into the following components: coarse wood (>5-mm diameter), fine wood (≤5-mm diameter), foliage of shrubs and forbs, leaves and culms of grasses, vizcacha feces, and miscellaneous (small unidentified particles and reproductive material). Samples were dried at 60°C and weighed to obtain the mass of each component. Three composite samples of each component from each burrow system and zone on the transects were ground and analyzed for C, N, and P content. Vizcacha feces also were analyzed for $\delta^{15}N$. Nutrient pools were calculated by multiplying the concentration of each component by its respective mass in each zone.

Soil from burrow systems was sampled at 3 depths: surface (0–10 cm), an intermediate depth between the surface and mean depth of floors of vizcacha burrows, and at mean depth of burrow floors encountered in each burrow system. Burrows were encountered in approximately 40% of the 9 auger holes in each burrow system. Mean depth of burrow floors was 67 cm ± 8 *SE* (range 50–90 cm), and soil from intermediate depths was sampled at 35 ± 9 cm (range 25–45 cm). Along transects, surface soil was collected at 9 random points within each 30-m zone, and subsurface soil was sampled at every 3rd point. Soil samples were analyzed for texture, total C, total N, inorganic N, and total P. In addition, surface soil and soil from the mean depth of burrow floors were analyzed for $\delta^{15}N$.

Laboratory analyses.—Total N and P in vegetation, litter, and soil samples were measured using wet oxidation with a sulfuric acid–hydrogen peroxide mixture. Approximately 0.25 g of dry plant tissue or 1.0 g of dry soil was digested on a Technicon BD-40 block digester at 340°C (Thomas et al. 1967). Digests were analyzed for NH_4^+ using an indophenol colorimetric technique after neutralization with 1.2 M NaOH (Scheiner 1976) and for PO_4^{3-} using a molybdenum blue colorimetric technique (Keeney and Nelson 1982; Olson and Sommers 1982). Soil texture was measured using the pipette method (United States Department of Agriculture Soil Conservation Service 1992). Organic matter in litter and soil was estimated using loss on ignition in a muffle furnace at 550°C for 24 h. Ammonium and NO_3^- in soil were extracted with 2 M KCl within 48 h of field collection, using 10-g equivalent dry weight of soil in 100 ml of KCl. Ammonium was analyzed using the indophenol technique. Nitrate + nitrite were analyzed colorimetrically after NO_3^- reduction in a copper–cadmium column (Keeney and Nelson 1982). Stable nitrogen isotope ($\delta^{15}N$) in foliage of *L. divaricata*, feces, and soil was measured at the Cornell University Stable Isotope Laboratory (Ithaca, New York) with an isotope ratio mass spectrometer (Finnigan MAT Delta Plus, Thermo Fisher Scientific, Pittsburgh, Pennsylvania) using atmospheric N_2 as a reference.

Data analysis.—We tested for significant differences in plant biomass, litter mass, N, and P content in foliage of *L. divaricata*, and N and P pools in plant tissues, litter, and soil along the gradient of vizcacha activity (burrow systems, adjacent heavily grazed zone, transition zone, and ungrazed zone) using mixed linear models that permit correlated error

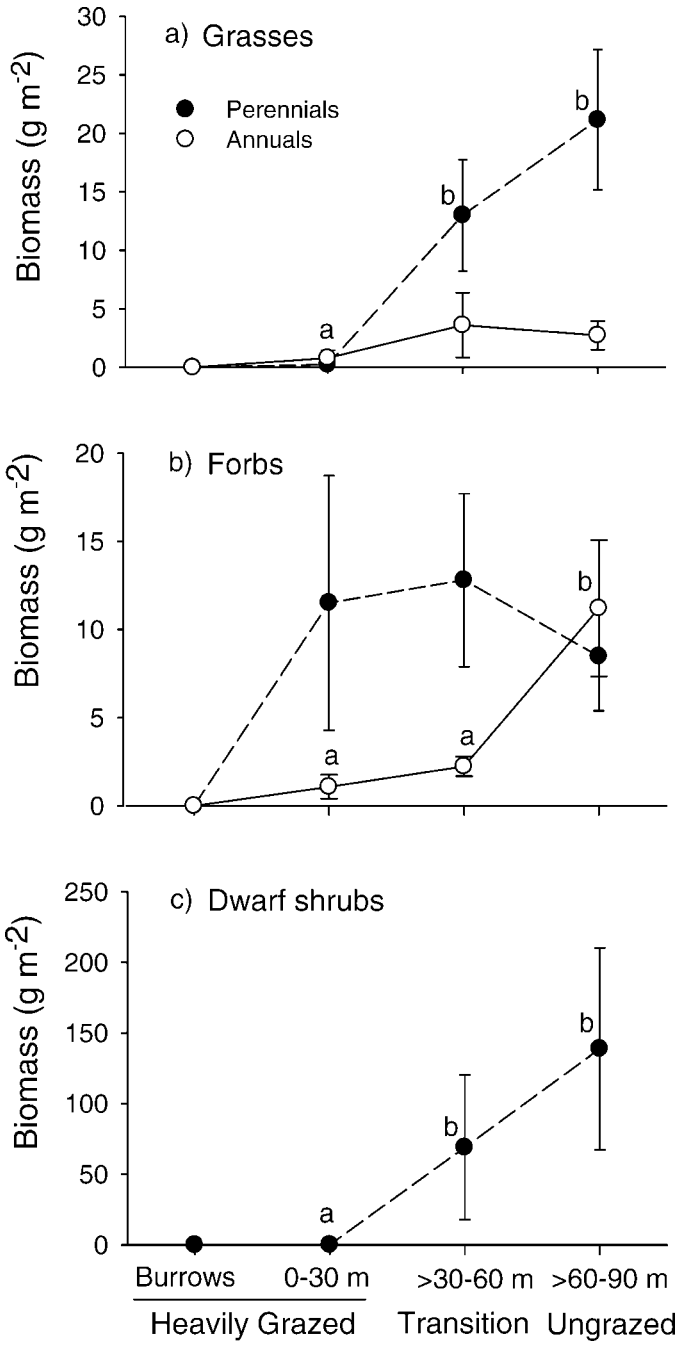

Fig. 1.—Biomass of functional groups of understory plants on colonial burrow systems of vizcachas and at increasing distances from the burrows. Values (mean ± 1 *SE*) with different letters are significantly different at $P < 0.05$, $n = 4$ colonies.

structure to account for lack of independence among zones at each colony site (Proc Mixed—SAS Institute Inc. 1996). Soil texture and $\delta^{15}N$ in foliage of *L. divaricata* were analyzed similarly. Understory species were combined into functional groups for analysis. Mean values of response variables for each zone for each colony were used as replicates ($n = 4$ for vegetation; $n = 3$ for litter and soil). Because biomass of herbaceous plants and dwarf shrubs was 0 g/m^2 on all burrow systems, statistical analyses for these variables only included the 3 zones along transects; zero values are shown for burrow systems on graphs for comparison with other zones. All other variables were analyzed across all 4 zones with colony entered into models as a repeated factor. We compared models with different covariance structures and chose the best model for each data set based on Akaike's information criterion and log-likelihood ratios (SAS Institute Inc. 1996). Comparisons among zones for all variables and among soil depths were made with Tukey's tests that adjust *P*-values for multiple comparisons. We tested for differences in N and P content in functional groups of plants with 1-way analysis of variance. The GT2 method was used to identify means that differed significantly because sample sizes (i.e., number of species per functional group) varied (Sokal and Rohlf 1995). We expected soil $\delta^{15}N$ belowground in burrow systems to reflect deposition of vizcacha feces, and we set up paired contrasts to compare $\delta^{15}N$ levels in surface soil and soil at mean depth of burrows for samples collected at the burrow systems and those in the 3 zones along the transect. Before analyses, data were transformed when necessary to meet assumptions of normality. Computations were conducted in SAS version 6.12 (SAS Institute Inc. 1996). All results are reported as means ± 1 *SE* and statistical significance level was $P \leq 0.05$.

Results

Aboveground biomass of vegetation.—Understory vegetation was absent from burrow systems, and little aboveground biomass occurred in heavily grazed zones adjacent to burrows (Fig. 1). Aboveground biomass of perennial grasses and dwarf shrubs increased with distance from burrow systems and comprised 87% of total understory biomass in the ungrazed matrix (Figs. 1a and 1c; Table 1). Biomass of annual forbs was higher in ungrazed areas than grazed areas, but biomass of perennial forbs did not differ along transects (Fig. 1b).

In contrast to understory vegetation, aboveground biomass of shrubs was greater on burrow systems compared to all other zones along the transects (Fig. 2a; Table 1). Greater shrub biomass resulted from larger individuals on the burrow systems rather than greater density (Figs. 2b and 2c; individual shrub mass by zone, $F = 28.9$, $d.f. = 3, 9$, $P < 0.001$). Individual shrubs in grazed zones adjacent to burrow systems also had significantly greater mass than shrubs in transition and ungrazed zones (Tukey's tests, $P < 0.04$ for pairwise tests). Shrub density exhibited the inverse pattern, with densities more than 3 times greater in ungrazed zones compared to grazed zones (Fig. 2c; $F = 27.4$, $d.f. = 3, 9$, $P < 0.0004$). Although stem biomass decreased from burrow systems to ungrazed zones, foliar biomass did not differ because small shrubs have a greater foliage to wood ratio than large shrubs (Table 1; foliage to wood ratio on burrow systems, 1:22; grazed zones, 1:19; transition zones, 1:11; ungrazed zones, 1:9—Hierro et al. 2000).

Nitrogen and P in vegetation.—Nitrogen and P content of live tissues of understory plants varied significantly among functional groups, with perennial grasses and dwarf shrubs having lower N and P contents than other groups (N, $F = 10.6$, $d.f. = 4$,

TABLE 1.—Summary statistics from mixed linear models for analyses of plant biomass, litter mass, and carbon to nitrogen (C:N) ratio in litter along a gradient of activity of vizcachas.

Response variable	*F*	*d.f.*	*P*
Understory biomass (g/m^2)			
Total biomass	6.0	2, 6	0.03
Annual forbs	9.2	2, 6	0.01
Perennial forbs	0.2	2, 6	0.84
Annual grasses	1.2	2, 6	0.35
Perennial grasses	58.5	2, 6	0.0001
Dwarf shrubs	10.8	2, 6	0.01
Shrub biomass (g/m^2)			
Total biomass	5.5	3, 9	0.02
Shrub foliage	2.0	3, 9	0.18
Shrub stems	6.8	3, 9	0.01
Litter mass (g/m^2)			
All litter	18.4	3, 6	0.002
Grass	13.3	3, 6	0.004
Foliage	0.7	3, 6	0.60
Fine wood	0.4	3, 6	0.75
Coarse wood	21.1	3, 6	0.001
Miscellaneous	1.4	3, 6	0.32
C:N ratio of litter			
All litter	147.8	3, 6	0.0001
Fine litter	7.2	3, 6	0.02

$P < 0.0001$; P, $F = 17.1$, $d.f. = 4$, $P < 0.0001$; Table 2). Nitrogen and P pools in understory vegetation corresponded with biomass along transects and were larger in ungrazed zones when compared to the heavily grazed zones adjacent to burrow systems (Table 3).

Foliage of *L. divaricata* on burrow systems had higher N and P content compared to foliage on transects, and similar N and P content along transects (Table 4). δ^{15}N content of foliage of *L. divaricata* on burrow systems was lower than in foliage in adjacent heavily grazed zones, and not significantly different among other sampling locations. N mass in shrub foliage also was greater on burrow systems than in adjacent grazed zones, and similar among other zones along transects (Table 3). Phosphorus mass in shrub foliage was not different among zones. Total aboveground N and P pools were larger for shrubs on burrow systems than along transects, but not different among zones along transects (Table 3).

Litter mass, N, and P.—Mass of grass litter on burrows and in adjacent heavily grazed zones was low compared to other zones along transects (Fig. 3a; Table 1). Mass of other fine litter did not change with distance from burrow systems (Table 1). Burrow systems had much greater coarse woody debris than any zone along the transects (Fig. 3a). In comparison to other fine litter, mass of vizcacha feces in litter samples on the soil surface was low on burrow systems (10.5 ± 5.4 g/m^2) and declined to 2.6 ± 1.7, 1.2 ± 0.7, and 0 g/m^2 in grazed, transition, and ungrazed zones, respectively. Mean contents of N and P in feces were 1.84% ± 0.03% and 0.26% ± 0.03%, respectively. δ^{15}N content of feces was 1.09‰ ± 0.46‰. Nitrogen and P pools in fine litter were not different among zones, but the large mass of coarse wood on burrows resulted in larger N and P pools and a much greater C:N ratio in total litter on the burrow systems compared to other zones along transects (Fig. 3b; Tables 1 and 3).

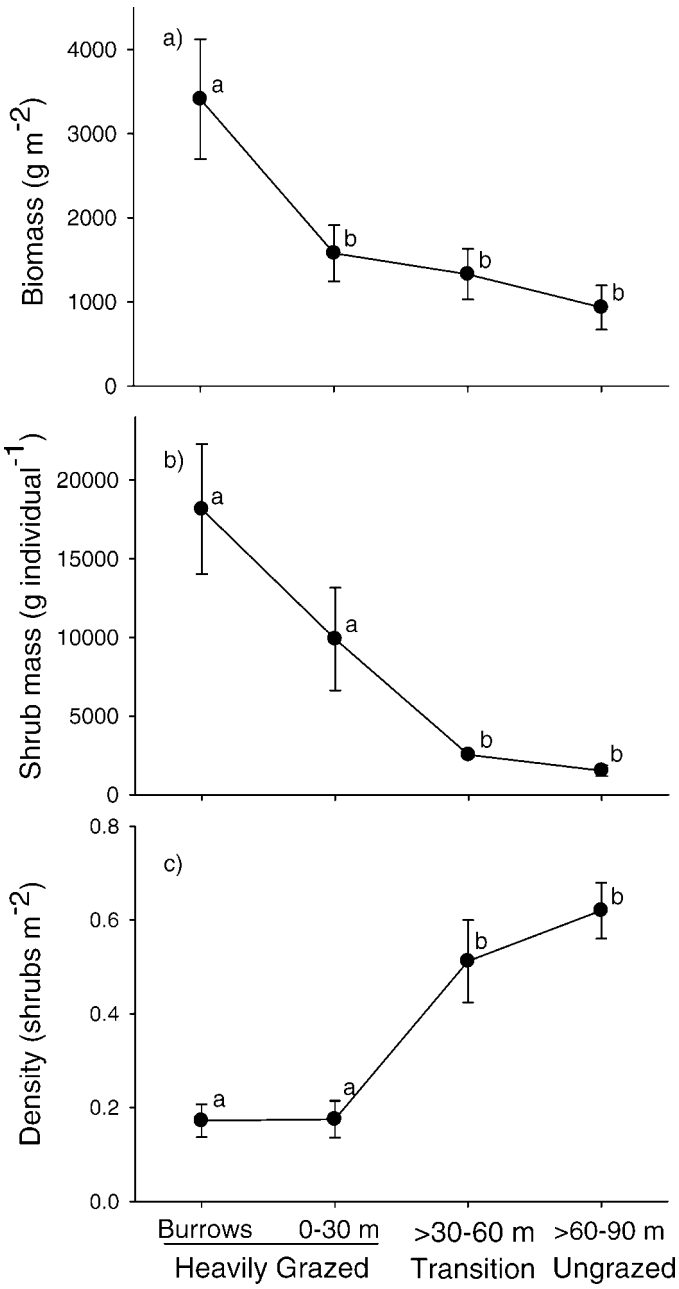

FIG. 2.—a) Total shrub biomass, b) mass of individual shrubs, and c) shrub density on colonial burrow systems of vizcachas and at increasing distances from the burrows. Data are means ± 1 *SE*, $n = 4$ colonies. Values with different letters are significantly different at $P < 0.05$.

Soil texture, C, N, and P.—Soil at all depths and zones was composed of 76–80% sand. Clay content was slightly higher in surface soil compared to deeper soil ($F = 5.8$, $d.f. = 3, 22$, $P < 0.01$), and this pattern was consistent across all zones, with no differences in clay content among zones ($P = 0.5$). Similarly, sand and silt content of soil did not vary among zones or depths ($P > 0.1$). Soil C did not vary among zones within each depth

Table 2.—Nitrogen (N) and phosphorous (P) contents (mean ± 1 *SE*) in aboveground live tissues of functional groups of understory plants. Means are unweighted by biomass.

Functional group	No. of species	N (%)[a]	P (%)[a]
Annual forbs	5	3.27A ± 0.41	0.39A ± 0.04
Perennial forbs	8	2.47A ± 0.18	0.23A ± 0.03
Annual grasses	2	3.18A ± 0.54	0.31A ± 0.06
Perennial grasses	7	1.52B ± 0.18	0.12B ± 0.03
Dwarf shrubs	3	1.21B ± 0.23	0.09B ± 0.05

[a] Different letters within a column indicate significant differences at $P < 0.05$ using Tukey's tests adjusted for multiple comparisons.

along the gradient of vizcacha activity (Table 5). Surface soil had higher C content than soil at a mean depth of 35 cm (16.5 ± 0.5 versus 13.8 ± 0.4 mg C/g soil, respectively, means for all zones combined ± 1 *SE*; $P = 0.02$). Soil C at the depth of burrows was more variable (15.5 ± 1.8 mg C/g soil) and did not differ from C contents at other depths ($P > 0.05$).

In surface soil, total N and inorganic N contents were similar among burrow systems, adjacent grazed zones, and ungrazed zones (Figs. 4a and 4b). In contrast, total N and inorganic N contents were significantly higher in soil at mean depth of burrow floors in burrow systems when compared to equivalent depths in all other zones (Table 5; $P < 0.0001$ for all pairwise comparisons). Surface and subsurface soil did not differ in total N on burrow systems ($P > 0.05$); whereas in all other zones, surface soil had higher total N than soil at the 2 other depths ($P < 0.05$). Inorganic N was an order of magnitude greater in soil at mean depth of burrow floors than in soil at any other location, with the exception of intermediate depths on burrow systems (Fig. 4a). At all sample locations, ammonium and nitrate contents followed a similar pattern, with nitrate comprising 71–96% of the inorganic N pool. $\delta^{15}N$ was similar for soil on the surface and at mean depth of burrows at the burrow systems ($P = 0.92$). In all other zones, $\delta^{15}N$ values were lower in surface soil than in soil at depth ($P < 0.02$; Fig. 5; Table 5). C:N ratios in surface soil were similar for burrow systems and zones along transects (Fig. 4c). In contrast, C:N ratios in subsurface soil in burrow systems were equivalent to C:N ratios in surface soil, and much lower than those in subsurface soil in all other areas. Total P content was greater in surface soil on burrow systems than in other zones ($P < 0.05$) and did not differ among grazed and ungrazed zones along transects ($P > 0.9$; Fig. 4d; Table 5). Total P content in soil at the mean depth of burrow floors was greater than that at equivalent depths along transects ($P < 0.05$).

Discussion

The activities of vizcachas resulted in reduced biomass of grasses, annual forbs, and dwarf shrubs; and greater biomass of shrubs and larger individuals on burrow systems compared to ungrazed areas. Shrubs growing on burrow systems had higher N and P contents in foliage, and soil N and P contents were higher at the mean depth of burrows compared to zones along the transects. Soil on the surface of burrow systems had higher P content than zones along transects.

Our conclusions are based on a comparative analysis that did not incorporate true experimental controls, and thus potentially could be confounded by other environmental factors (e.g., gradients in slope, and soil type and texture) along the transects. However, this is unlikely because analysis of soil texture demonstrated that soils were homogeneous throughout the study area, and transects were located in a random direction at each burrow system, and thus were unlikely to consistently follow any unmeasured environmental gradients. Although impacts of vizcachas on herbaceous vegetation have been demonstrated using experimental exclosures (Branch et al. 1996), assessment of effects of vizcachas on woody vegetation and soils are not as amenable to short-term experimentation. This study focused primarily on spatial patterns in ecosystem structure and processes. Long-term measurements of changes in vegetation and soil from the time of establishment of new colonies to post extinction would aid greatly in understanding temporal dynamics of changes in ecosystem structure induced by vizcachas.

Table 3.—Nitrogen (N) and phosphorous (P) pools (mean ± 1 *SE*) in vegetation and litter along a gradient of activity of vizcachas, and summary statistics from mixed linear models for comparison of pools along the gradient.[a]

	Burrow system	Adjacent grazed	Transition	Ungrazed	*F*	*d.f.*	*P*
N pools (g/m^2)							
Understory vegetation	—	0.34A ± 0.20	1.41A,B ± 0.49	2.37B ± 0.53	5.9	2, 6	0.04
Total shrubs	37.31A ± 7.08	17.94B ± 3.79	16.21B ± 3.89	11.73B ± 3.25	5.7	3, 9	0.02
Shrub foliage	4.43A,C ± 0.57	2.31B ± 0.45	2.91B,C ± 0.61	2.44B,C ± 0.56	3.7	3, 9	0.05
Fine litter	3.28 ± 0.76	3.28 ± 0.37	5.79 ± 1.56	5.80 ± 0.92	3.0	3, 6	0.11
Coarse litter	13.09A ± 3.97	0.18B ± 0.06	0.44B ± 0.22	0.43B ± 0.19	37.1	3, 6	0.0003
Feces	0.17 ± 0.09	0.04 ± 0.03	0.02 ± 0.01	0.000	3.8	3, 6	0.07
P pools (g/m^2)							
Understory vegetation	—	0.03A ± 0.01	0.13A,B ± 0.03	0.24B ± 0.03	10.0	2, 6	0.01
Total shrub	1.71A ± 0.32	0.85B ± 0.17	0.77B ± 0.17	0.55B ± 0.15	5.5	3, 9	0.02
Shrub foliage	0.20 ± 0.03	0.11 ± 0.02	0.14 ± 0.03	0.12 ± 0.02	2.3	3, 9	0.14
Fine litter	0.12 ± 0.02	0.13 ± 0.02	0.24 ± 0.07	0.26 ± 0.06	3.4	3, 6	0.09
Coarse litter	0.30A ± 0.09	0.004B ± 0.001	0.01B ± 0.005	0.01B ± 0.004	12.8	3, 6	0.005
Feces	0.023 ± 0.011	0.005 ± 0.004	0.002 ± 0.001	0.000	4.4	3, 6	0.06

[a] Different letters within a row indicate significant differences at $P < 0.05$ using Tukey's tests adjusted for multiple comparisons.

TABLE 4.—Nitrogen (N) and phosphorous (P) contents and stable nitrogen isotope ($\delta^{15}N$; mean ± 1 *SE*) in foliage of *Larrea divaricata* along a gradient of activity of vizcachas, and summary statistics from mixed linear models for comparison of variables along the gradient.[a]

	Burrow system	Adjacent grazed	Transition	Ungrazed	*F*	*d.f.*	*P*
N content (%)	3.30A ± 0.03	2.80B ± 0.05	2.65B ± 0.04	2.72B ± 0.11	11.7	3, 9	0.002
P content (%)	0.15A ± 0.002	0.12B ± 0.005	0.13B ± 0.006	0.13B ± 0.006	8.0	3, 9	0.006
$\delta^{15}N$ (‰)	4.66A,C ± 0.52	6.48B ± 0.61	5.65B,C ± 0.55	5.12B,C ± 0.19	4.7	3, 9	0.03

[a] Different letters within a row indicate significant differences at $P < 0.05$ using Tukey's tests adjusted for multiple comparisons.

Vizcachas foraged on grasses and forbs and clipped dwarf shrubs, which favored annual and perennial forbs with higher N and P contents over perennial grasses and dwarf shrubs with relatively low N and P contents. Alteration of plant species composition is a primary indirect mechanism by which herbivores affect decomposition and nutrient turnover of litter (Coppock et al. 1983; McInnes et al. 1992; Sirotnak and Huntly 2000). Grazing also can alter nutrient content of plant species that are grazed (Coppock et al. 1983; Green and Detling 2000; McNaughton et al. 1988). Our samples of understory vegetation were collected from ungrazed areas; thus, we did not account for potential variation in N and P contents within understory species along the gradient of herbivory by vizcachas. However, because herbaceous vegetation in grazed areas constitutes only a minor proportion of the overall biomass, and nutrient pools in the understory strongly reflect differences in biomass along the gradient of herbivory, this limitation is not likely to substantially alter observed patterns in understory nutrient pools.

Although vizcachas do not consume shrubs, the structure of woody vegetation differed markedly with activity of vizcachas. The larger shrubs on burrows and in adjacent grazed areas, and the greater biomass of shrubs growing on burrow systems, suggest that vizcachas facilitated growth, persistence of shrubs, or both, in these areas. Alternatively, vizcachas may choose to place their burrows in areas with larger shrubs. However, this hypothesis is inconsistent with field data on populations of vizcachas. Vizcachas colonize sites where fire or other disturbance has reduced aboveground biomass of vegetation, and populations of vizcachas decline when shrubs on burrow systems become large (Branch et al. 1994a; Machicote 2001). In addition, soil texture, which can influence both activity of burrowing mammals (Laundre and Reynolds 1993) and size of shrubs (Hamerlynck et al. 2002), was similar at burrow systems, grazed areas, and ungrazed areas.

Facilitation of shrubs by vizcachas could occur through at least 3 mechanisms. First, the large size of individual shrubs and greater biomass of shrubs on burrow systems could be explained by greater availability of N and P associated with burrowing and deposition of waste belowground. Consistent with this hypothesis, foliar N content of *L. divaricata* was higher in individuals growing on burrow systems (range, 3.2–3.4% N) compared to those in surrounding grazed and ungrazed areas (2.4–2.8% N). Also, foliage of *L. divaricata* on burrow systems was depleted in ^{15}N, indicating a link between belowground N deposition by vizcachas, whose feces were relatively low in ^{15}N, and N uptake by shrubs. Foliar N content of *L. divaricata* on burrow systems exceeded values reported for other shrub species in southwestern Argentina (0.9–2.9% N—Carrera et al. 2000; Mazzarino et al. 1998) and those reported for *L. tridentata* in North America (1.3–2.6% N—Hamerlynck et al. 2004; Killingbeck and Whitford 1996). Foliar P content of *L. divaricata* showed a similar pattern and also was higher than values reported for *L. tridentata* in North America (0.06–0.1% P—Lajtha 1987). Higher foliar P content in shrubs growing on burrow systems could result from both weathering of caliche deposited on the soil surface during burrow excavation by vizcachas and from deposition of organic forms of P in feces in

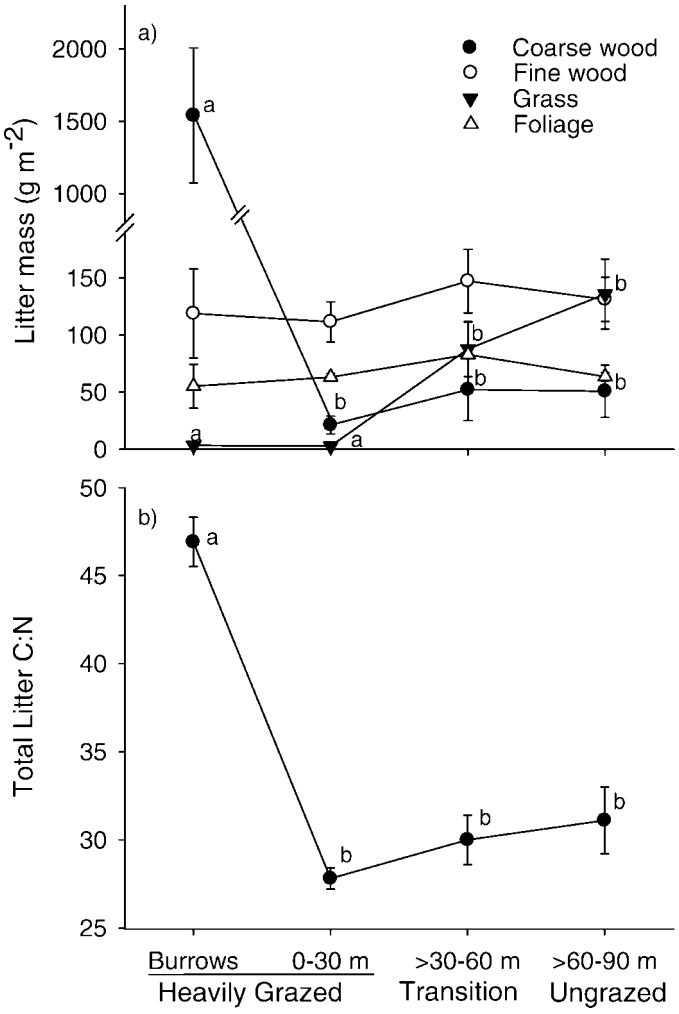

FIG. 3.—a) Mass of litter components and b) carbon to nitrogen ratio of all litter on vizcacha burrows and at increasing distances from the burrows. Values (mean ± 1 *SE*) of components with different letters are significantly different at $P < 0.05$, $n = 3$ colonies.

TABLE 5.—Summary statistics from mixed linear models for analyses of soil carbon (C), total soil nitrogen (N), inorganic soil N, stable isotope of nitrogen ($\delta^{15}N$), and total soil phosphorous (P) at the surface and belowground along a gradient of activity of vizcachas.

	Zone along the transect			Depth			Zone × depth interaction		
Response variable	*F*	*d.f.*	*P*	*F*	*d.f.*	*P*	*F*	*d.f.*	*P*
Total C	0.2	3, 22	0.84	4.5	2, 22	0.02	0.7	6, 22	0.68
Total N	11.5	3, 22	0.0001	44.4	2, 22	0.0001	12.7	6, 22	0.0001
Inorganic N	43.8	3, 22	0.0001	13.7	2, 22	0.0001	18.7	6, 22	0.0001
$\delta^{15}N$	0.4	3, 14	0.77	20.5	1, 14	0.0005	2.7	3, 14	0.08
Total P	4.1	3, 22	0.01	21.4	2, 22	0.0001	0.9	6, 22	0.45

burrows and subsequent mineralization. Higher foliar N content in *L. tridentata* has been linked to higher photosynthetic rates, higher stomatal conductances, and higher productivity (Hamerlynck et al. 2004). Both N and P fertilization can increase growth rates of seedlings of *L. tridentata* (Lajtha and Klein 1988). Therefore, shrubs on vizcacha burrows are likely to have greater rates of net assimilation and productivity when compared to shrubs in other areas.

Second, greater size of individuals and lower density of *L. divaricata* on burrow systems and in heavily grazed areas could occur because these shrubs are older. Fires are common in shrub-dominated ecosystems of central Argentina, and rates of spread and fire intensity strongly depend on fine-fuel loads, particularly perennial grasses and standing dead litter (Bóo et al. 1997; Scott and Burgan 2005). By grazing the understory, vizcachas reduce fine-fuel loads and may alter fire frequency and intensity, potentially leading to lower shrub mortality. We are investigating this hypothesis using fire history and dendrochronological techniques to age stems of *L. divaricata*.

Third, shrubs may be larger on burrow systems and grazed areas because vizcachas reduce competition between shrubs and herbaceous vegetation for nutrients, water, or both by removing understory vegetation. However, in our study area, foliar N and P contents in *L. divaricata* and N and P pools in shrub foliage did not differ between ungrazed or lightly grazed areas and heavily grazed areas, suggesting that grazing alone does not alter availability of nutrients to shrubs. Although experimental removal of grasses in other semiarid ecosystems has been shown to increase soil water potential and augment productivity of shrubs by up to 25% (Aguiar and Sala 1998; Sala et al. 1989), predawn xylem pressure potentials were similar for *L. divaricata* in areas grazed heavily by vizcachas and ungrazed areas during severe droughts (Hierro 1999). Therefore, reduced competition between understory vegetation and shrubs for nutrients, water, or both does not appear to be the major mechanism by which vizcachas facilitate shrubs in grazed areas.

Vizcachas alter distribution of litter by grazing herbaceous vegetation and piling wood on burrows during territorial displays (Branch 1993a). These activities resulted in greater heterogeneity of litter across the landscape but did not lead to detectable differences in C, total N, or inorganic N contents in surface soil. Coarse wood has a high C:N ratio, likely leading

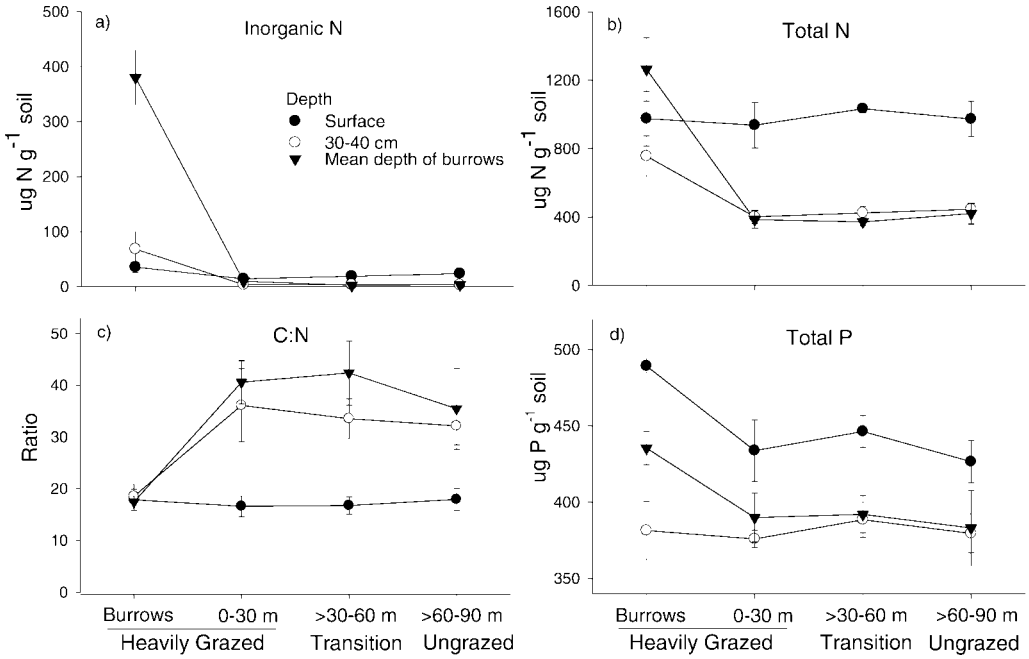

FIG. 4.—a) Inorganic nitrogen, b) total nitrogen, c) carbon to nitrogen ratio, and d) total phosphorus in soil sampled at the soil surface (0–10 cm), intermediate depth (30–40 cm), and mean depth of burrows (50–90 cm) at vizcacha burrow systems and at increasing distances from the burrows. Data are means ± 1 *SE*, $n = 3$ colonies.

to slow turnover as reported for dynamics of coarse wood in other semiarid ecosystems (Schaefer et al. 1985). Grazing has been shown to have relatively little effect on total C or N pools in surface soil in some other systems, while at the same time altering labile N pools and rates of N mineralization (Frank and Groffman 1998; Sirotnak and Huntly 2000). We currently are investigating rates of N mineralization and microbial respiration on burrow systems and along transects to examine effects of grazing by vizcachas on these processes.

In contrast to the lack of changes in total N and inorganic N on the soil surface with grazing, waste deposition in burrow systems and biopedturbation by vizcachas significantly altered vertical distributions of N and P in this ecosystem. Vizcachas redistribute and concentrate nutrients by foraging over large areas (e.g., mean home range, 13,000 ± 2,000 m^2—Branch 1993b) and depositing feces and urine belowground in the much smaller area occupied by the burrow system (150 ± 9 m^2). Deposition in burrows resulted in total N concentrations that are similar to those in surface soil and much greater than at equivalent depths in other areas. Surface soil, in general, is depleted in ^{15}N relative to soil at depth (Martinelli et al. 1999). However, surface soil and soil at the depth of vizcacha burrows exhibited similar $\delta^{15}N$ contents, reflecting the low values of ^{15}N in feces deposited in burrows and likely mixing of soil during construction of burrows. Inorganic N content, particularly NO_3^-, in burrow soil was an order of magnitude higher than that in surface soil, and likely resulted from decomposition and mineralization of N in feces and hydrolysis of urea. Increases in total and inorganic N in subsurface soil may be one of the major effects of a broad range of burrowing animals on nitrogen cycling (Chew and Whitford 1992; Whitford and Kay 1999). Belowground N storage may be particularly important in ecosystems that experience high frequency of fires, because storage in burrows should conserve N during intense fires if these pools persist for long periods of time.

By burrowing and excavation, vizcachas redistributed caliche from subsurface layers at approximately 50–150 cm in depth up to the surface, resulting in total P content of surface soil on burrow systems that was greater than any other location sampled. Transport of soil by animals and subsequent weathering may play a particularly important role in enhancing plant-available P in arid and semiarid ecosystems, where much of the P is precipitated as caliche or other secondary calcium phosphate minerals (Lajtha and Schlesinger 1988; Whitford and Kay 1999). Genesis of caliche layers and accumulation of weathered clays and oxides occurs on geologic time scales, but transport to the soil surface by burrowing animals can occur rapidly. Fecal and urine deposition in burrows also may increase organic P in subsurface soil.

Four major processes have been proposed as determinants of vertical distribution of nutrients within a soil profile: biological cycling by plants, weathering, leaching, and atmospheric deposition (Jobbagy and Jackson 2001). Biological cycling processes associated with plants often dominate distributions of nutrients most limiting to plant productivity, and these typically have the shallowest vertical distributions. For example, total N and extractable P contents are significantly higher in the top 20 cm of soil in a range of soil types, consistent with our data for total N, inorganic N, and total P in the absence of burrowing activities. However, examination of our data indicates that animals also play an important role in determining vertical distribution of soil nutrients by deposition and transport of materials within the soil profile, and they may enhance weathering of minerals in transported materials.

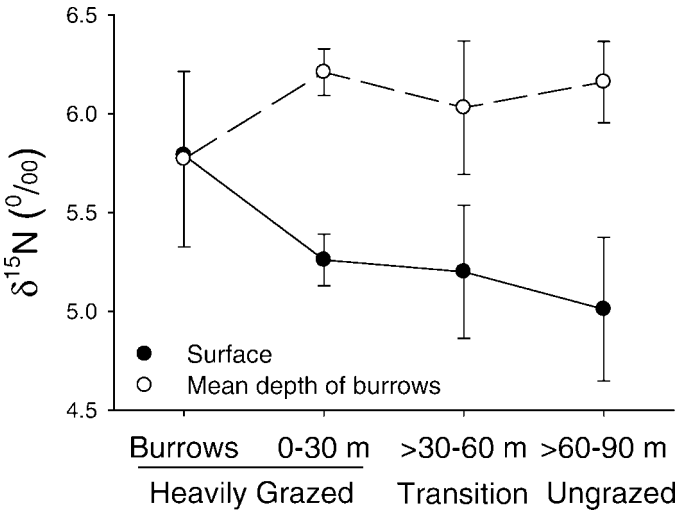

Fig. 5.—Stable nitrogen isotope ($\delta^{15}N$) in soil sampled at the soil surface (0–10 cm) and mean depth of burrows (50–90 cm) at vizcacha burrow systems and at increasing distances from the burrows. Data are means ± 1 *SE*, $n = 3$ colonies.

Landscape-level effects of vizcachas in semiarid scrub.—Through their effects on understory vegetation, soil nutrients, fire regimes, or a combination of these, vizcachas produce patches of large shrubs with greater biomass and little understory vegetation in a matrix of smaller shrubs, subshrubs, and perennial grasses. This results in both greater structural heterogeneity and greater absolute amounts of biomass and N and P pools in vegetation at the landscape level. We estimated the area grazed by vizcachas as 1.4 ha per colony based on the distribution of vizcacha feces at colonies and with grazed and transition areas calculated as concentric rings of 30-m width around the burrow system. This value is similar to mean home-range size of colonies calculated from behavioral observations (1.3 ha—Branch 1993b). Based on this estimate of area, density of burrow systems (0.3 ± 0.05 burrow systems/ha—Branch et al. 1996), and mean biomass and nutrient pools on burrow systems and in grazed, transition, and ungrazed zones weighted by area, we calculated that the landscape at our study site contains 14.7% more biomass, 11.9% more N, and 6.1% more P in aboveground vegetation than a landscape without vizcachas (i.e., a landscape equivalent to the ungrazed matrix). Similarly, total aboveground pools of N and P (vegetation + litter) were estimated to be 6.8% and 2.4% greater, respectively.

As a result of their deposition of N below the soil surface and transport of P from subsurface to surface soil, vizcachas alter the spatial distribution of plant-essential nutrients. The size of nutrient-enriched patches averages 150 ± 9 m^2 (i.e., the size of

a burrow system), and based on the density of vizcacha colonies present during this study, approximately 0.5% of the landscape consists of patches enriched with N and P associated with burrow systems. Vizcacha colonies are dynamic with recurrent local extinctions and colonization occurring across the landscape (Branch et al. 1994a, 1996). Because total N pools belowground are large and caliche weathers slowly on the soil surface, nutrient-enriched patches associated with burrow systems of vizcachas probably persist much longer than active vizcacha colonies themselves. Our landscape-level calculation of the area of nutrient patches associated with vizcacha colonies only incorporates extant colonies and, therefore, likely underrepresents the total amount of the landscape with vizcacha-induced nutrient patches.

Our research on vizcachas highlights several themes that are important for understanding effects of animals on structure and dynamics of ecosystems. First, the largest impacts of herbivores on ecosystem structure may occur through their effects on plants they do not consume. In our study, vizcachas altered individual size, biomass, and nutrient pools in shrubs, the dominant vegetation in this ecosystem. These changes are likely to affect processes such as productivity and nutrient cycling and are known to affect distribution and dynamics of other animal species (Machicote et al. 2004). Second, animals can create sites of enhanced soil nutrients that differ in spatial scale from the nutrient-enriched patches typically associated with shrubs in semiarid ecosystems. Animals are highly mobile, and their activities potentially disrupt tight feedbacks between plants and soil properties that control a number of processes in these ecosystems (Schlesinger et al. 1990). Third, transport of materials by animals has the potential to alter temporal dynamics of processes such as decomposition and mineral weathering by exposing materials to different sets of biotic and abiotic conditions. In systems where biopedturbation is frequent, animal transport should be included in the set of key processes (e.g., Jobbagy and Jackson 2001) that determine vertical distribution of nutrients within a soil profile. Finally, animal populations are highly dynamic, but their effects on ecosystem structure, and subsequent feedbacks on ecosystem processes, may persist much longer on landscapes than do the animals themselves (Naiman et al. 1994; Pastor and Naiman 1992). Potential long-term effects of animals on ecosystems are likely to be underestimated because human activities have markedly reduced populations of many animal species, and because the link between animal populations and animal-generated modifications may not be obvious once animals have disappeared from the landscape.

Resumen

El rol de los animales en alterar la estructura y dinámica de los ecosistemas ha recibido considerable atención en los últimos años. Sin embargo, aún existen falencias en el conocimiento que limitan la capacidad de incorporar efectos de los animales en modelos de dinámica de ecosistemas. Nuestra investigación sobre vizcacha (*Lagostomus maximus*, familia Chinchillidae) indaga sobre 3 de esas falencias—impactos subterráneos de vertebrados en el suelo, efectos netos de varios tipos de actividad animal sobre la estructura del ecosistema y magnitud a nivel del paisaje de los efectos locales. Nuestro estudio demuestra que como resultado del pastoreo a partir de las cuevas, las vizcachas producen fuertes patrones espaciales en la composición, biomasa y niveles de nutrientes de la vegetación herbácea. En la profundidad del suelo de las cuevas, los contenidos de nitrógeno (N) y fósforo (P) totales y el N inorgánico fueron mayores que a profundidades similares de suelos no disturbados por la actividad de vizcachas. Debido a los efectos de las heces de vizcacha, el suelo de las cuevas y el follaje de los arbustos que crecen sobre las mismas están reducidos en ^{15}N. El transporte de piedras calizas por las vizcachas resultó en mayores y significativas concentraciones de P en el suelo de la superficie de las cuevas. Los efectos indirectos sobre los arbustos, debido a la alteración de los nutrientes del suelo, transporte de calizas a la superficie y la posible modificación de los regímenes de fuego resultan en mayor biomasa y contenido de N y P foliar y cantidad total de N y P en arbustos. Los efectos netos de las vizcachas sobre la estructura tanto aérea como subterránea del ecosistema son extensos espacialmente y posiblemente persisten mucho más que las colonias que produjeron esos efectos. Este estudio demuestra que los mayores efectos de los herbívoros sobre la estructura de los ecosistemas pueden ocurrir a través de los impactos sobre las plantas que no consumen. En sistemas adonde la perturbación biológica del suelo es frecuente, el transporte animal está entre los procesos clave que determinan la distribución vertical de nutrientes en el perfil del suelo.

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Literature Cited

Aguiar, M. R., and O. E. Sala. 1998. Interactions among grasses, shrubs, and herbivores in Patagonian grass–shrub steppes. Ecología Austral 8:201–210.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165–1183.

Ben-David, M., G. M. Blundell, J. W. Kern, J. A. K. Maier, E. D. Brown, and S. C. Jewett. 2005. Communication in river otters: creation of variable resource sheds for terrestrial communities. Ecology 85:1331–1345.

Ben-David, M., R. T. Bowyer, L. K. Duffy, D. D. Roby, and D. M. Schell. 1998. Social behavior and ecosystem processes: river otter

latrines and nutrient dynamics of terrestrial vegetation. Ecology 79:2567–2571.

Bóo, R. M., D. V. Peláez, S. C. Bunting, M. D. Mayor, and O. R. Elia. 1997. Effect of fire on woody species in central semi-arid Argentina. Journal of Arid Environments 35:87–94.

Boogert, N. J., D. M. Paterson, and K. N. Laland. 2006. The implications of niche construction and ecosystem engineering for conservation biology. BioScience 56:570–578.

Branch, L. C. 1993a. Social organization and mating system of the plains vizcacha (*Lagostomus maximus*). Journal of Zoology (London) 229:473–491.

Branch, L. C. 1993b. Intergroup and intragroup spacing in the plains vizcacha, *Lagostomus maximus*. Journal of Mammalogy 74:890–900.

Branch, L. C., D. Villarreal, and G. S. Fowler. 1994a. Factors influencing population dynamics of the plains vizcacha (*Lagostomus maximus*, Mammalia, Chinchillidae) in scrub habitat of central Argentina. Journal of Zoology (London) 232:383–395.

Branch, L. C., D. Villarreal, J. L. Hierro, and K. Portier. 1996. Effects of local extinctions of the plains vizcacha (*Lagostomus maximus*) on vegetation of the semi-arid scrub of central Argentina. Oecologia 106:389–399.

Branch, L. C., D. Villarreal, A. P. Sbriller, and R. A. Sosa. 1994b. Diet selection of the plains vizcacha (*Lagostomus maximus*, family Chinchillidae) in relation to resource abundance in semi-arid scrub. Canadian Journal of Zoology 72:2210–2216.

Carrera, A. L., C. L. Sain, and M. B. Bertiller. 2000. Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. Plant and Soil 224:185–193.

Chew, R. M., and W. G. Whitford. 1992. A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosote bushes (*Larrea tridentata*). Journal of Arid Environments 22:375–386.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I . Dyer. 1983. Plant–herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1–9.

Detling, J. K. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. Wildlife Society Bulletin 26:438–448.

Eviner, V. T., and F. S. Chapin III. 2005. Selective gopher disturbance influences plant species effects on nitrogen cycling. Oikos 109:154–166.

Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229–2241.

García, L. V., T. Marañón, F. Ojeda, L. Clemente, and R. Redondo. 2002. Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. Oikos 98:75–86.

Green, R. A., and J. K. Detling. 2000. Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. Oikos 91: 280–284.

Hamerlynck, E. P., T. E. Huxman, J. R. McAuliffe, and S. D. Smith. 2004. Carbon isotope discrimination and foliar nutrient status of *Larrea tridentata* (creosote bush) in contrasting Mojave Desert soils. Oecologia 138:210–215.

Hamerlynck, E. P., J. R. McAuliffe, E. V. McDonald, and S. D. Smith. 2002. Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. Ecology 83:768–779.

Hierro, J. L. 1999. Cold spots–hot spots: facilitation and interference of shrubs by a native herbivore in a semiarid ecosystem. M.S. thesis, University of Florida, Gainesville.

Hierro, J. L., L. C. Branch, D. Villarreal, and K. L. Clark. 2000. Predictive equations for biomass and fuel characteristics of Argentine shrubs. Journal of Range Management 53:617–621.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Jackson, J. E., L. C. Branch, and D. Villarreal. 1996. *Lagostomus maximus*. Mammalian Species 543:1–6.

Jobbagy, E. G., and R. B. Jackson. 2001. The distribution of soil nutrients with depth: global patterns and the imprint of plants. Biogeochemistry 53:51–77.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen—inorganic forms. Pp. 643–698 in Methods of soil analysis, part 2: chemical and microbial properties (R. H. Miller and D. R. Keeney, eds.). American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin.

Kielland, K., and J. P. Bryant. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. Oikos 82:377–383.

Killingbeck, K. T., and W. G. Whitford. 1996. High foliar nitrogen in desert shrubs: an important ecosystem trait or defective desert doctrine? Ecology 77:1728–1737.

Lajtha, K. 1987. Nutrient reabsorption efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata* (DC) Cov. Biogeochemistry 4:265–276.

Lajtha, K., and M. Klein. 1988. The effect of varying nitrogen and phosphorus availability on nutrient use by *Larrea tridentata*, a desert evergreen shrub. Oecologia 75:348–353.

Lajtha, K., and W. H. Schlesinger. 1988. The biogeochemistry of phosphorus cycling and phosphorus availability along a desert soil chronosequence. Ecology 69:24–39.

Laundre, J. W., and T. D. Reynolds. 1993. Effects of soil structure on burrow characteristics of five small mammal species. Great Basin Naturalist 53:358–366.

Machicote, M. 2001. Facilitation–inhibition: burrowing owls and their hosts in central Argentina. M.S. thesis, University of Florida, Gainesville.

Machicote, M., L. C. Branch, and D. Villarreal. 2004. Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? Oikos 106:527–535.

Martinelli, L. A., et al. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. Biogeochemistry 46:45–65.

Mazzarino, M. J., M. Bertiller, T. Schlichter, and M. Gobbi. 1998. Nutrient cycling in Patagonian ecosystems. Ecología Austral 8: 167–181.

McInnes, P. F., R. J. Naiman, and J. Pastor. 1992. Effects of moose browsing on vegetation and liter-fall of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075.

McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. BioScience 38:794–800.

Naiman, R. J., G. Pinay, C. A. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905–921.

Olofsson, J., H. Kitti, P. Rautiainen, S. Stark, and L. Oksanen. 2001. Effects of summer grazing by reindeer on composition

of vegetation, productivity and nutrient cycling. Ecography 24: 13–24.

Olson, S. R., and L. E. Sommers. 1982. Phosphorus. Pp. 403–430 in Methods of soil analysis, part 2: chemical and microbial properties (R. H. Miller and D. R. Keeney, eds.). American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:690–705.

Reichman, O. J., and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution 17:44–49.

Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81:501–505.

SAS Institute Inc. 1996. SAS/STAT software: changes and enhancement. SAS Institute Inc., Cary, North Carolina.

Schaefer, D., Y. Steinberger, and W. G. Whitford. 1985. The failure of nitrogen and lignin control of decomposition in a North American desert. Oecologia 65:382–386.

Scheiner, D. 1976. Determination of ammonia in Kjeldahl nitrogen by the indophenol method. Water Resources Research 10:31–36.

Schlesinger, W. H., et al. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Scott, J. H., and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. United States Department of Agriculture Forest Service General Technical Report RMRS-GTR-153:1–72.

Sherrod, S. K., and T. R. Seastedt. 2001. Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. Biogeochemistry 55:195–218.

Sirotnak, J. M., and N. J. Huntly. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. Ecology 81:78–87.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd ed. W. H. Freeman and Company, San Francisco, California.

Thomas, R. L., R. W. Sheard, and J. R. Moyer. 1967. Comparison of conventional and automated procedures for nitrogen, phosphorus, and potassium analyses of plant material using a single digestion. Agronomy Journal 59:240–243.

United States Department of Agriculture Soil Conservation Service. 1992. Soil survey laboratory methods manual. Soil Survey Investigations Report 42:1–716.

Weltzin, J. E., S. Archer, and R. K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. Ecology 78:751–763.

Whitford, W. G., and R. R. Kay. 1999. Biopedturbation by mammals in deserts: a review. Journal of Arid Environments 41:203–230.

Wilby, A., M. Shachak, and B. Boeken. 2001. Integration of ecosystem engineering and trophic effects of herbivores. Oikos 92:436–444.

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