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Effect of Herbivory and Disturbances by Tuco-Tucos (*Ctenomys mendocinus*) on a Plant Community in the Southern Puna Desert

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Abstract

We studied the differences between areas undisturbed and disturbed by *Ctenomys* in the structure, diversity, and composition of a Puna desert plant community. We also studied differences in nutrient distribution in the soil produced by the activity of tuco-tucos. Within the plant community, plant and soil samples were taken from different sites, and at each site, both disturbed and undisturbed areas were sampled. We hypothesized that the activity of this rodent affected plant community structure, specific composition, diversity, and nutrient distribution (N, K, and P). Results at the plant population and community level and for soil nutrient concentration suggest that *Ctenomys mendocinus* could be a keystone species, capable of orienting the dynamics of the plant community studied in this ecosystem. Nevertheless, further manipulative experiments are necessary to confirm that the differences found between disturbed and undisturbed areas are indeed caused by the activity of *Ctenomys*.

Introduction

Subterranean rodents may affect the structure of plant communities both indirectly (movement of soil and alteration of physical and chemical features by excavation) and directly (Andersen, 1987; Huntly and Reichman, 1994; Whitford and Kay, 1999; Cameron, 2000; Campos et al., 2001; Reichman and Seabloom, 2002). Subterranean and burrowing species often have been described as keystone species in their ecosystems (e.g. Ceballos et al., 1999), as their impact on the community is disproportionately strong relative to their abundance (Mares and Hulse, 1977; Power et al., 1996; Reichman and Seabloom, 2002). Thus, they have been considered as keystone ecosystem engineers due to their ability to modulate resource availability (i.e. nutrients, food, water, habitat) for other species (Reichman and Seabloom, 2002).

Subterranean and fossorial mammals build burrow systems where they store food, feces, seeds, plant propagules, and several types of organic matter, creating patches rich in organic content and affecting nutrient dispersion and plant distribution (Huntly and Reichman, 1994; Borghi and Giannoni, 1997; Gómez-García et al., 1999; Cameron, 2000). Also, soil disturbances caused by subterranean mammals result in improved water balance for plants (Grant et al., 1980; Williams et al., 1986) and can increase concentration of soil nutrients by accumulating them on the surface of disturbed areas (Grant and McBrayer, 1981; Huntly and Inouye, 1988). Thus, the activity of subterranean rodents produces nutrient-rich microsites that favor germination and establishment of annual plant species with high nitrogen requirements (Mun and Whitford, 1998). In other cases, their foraging activity and generation of mounds alter successional plant processes (Andersen and MacMahon, 1985; Inouye et al., 1987; Stromberg and Griffin, 1996). Therefore, by affecting soil properties, subterranean mammals strongly influence vegetation dynamics. Also, subterranean rodents, through herbivory, can eliminate plant species by cutting their roots and feeding on them or on their seeds (Mares and Hulse, 1977; Cantor and Whitham, 1989; Huntly and Reichman, 1994; Campos et al., 2001).

Arid environments are characterized by great variability in climate, topography, and soil, which produces a complex patch structure, with frequent occurrence of nutrient islands (i.e. areas rich in nitrogen and phosphorus; Crawford and Gosz, 1982; Noy-Meir, 1985). Some studies suggest that such islands could arise from the presence of shrubs which relocate soil nutrients beneath them (Crawford and Gosz, 1982), and from litter decomposition which is ecologically important in these zones (Martínez Carretero and Dalmaso, 1992). Since fertility islands arise from shrubs, these would probably be more resistant to environmental disturbances and more persistent within the community (Shlesinger et al., 1990; Tongway and Ludwig, 1994). This environmental heterogeneity is increased by continuous water and wind erosion, soil disturbance by animals, and grazing by domestic and wild herbivores (Wiens, 1985; Ceballos et al., 1999; Dean et al., 1999; Shlesinger et al., 1990).

Ctenomys are small or medium-sized rodents that share almost all their characteristics with subterranean species (Reig et al., 1990; Giannoni et al., 1996; Busch et al., 2000). They build complex burrow systems with several entrances (usually closed), some of them with soil mounds near the entrances, and others, called feeding holes, immediately beside the plants they consume (Pearson, 1959; Reig et al., 1990; Rosi et al., 1996).

In general, when individuals of the genus *Ctenomys* browse on shrubs, they cut the branches transversally into small pieces (Mares and Hulse, 1977; Borrueal et al., 1998) and carry them into their galleries so as to feed inside (Mares and Hulse, 1977). In South American deserts, herbivory by subterranean rodents has been studied in some arid zones (Contreras and Gutierrez, 1991; Borrueal et al., 1998; Campos et al., 2000, 2001; see also Cameron, 2000), but little is known about this animal-plant interaction in the cold Puna desert. An early study on the Peruvian Puna suggested a negative interaction between the activities of *Ctenomys* and those of larger herbivores such as the vicuña (Pearson, 1951). Antagonistic action of tuco-tucos (*Ctenomys* spp.) with camelids was also suggested for another Puna site (San Guillermo Reserve), due mainly to competition for the use of plant resources (Cajal et al., 1981).

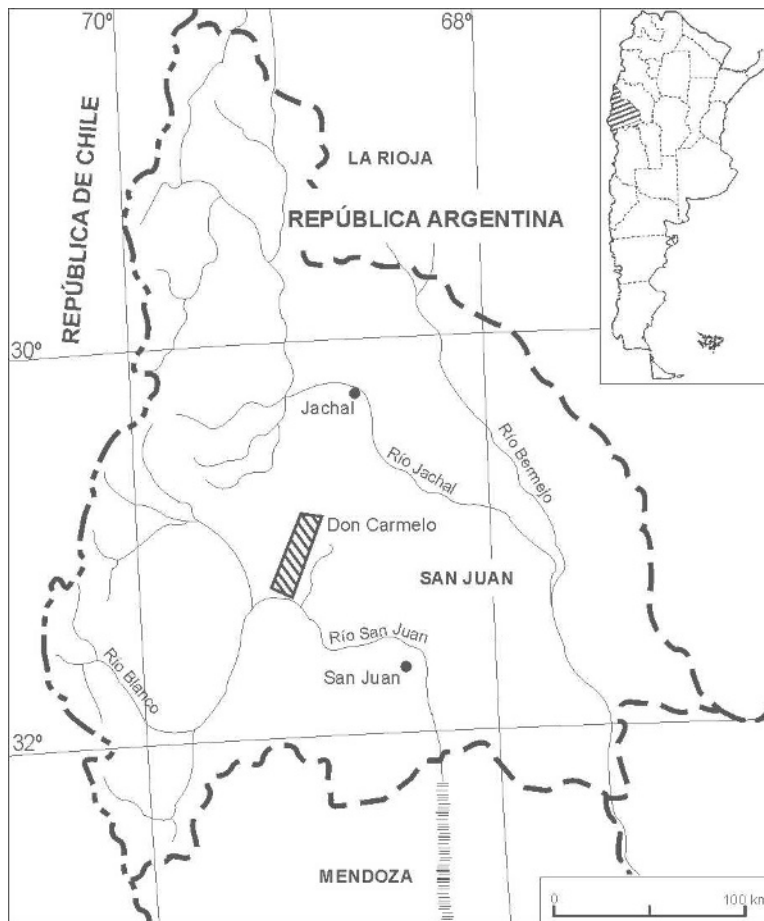


FIGURE 1. Location of the Puna Desert Private Reserve “Don Carmelo” in San Juan Province, Argentina.

The main objective of this study was to conduct a comparative study (mensurative experiment *sensu* Underwood, 1998) to assess the effect of the activity and feeding behavior of *Ctenomys mendocinus* on vegetation and soil in a Puna desert plant community. The specific aim of this study was to determine the effect of tuco-tucos on plant cover, community structure, diversity, specific composition, plant mortality, and nutrient distribution in the soil.

Materials and Methods

STUDY SITE

The study was conducted in the multiple-use private reserve “Don Carmelo” (30°57’S, 69°05’W), which is located in the precordillera of San Juan Province, Argentina (Márquez, 1999; Fig. 1). The reserve covers approximately 36,000 ha of the valley that lies between Sierra del Tigre and Sierra La Invernada, at an altitude ranging between 3000 and 3700 m a.s.l. The vegetation includes low, sparse, xerophytic shrubs and grasses. The climate is cold and dry, with a wide daily thermal range; rainfall occurs mainly in summer (December to March), and snow may fall at any time of the year (Martínez Carretero, 1995).

In the study area, we have observed individuals of *Ctenomys mendocinus* when burrowing and foraging on the surface. We have also collected a voucher specimen, which is deposited in the Mammal Collection at the Institute and Museum of Natural Sciences, San Juan National University (IMCN CM-059). This specimen was determined to be *Ctenomys mendocinus*.

SAMPLING DESIGN

Impact of *Ctenomys* on Vegetation

Fieldwork was conducted in February 2001. Vegetation was sampled at five sites encompassing both disturbed and undisturbed areas. To assess the impact of *Ctenomys* on vegetation, we selected five sites within the community, and two types of areas were sampled at each site: (1) areas highly disturbed by tuco-tucos (with a high density of holes [3.46/2 m²] and mounds [1.82/2 m²]; = “disturbed”), and (2) areas relatively undisturbed by *Ctenomys* (with a low density of holes [0.36/2 m²] and mounds [0.25/2 m²]; = “undisturbed”). In each area we randomly established three 30-m transects. Ten 2-m² samples, 1 m apart, were taken along each transect. For each of the 300 plant samples (5 × 2 × 3 × 10), we recorded plant cover, total number of individuals of each plant species, and number of dead plants (shrubs). For analysis of herb and shrub cover, we considered succulents as belonging to the herb stratum.

We used a blocked MANOVA analysis (site used as blocking factor) for comparing disturbed and undisturbed areas (Underwood, 1998). Data on plant cover (measured as percentages) were arc-sin transformed to meet MANOVA requirements. Newman-Keuls post-hoc test were used to assess differences between means.

A modified *t*-test was used to compare diversity indexes (Hutcheson, 1970) between disturbed and undisturbed areas (Zar, 1999). Statistical analyses were made using STATISTICA (version 6; STATSOFT, 2001), and InfoStat (professional version 1.1; INFOSAT, 2002). For analyzing diversity, the Shannon-Wiener index was calculated using log₂ (Krebs, 1989).

TABLE 1

Plant cover, number of holes, number of mounds, density of live plants, and density of dead shrubs in both areas (disturbed/undisturbed). A Blocked MANOVA test was used for comparing both areas. Disturbed areas were different from undisturbed ones (Wilks lambda = 0.38, $F_{(5, 290)} = 94.64$, $p = 0.0000$). Standard deviation in parentheses. Asterisk indicates a significant difference using a Newman-Keuls post-hoc test.

	Disturbed	Undisturbed	p -level	
Holes	3.46 (2.63)	0.36 (1.17)	<0.0001	*
Mounds	1.82 (0.85)	0.25 (0.57)	<0.0001	*
Plant cover	11.59 (7.39)	20.81 (8.70)	<0.0001	*
Mean number of live plants per sample	18.68 (8.97)	21.70 (11.22)	0.0063	*
Mean number of dead shrubs per sample	3.57 (2.93)	1.43 (1.66)	<0.0001	*

Impact of *Ctenomys* on Soil

Soil samples were taken from disturbed areas (only bare soil, because the other strata were absent), and from relatively undisturbed areas (samples from bare soil, recent mounds, soil under shrubs, and deep soil [four samples from a depth of 15 cm]) at eight sites within each type of area. Sampling was made in two seasons: summer (February) and spring (November). Soil samples were collected at 0–5 cm depth, and each one was made up of 10 subsamples. Total nitrogen, phosphorus, potassium, and organic matter were analyzed for each of the 36 soil samples. Nitrogen was determined by Kjeldhal method (expressed in ppm), extractable phosphorus was determined colorimetrically (expressed in ppm), potassium by nitric extraction using Pratt's method and then with flame photometer (expressed in ppm), and organic matter by chromic acid method (expressed in %/weight; Jackson, 1976). Differences in nutrient concentration between areas were determined with a one-way ANOVA analysis, because the blocked ANOVA analysis using season as a blocking factor did not produce a significant result. In analyzing different nutrient concentrations in undisturbed areas (bare soil, recent mounds, soil under shrubs, and deep soil), ANOVA and *a posteriori* Tukey test for unequal N were used to test for differences among sampling situations. Also, a multisample hypotheses test (Levene's test) was employed to compare the variances in the different soil variables measured within each situation (disturbed bare soil, and relatively undisturbed bare soil, recent mounds, soil under shrubs, and deep soil). As we rejected the null hypotheses that all variances are equal, we performed a post-hoc multiple comparison test, using also the Levene's test, correcting the results with the Bonferroni sequential adjustment (Rice, 1989). However, we take into account that the above procedures are now under debate (Moran, 2003).

Results

Total plant cover was significantly lower (44%) in areas disturbed by tuco-tucos. With respect to live plants and dead

TABLE 2

Mean density of plants from herb and shrub strata in disturbed and undisturbed areas. Standard deviation in parentheses. Disturbed areas were different from undisturbed ones (a Blocked MANOVA test was used for comparing both areas; Wilks lambda = 0.50, $F_{(2, 293)} = 146.15$, $p < 0.0001$). Asterisk indicates a significant difference using a Newman-Keuls post-hoc test.

	Disturbed	Undisturbed	p -level	
	Mean (SD)	Mean (SD)		
Herbs	1.93 (2.54)	9.01 (4.70)	<0.0001	*
Shrubs	16.34 (8.96)	12.41 (9.94)	0.0002	*

shrubs, we found that live plants were more abundant in undisturbed areas, and dead shrubs appeared in greater number in disturbed areas (Table 1). Herbs were significantly more abundant in undisturbed areas, and shrubs in disturbed areas (Table 2). Three shrub species showed significant differences in abundance in both areas; *Artemisia mendocana* and *Lycium tenuipinosum* were more abundant in disturbed areas, and *Lycium chazar* in undisturbed ones. With respect to herb species, *Poligala kurtzii* was more abundant in disturbed areas and species of *Stipa* in undisturbed ones (Table 3). Plant community diversity and species density were significantly higher in undisturbed areas, but species richness (17 vs. 14) and mean species richness were higher in disturbed areas (Table 4).

As regards soil, we found no significant differences in organic matter among different situations, but the tendency was similar to the concentration of N, K, and P: higher under shrubs, generally intermediate in disturbed bare soil and recent mounds, and the lowest in bare soil (Fig. 2). Concerning variability in soil data, we found significant differences in the variance in organic matter among different situations (Levene's test, $F = 7.53$, $P = 0.0003$), and the post-hoc test showed that the variance in undisturbed bare soil was significantly higher than others. But if the probabilities are corrected by sequential Bonferroni adjustment, all differences remain, with the exception of differences between undisturbed bare soil and disturbed bare soil. We did not find any significant differences in the variability of the other soil data (concentration of N, K, and P).

Discussion

The influence of *Ctenomys mendocinus* on this community (44% reduction of biomass) was stronger than that on grasslands of Buenos Aires Province (31% reduction of biomass; Malizia et al., 2000), but intermediate compared to the effect on some Monte desert plant communities (67% reduction in a community of *Larrea cuneifolia*; and 20% in a community of *L. divaricata*; Campos et al., 2001), and within the range of other herbivorous subterranean rodents (plant biomass reduced by 25 to 50%; Reichman and Smith, 1985). In disturbed areas, density of almost all plant forms decreases significantly, but a significant increase in the number of shrubs was observed (Table 2). Contradictory results about the effect of subterranean herbivores on shrubs have been reported for *Ctenomys* and other subterranean rodents (Busch et al., 2000; Cameron, 2000; Campos et al., 2001; Tort et al., 2004), which could be related to regional differences in the environmental conditions under which *Ctenomys* species live (Humid Pampa, Temperate Monte Desert, and Cold Puna Desert; Cameron, 2000; Malizia et al., 2000; Campos et al., 2000, 2001). Nevertheless, our results (increase in shrub cover in disturbed areas) could be explained by the difference of defense strategies of

TABLE 3

Mean density of plants (individuals/2 m²) of species recorded in disturbed and undisturbed areas. Standard deviation in parentheses. Disturbed areas were different from undisturbed ones (a Blocked MANOVA test was used for comparing both areas; Wilks lambda = 0.43, $F_{(10, 285)} = 37.17$, $p < 0.0001$). Asterisk indicates a significant difference using a Newman-Keuls post-hoc test.

	Disturbed	Undisturbed	p-level
Compositae			
<i>Artemisia mendozaana</i>	14.93 (9.26)	10.45 (10.28)	<0.0001 *
Ephedraceae			
<i>Ephedra aff. multiflora</i>	0.10 (0.38)	0.18 (0.80)	0.2642
Solanaceae			
<i>Lycium chandar</i>	0.40 (1.02)	1.55 (2.42)	<0.0001 **
<i>Lycium tenuipinosum</i>	0.96 (2.08)	0.26 (0.94)	0.0002 *
Portulacaceae			
<i>Montiopsis aff. gilliesii</i>	0.15 (0.93)	0.03 (0.21)	0.1203
Poligalaceae			
<i>Poligala kurtzii</i>	0.19 (0.69)	0.01 (0.12)	0.0022 *
Gramineae			
<i>Stipa speciosa</i>	0.19 (0.90)	1.99 (4.37)	<0.0001 *
<i>Stipa vaginata</i>	1.32 (2.37)	6.98 (5.55)	<0.0001 *
Cactaceae			
<i>Maihuenopsis glomerata</i>	0.23 (0.60)	0.21 (0.47)	0.7352
Cactus sp.	0.12 (1.47)	0.01 (0.12)	0.3764

shrubs against herbivores, because increase in shrub cover could only be accounted for by the increase in one species, *Artemisia mendozaana*.

With respect to the relationship between *Ctenomys* and plant diversity at Puna, our results disagree with most obtained until now (see Cameron, 2000). Species richness was higher in disturbed areas, suggesting that *Ctenomys* activity favors the persistence of some fugitive species that could be absent without perturbation (Platt, 1975). If this pattern is confirmed at a larger geographic scale, *Ctenomys* would have an important role in conserving fugitive Puna species.

On the other hand, diversity and species density were lower in disturbed situations. However, lower diversity in disturbed areas was not due to lower species richness, but to increase in the abundance of a dominant species, *Artemisia mendozaana*. This was the most dominant species in undisturbed areas, representing 47% of the total individuals recorded, but in disturbed areas its presence increased up to 80% of all plants sampled.

Density of the grasses *Stipa vaginata* and *S. speciosa* significantly decreased in disturbed areas as reported by Campos et al. (2001). Densities of *Artemisia mendozaana*, *Lycium tenuipinosum*, and *Poligala kurtzii* were higher in disturbed areas, which suggests a positive effect of *Ctenomys* activity on these plants. They are probably favored by *Ctenomys* herbivory, releasing interspecific competition when other plants are damaged. The effect of *Ctenomys* on plant density could be due to herbivory, competition relaxation, and facilitation of sexual and asexual reproduction, as suggested for other subterranean rodent-plant interactions (Contreras and Gutierrez, 1991; Borghi and Gianoni, 1997). In the case of the increase in the shrub *Artemisia mendozaana* var. *paramilloensis*, even though tuco-tucos can eat *Artemisia* plants, if there are more palatable species in their environment, i.e. *Lycium* spp., they avoid *Artemisia* (Riveros, 2003), probably because of the high contents of secondary plant compounds the genus has (saponins and terpenoids), which function as defense compounds (Golob et al., 1999). Consequently, tuco-tucos feed on and kill competing shrubs instead of

TABLE 4

Mean plant diversity, with Shannon-Wiener index (log₂; Krebs, 1989). t test for differences between two diversity indices in disturbed/undisturbed areas (Zar, 1984; * $p < 0.001$)

	Disturbed	Undisturbed	p-level
Total species richness	17	14	
Mean species richness			
($n = 10$)	8.4	7.4	0.089
Diversity (H)	1.32 (0.04)	1.94 (0.02)	0.001 *
Species density ¹			
(spp./2 m ²)	2.53 (1.02)	2.87 (0.93)	0.001 *

¹ t test.

Artemisia (the number of dead shrubs was significantly higher in disturbed areas).

Nutrient islands develop rapidly in desert soils (Schlesinger et al., 1990), and one of the mechanisms suggested for their formation is retention of humidity under shrubs. Another mechanism suggested is retention of plant material and soil nutrients by shrubs under their canopy when surface water flows after rainfall (Parsons et al., 1992). These shrub islands concentrate the biotic activity and biogeochemical cycles in desert ecosystems across continents (Noy Meir, 1985; Mazzarino et al., 1991; Herman et al., 1995). In North American deserts, high concentrations of N, P, and K under *Larrea tridentata* shrubs underscore the importance of biotic processes (decomposition and relocation of nutrients through the root system) to the development of fertility islands, especially with respect to N, which limits primary production in the Chihuahuan and Mojave deserts (Fisher et al., 1987; Sharifi et al., 1988). In the Monte desert, Martinez Carretero and Dalmasso (1992) found that litter under *Larrea divaricata* and *L. cuneifolia* shrubs is very important in the generation of fertility islands, since it is a source of N for microorganisms that mineralize soils in these zones. Similar data were found by Maggs and Pearson (1977) for coastal shrublands of Australia.

The disturbing activity of *Ctenomys mendocinus* in the studied areas increased nutrient concentration (N, K, P) in bare soil compared to bare soil in undisturbed areas. Differences in nutrient concentration between mounds of subterranean rodents and surrounding soil have been found in almost all studies performed, though not always for the same elements (nutrients) or in the same direction (increase or decrease; see Cameron, 2000, and Malizia et al., 2000). This has been attributed to the composition of the parent material in each region, and to the horizontal distribution of nutrients in the studied areas. The disturbing activity of *Ctenomys*, particularly in the southern Puna, modifies the distribution of nutrients, increasing their concentration in bare soils. The activity of *Ctenomys* also affects variability (variance) in organic matter, decreasing it in mounds and disturbed soils, probably redistributing nutrients from the "nutrient islands" found under shrubs, as suggested by the tendency shown by almost all nutrients studied (see Fig. 2). Therefore, the disturbing/grazing effects of tuco-tucos decrease the heterogeneity of soil nutrients. In undisturbed areas some patches have high concentrations and others low concentrations, while all areas have intermediate concentrations in disturbed areas. Also, increased nutrient concentrations in bare soil could increase the possibility for new plants to establish, increasing plant reproduction.

Results found in this work suggest that herbivory of *Ctenomys* affects plant cover, community structure, plant diversity, plant mortality, and floristic composition in the studied

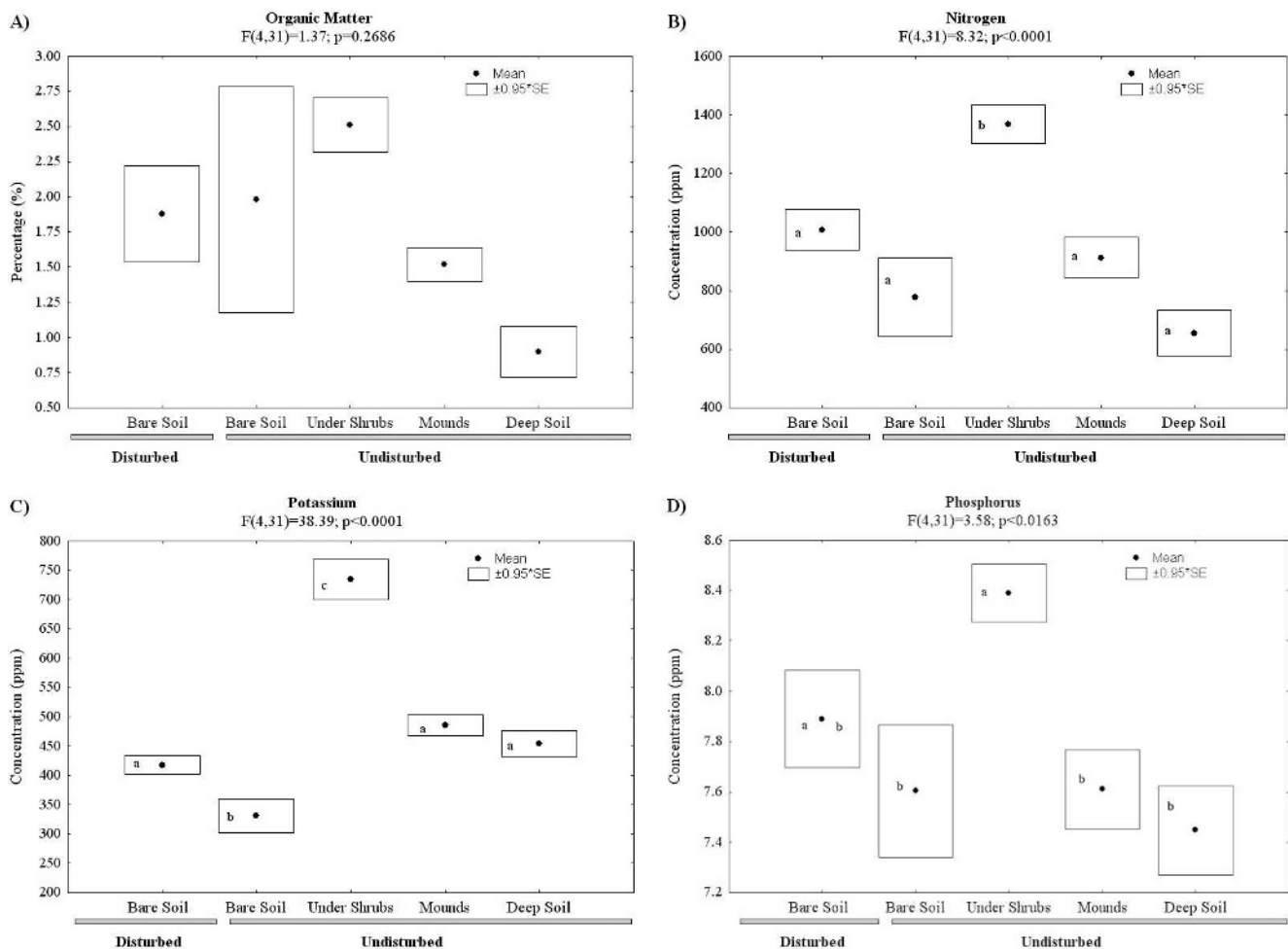


FIGURE 2. Organic matter content and nutrient concentration in areas under different levels of disturbance by *Ctenomys*, and in different microhabitats. Letters (a, b, c) indicate the result of an *a posteriori* Tukey test for unequal *N* among means ($p < 0.05$). (A) Organic matter content (%). (B) Nitrogen concentration (ppm). (C) Potassium concentration (ppm). (D) Phosphorus concentration (ppm).

Puna community. In addition, the burrowing activity on soil nutrients would suggest that *Ctenomys* sp. could be acting as a “key species” by establishing potential facilitation and mutualistic and predatory relationships with many species of the community, as has already been found for other keystone subterranean herbivores (Andersen and MacMahon, 1981; Ceballos et al., 1999; Reichman and Seabloom, 2002). Finally, further manipulative experimental studies are necessary to validate the conclusions suggested by this descriptive study and to confirm the role of *C. mendocinus* as a keystone species in the south of the Puna desert.

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