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SOIL MICROBIOLOGY

Subterranean Desert Rodents (Genus *Ctenomys*) Create Soil Patches Enriched in Root Endophytic Fungal Propagules

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Abstract

Subterranean rodents are considered major soil engineers, as they can locally modify soil properties by their burrowing activities. In this study, the effect of a subterranean rodent of the genus *Ctenomys* on soil properties and root endophytic fungal propagules in a shrub desert of northwest Argentina was examined. Our main goal was to include among root endophytic fungi not only arbuscular mycorrhiza but also the dark septate endophytes. We compared the abundance of fungal propagules as well as several microbiological and physicochemical parameters between soils from burrows and those from the surrounding landscape. Our results show that food haulage, the deposition of excretions, and soil mixing by rodents' burrowing promote soil patchiness by (1) the enrichment in both types of root endophytic fungal propagules; (2) the increase in organic matter and nutrients; and (3) changes in soil edaphic properties including moisture, field capacity, and texture. These patches may play a critical role as a source of soil heterogeneity in desert ecosystems, where burrows constructed in interpatches of bare soil can act, once abandoned, as "islands of fertility," promoting the establishment of plants in an otherwise hostile environment.

Keywords Biopedturbation · Fungal dispersion · Dark septate endophytes · Arbuscular mycorrhiza · Monte Desert

Introduction

Since the seminal work of Darwin [1], we know that the activity of soil biota affects soil properties and strongly influences vegetation dynamics. Soil biota comprises an enormous diversity of organisms, including microorganisms (i.e., bacteria, fungi) and soil fauna (microscopic and macroscopic animals). They have major control over nutrient availability for plants, both directly, throughout their role in organic matter turnover, and indirectly, when fungi and bacteria establish mutualistic symbioses with roots that enhance plant nutrient uptake [2]. Among mutualistic fungi, arbuscular mycorrhizae (AM) are well known to promote plant growth by increasing the root surface area with their mycelial network [3, 4]. More recently, a less studied group of root-colonizing fungi, the dark septate endophytes (DSE), have been reported as plant growth promoters [5, 6], though little is known about the mechanisms underlying their positive effect [7–9].

Soil microbiological activity strongly depends on the availability of organic matter as food source. In arid environments, due to the low vegetation cover compared with other ecosystems, organic matter together with water are main limitants for the establishment and growth of an active soil community [10]. Nutrients in deserts are not only scarce, but also not uniformly distributed. Patchiness is a pervasive characteristic of arid lands, determining a mosaic of vegetation patches (fertility islands), with high concentrations of organic matter and microbial activity, alternated with low-nutrient interpatches of sparse cover or bare soil (e.g., [11, 12]).

Under this scenario, animals that spend most of their life beneath earth can significantly affect the distribution of organic matter in desert soils. When they store their food or deposit

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their feces in their nests or burrows, they create soil patches enriched in organic matter (e.g., [13, 14]). Also, the movement of soil by digging activities change the concentration of soil nutrients [15, 16] and soil physical features [17]. Thus, their activities produce microsites enriched in organic matter, which in turn, increase soil microbial abundance and activity [18]. In deserts, any mechanism or activity that increases the availability of nutrients to plants can have profound effects on community dynamics; therefore, the generation of these patches may eventually lead to a new fertility island by facilitating the germination and establishment of plants [19, 20].

Among subterranean animals, desert rodents have been demonstrated to change soil properties within their burrow environment (e.g., [21–26]). However, most of these studies focused on soil physicochemical changes due to rodents' burrowing, while few have addressed a modification on soil microbiological composition and activity (e.g., [27, 28]). In particular, only two studies, to our knowledge, have studied how subterranean rodents affect root endophytic fungal communities through their burrowing activity [29, 30], but only taking the AM fungi into account.

In this work, we aimed to study changes in the abundance of root endophytic fungi propagules (AM and DSE) in relation with the burrowing activity of the subterranean rodent *Ctenomys* aff. *knighti* in semiarid northwestern Argentina. In a previous study, we demonstrated that this rodent species disperse viable AM and DSE propagules within their scats, and that these fungal propagules successfully colonize the roots of native plants under lab conditions [31]. Given that *C.* aff. *knighti* rodents commonly construct their burrows in interpatches of bare soil or sparse cover (V. Valentinuzzi, personal communication), we wondered whether rodents' burrowing activities promote soil patches enriched in endophytic fungal propagules. As burrowing activity, we include not only digging for constructing their burrow, but also their subterranean habits (e.g., taking their food and depositing their feces inside the burrow). To test this, we look for differences in the abundance of infective AM and DSE propagules and AM spore density between soils within the burrow environment and soils without burrows. Additionally, we also wondered whether the soil from burrows would have higher microbial activity, higher levels of nutrients, different pH, electrical conductivity, particle-size distribution, and field capacity compared to non-burrow soils.

Materials and Methods

Study Site

This study was carried out in a relatively undisturbed natural area located 8 km east of Anillaco, La Rioja, northwestern Argentina. This area corresponds to the Monte Desert biome, a shrub desert characterized by bolson landforms and valleys (see [32, 33] for a further description of the region). Climate is arid: Mean annual rainfall ranges from 100 to 200 mm and is almost exclusively limited to the summer months (between December and February), and mean annual temperatures range between 15 and 17 °C. Soils are sandy and poor in nutrients (entisols type), and the predominant vegetation is a shrubby steppe with flora mainly of the families Zygophyllaceae (*Larrea cuneifolia*, *Bulnesia retama*), Fabaceae (*Acacia aroma*, *Senna aphylla*, *Cercidium praecox*), and Cactaceae (*Trichocereus candicans*, *Tephrocactus articulatus*, *Opuntia sulphurea*). The vegetation is organized as a two-phase mosaic composed by a phase of shrub-dominated patches alternating with areas with sparse cover or bare soil [34].

The subterranean rodent genus *Ctenomys* includes more than 60 species that inhabit arid and semiarid regions of South America [35–38]. In our study area, *C.* aff. *knighti* (currently under process of taxonomic identification) is common and abundant (20 individuals/ha, distance between burrows ~ 100 m, V. Valentinuzzi, personal communication). Popularly known as "tuco-tucos," they are large (150–180 g), ,solitary and herbivorous, who emerge aboveground only for short bouts (Fig. 1a) [39, 40]. Burrows have tunnel systems (15 to 80 cm depth) with several entrances (usually closed and with soil mounds near the openings) and can cover an area up to 50 m^2 (Fig. 1b) [31]. The tuco-tucos browse on nearby shrubs and herbs, cut the branches and roots into small pieces, and carry them into their burrows to feed inside [41, 42]. Tunnels with dead ends are used for food stock, sleeping nests, or latrines [43].

Soil Sampling

We collected samples of active burrows and adjacent soils without burrows (hereafter, burrow and non-burrow soils, respectively) in eight 10 × 10 m plots separated ~ 5 km from each other, covering a total area of about 75 km^2. The eight plots exhibit similar characteristics in terms of geology, vegetation cover, and rainfall (exact locations are shown on the Table 1). Sampling was performed during February 2015. During this month, the biological activity in general is high after the summer rains. Prior sampling, occupation of the burrows was verified by field observations.

Each burrow was excavated until reaching the subterranean galleries. We collected five soil subsamples with a core (10 cm wide × 10 cm deep) from different burrow galleries and at different distances from each entrance (0.5 to 5 m away). Five subsamples of control soil were collected from adjacent bare soil, at least 10 m away. The subsamples were pooled in a composite sample of about 2 kg for each plot and treatment (burrow and non-burrow soil) and transported to the lab. The pooled samples (hereafter soil samples) were stored at room temperature until analyzed. For microbiological analyses, soil

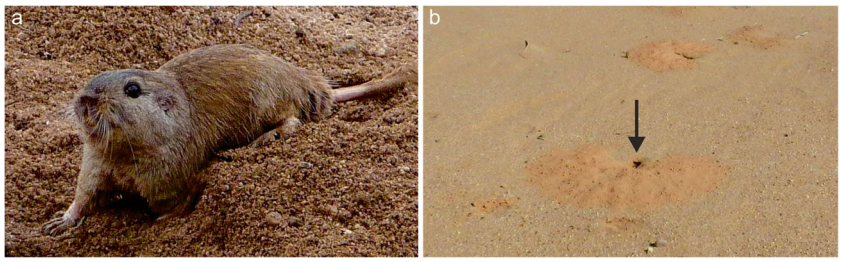

Fig. 1 **a** General aspect of *Ctenomys* aff. *knighti*. **b** An active *Ctenomys* burrow in the Monte Desert of northwestern Argentina. The black arrow shows one of the burrow entrances surrounded by the ejected mound

samples were processed within 24 h after their collection in the field.

Abundance of AM and DSE Propagules

Abundance of infective fungal propagules (spores and hyphae for AM and microsclerotia and melanised hyphae for DSE) in soil samples was assessed by the most probable number (MPN) method, following an adaptation by Sieverding et al. [44]. This method allows us to discriminate each endophyte type (AM and DSE). The assay was conducted in eightfold dilution series for 100 g of each soil sample, using sterile sandy soil as diluent substrate. As test plant, we used *Lactuca sativa*. Surface-sterilized seeds were pregerminated and planted into 500-ml pots (one per pot) filled with each dilution soil series (five replicates for each dilution series). As control, we used pots filled with sterile soil. The plants were randomly arranged, grown in greenhouse conditions at 23–28 °C, and watered daily with sterile water. After 5 weeks, the roots were harvested, stained with the dual Trypan Blue-Sudan IV method Barrow [45], and scored under binocular microscope for the presence or absence of AM and DSE colonization. Root colonization was quantified, according to the method of McGonigle et al. [46].The bioassay was performed in duplicate for each soil sample. The results were averaged for each type of endophyte and expressed as the number of each type of propagules per gram of soil, following Table VIII of Fisher and Yates [47].

To evaluate AM spore density, two 50-g subsamples of each soil sample were sieved with a 2-mm mesh to remove coarse debris and thoroughly wetted for 1 h before sieving and decanting following An et al. [48]. Briefly, spores were collected on 300-, 150-, and 60-μm sieves with tap water and placed in a 9-cm Petri dish for examination under a binocular stereomicroscope Leica MZ12. We counted the AM spores present in the three fractions and expressed the result as density of AM spores (no. of AM spores/g soil). When spores were tightly grouped in rigid dark sporocarps (aff. *Sclerocystis*), so that it was difficult to count them, we considered each sporocarp as one spore. For each sample, spore densities from the two subsamples were averaged.

Table 1 Geographic coordinates and elevations of the eight plots sampled in La Rioja Province, Argentina

Plot	Geographic coordinates	Elevation (m)
1	28° 48′ 24.4″ S 66° 54′ 36.8″ W	1306
2	28° 46′ 28.8″ S 66° 53′ 30.5″ W	1225
3	28° 48′ 18.6″ S 66° 52′ 13.9″ W	1233
4	28° 47′ 26.8″S 66° 51′ 31.3″ W	1203
5	28° 47′ 16.8″ S 66° 50′ 09.6″ W	1161
6	28° 44′ 59.9″ S 66° 50′ 12.3″ W	1098
7	28° 46′ 32.4″ S 66° 48′ 24.5″ W	1127
8	28° 43′ 51.6″ S 66° 48′ 23.2″ W	1038

Microbial Activity

Microbial activity was assessed by measuring respiration of incubated soil samples, using NaOH solution as the CO_2 trap [49]. The samples were kept in sealed jars at 25 °C in the darkness for 10 days. Blanks were also incubated. After that time, the CO_2 released from the soil was confined and absorbed by the alkaline solution, and the amount of the remaining NaOH was determined by titration with HCl. The analysis was replicated three times and averaged for each soil sample. Microbial activity is expressed as milligrams of CO_3^{-2} respired per gram of soil per day (mg CO_3^{-2}/g/d).

Soil Physicochemical Analyses

Soil samples were analyzed by Soil Laboratory (INGEIS, UBA—CONICET) Buenos Aires, Argentina, for organic carbon (g/kg) by Walkley-Black method, total nitrogen (g/kg) by Kjeldahl method [50], and available phosphorous (mg/kg) following Bray and Kurtz [51], and nitrate (mg/kg) was determined using the $CuSO_4$ method [52]. Soil pH and electric conductivity (EC, dS/m) were measured in a 1:2.5 suspension of soil in water. Field capacity (%) and moisture (%) were also determined [53]. The particle size distributions were

calculated by sieving the coarse (> 2 mm), medium (between < 2 mm and > 50 μm), and fine (< 50 μm) fractions of 100 g of each soil sample, and their weights were expressed as percentage.

Statistical Analyses

First, we tested whether the abundance of endophytic fungi differed between burrow and non-burrow soils using a multivariate analysis of variance (MANOVA). Response variables were abundance of AM propagules, abundance of DSE propagules, and density of AM spores and fixed factor plot and treatment (burrow and non-burrow soils). Differences in the overall abundance of AM and DSE propagules were analyzed with one-way ANOVA.

To test differences between burrow and non-burrow soils for the remaining soil parameters (microbial activity and physicochemical measures), we also used a MANOVA with plot and treatments as fixed factors. Wilks lambda was used as the multivariate criterion.

Tukey's post hoc tests were performed when the analyses yielded significant differences ($p < 0.05$), to assess differences between means of the individual parameters. Prior to analyses, all response variables were examined to meet parametric assumptions and either log or square root-transformed when necessary. All analyses were performed using the statistical computing language R v. 3.4.3 [54] and standard packages.

Results

Abundance of AM and DSE Propagules

Burrow and non-burrow soils differed significantly in the overall abundance of endophytic fungal propagules (Wilks lambda = 0.0011, $F = 1533.63$, $df = 3, 5$, $p < 0.0001$). Plots sampled showed no significant difference among them (Wilks lambda = 0.0946, $F = 0.9037$, $df = 21, 15$, $p = 0.5933$). The overall abundance of DSE propagules was significantly higher than that of AM (means ± SD; 5.61 ± 3.79 and 2.15 ± 1.36, respectively, one-way ANOVA: $F = 11.7906$, $df = 1, 30$, $p < 0.01$). The abundance of AM propagules was almost three times higher in burrows compared to non-burrow soils ($F = 383.403$, $df = 1, 14$, $p < 0.0001$). The abundance of DSE propagules was almost five times higher in burrows than non-burrow soils ($F = 5522.14$, $df = 1, 14$, $p < 0.0001$; Table 2, Fig. 2a). Regarding root colonization of *L. sativa*, we found significant differences among burrow and non-burrow soils, in both percent of DSE and AM colonization (Table 1 S).

In general, the density of AM spores was low in both microenvironments (< 1 spore/g/soil), but also significantly higher in burrow than in non-burrow soils ($F = 71.687$, $df = 1, 14$, $p < 0.0001$; Table 2, Fig. 2b). The most abundant morphotype, and present in almost all soil samples, were dark and rigid sporocarps of the former genus *Sclerocystis*.

Table 2 Abundance of root endophytic fungal propagules (DSE and AM) in *Ctenomys* burrow and adjacent non-burrow soils. Values are means ± standard deviations of eight soil samples for each microenvironment. Letters (a, b) indicate significant differences using a Tukey post hoc tests ($df = 1, 14$; $p < 0.05$)

Micro-environment	Spores	Propagules		
	AM	DSE	AM	Total
AB	0.12 ± 0.02b	9.27 ± 0.33b	3.39 ± 0.28b	12.66
BS	0.02 ± 0.02a	1.95 ± 0.18a	0.87 ± 0.24a	2.82

The total of endophytic propagules (DSE + AM) in burrow was four times higher than in non-burrow soils (Table 2), while the percent of root colonization of *L. sativa* was almost

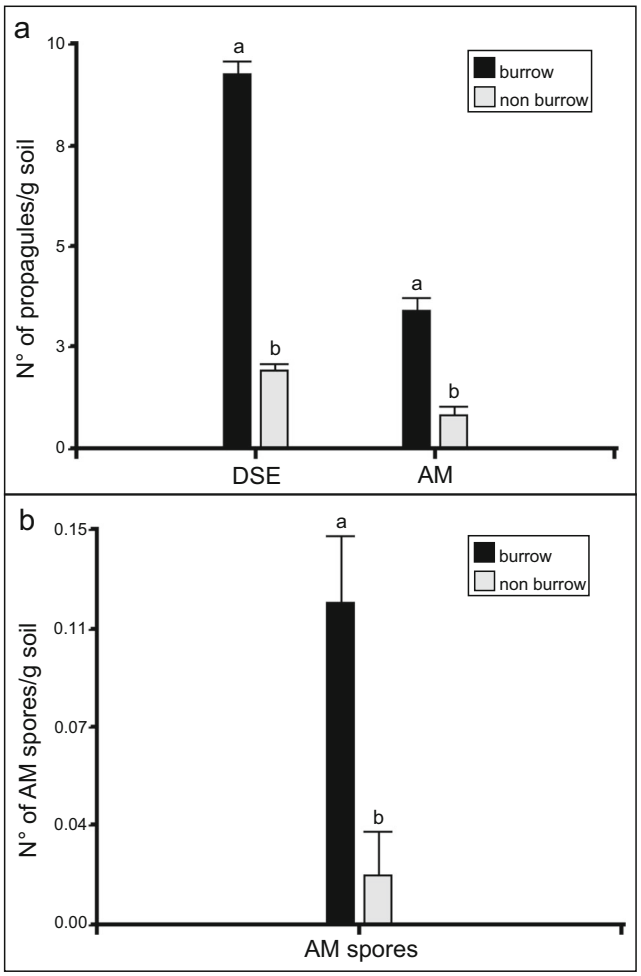

Fig. 2 Abundance of root endophytic fungal propagules in *Ctenomys* burrow and adjacent non-burrow soils. **a** Abundance of AM and DSE fungal propagules. **b** Density of AM spores. Each bar represents the mean value of eight soil samples from each microenvironment; error bars represent standard errors. Bars with different letters indicate significant differences between treatments (Tukey's post hoc tests, $p < 0.0001$)

five times higher in burrows with respect to non-burrow soils (Table 1 S).

Soil Microbial Activity and Physicochemical Parameters

Except for soil electrical conductivity, the rodent digging activity significantly modified all the measured physicochemical and microbiological parameters within their burrow environment when compared to non-burrow soils (Wilks lambda = 0.00003, $F = 3889.093$, $df = 7, 1$ $p < 0.05$, see Table 3 for the univariate results and their significances). Plots showed no significant effect (Wilks lambda = 0.000004, $F = 2.1$, $df = 49, 10$ $p = 0.1084$). Soil microbial activity, assessed as soil respiration rate, was approximately seven times higher in burrow than in non-burrow soils. Organic carbon, total nitrogen, and nitrates almost doubled that of non-burrow soils. In contrast, available phosphorus was slightly lower in burrow compared to non-burrow soils. Also, the field capacity and moisture were higher in burrows, whereas soil pH was slightly more alkaline than in non-burrow soils. The fine fraction of the soil particles increased in burrows, while medium fractions predominated in non-burrow soils.

Discussion

Our results show that the burrowing activities of the desert subterranean rodent *C.* aff. *knighti* promotes soil patchiness in the desert shrub biome. First, they increase the abundance of AM and DSE fungal propagules, and second, they change edaphic properties in terms of microbiological activity, nutrient concentration, and soil physicochemical features (see Fig. 3 for summarizing both microbiological and physicochemical effects). All together, these changes promote soil patchiness by creating microniches that could act as "islands of opportunity" for seedling establishment and plant growth, as will be discussed below.

Root endophytic fungi as a microbiological variable related to subterranean rodent burrowing activities have been scarcely addressed, and DSE fungi have been even less studied. An early work of Allen and MacMahon [29] demonstrated the key role of pocket gophers in a post-volcanic scenario, by moving buried soil containing viable AM spores and mycorrhizal root fragments, thus creating microniches for pioneer plants in early successional stages. Later, Titus et al. [30] found no significant differences in AM spore density and their inoculum potential between burrow and non-burrow soils of the Mojave Desert. In contrast, our results show that the abundance of both AM and DSE fungal propagules increased significantly in tuco-tuco burrows compared to non-burrow soils.

The effect of symbiotic endophytic fungi on plant performance is particularly relevant in harsh environments [55], and most perennial desert plants are mycorrhizal [30, 56–60]. The symbiosis with AM fungi increases drought tolerance, facilitates the acquisition of nutrients, and is critical for the success of the seedling establishment and the early stages of plant growth [55, 60–63]. As with the AM symbiosis, DSE fungi have been shown to promote plant growth [3, 5, 6, 64], mitigate plant stress related to high temperatures [63], and provide higher survival under water stress conditions [65].

Moreover, there is an increasing interest on DSE fungi, as new insights in this polyphyletic group showed that their ubiquitous presence in plant communities of extreme environments would indicate a key relevance in ecosystem functioning [5].

Indeed, our results showed overall a higher abundance of DSE infective fungal propagules compared to that of AM. In turn, both DSE and AM fungi were more abundant in burrow soils compared to non-burrow soils and, together with our previous study showing that viable DSE and AM propagules are contained in the tuco-tuco scats [31] and that the rodents deposit their feces inside the burrows, suggest that rodents are responsible for this concentration. Additionally, recent works have shown that coprophilous fungi can behave as DSE by colonizing asymptomatically roots of different plant species

Table 3 Microbiological activity and physicochemical soil parameters measured in *Ctenomys* burrow and adjacent non-burrow soils. Values are means ± standard deviations of eight soil samples for each microenvironment. Asterisks indicate significant differences using a Tukey post hoc test ($df = 1, 7$; $p < 0.05$)

Variable	Burrow	Non-burrow	*F* values	*p* level
Microbial activity(mg CO_3^{-2}/g/d)	0.72 ± 0.07	0.10 ± 0.02	485.8283	< 0.0001*
Organic carbon (g/kg)	4.42 ± 0.75	1.80 ± 0.36	78.6650	< 0.0001*
Total nitrogen (g/kg)	0.32 ± 0.07	0.14 ± 0.02	56.0000	< 0.0001*
Nitrate (mg/kg)	0.93 ± 0.05	0.47 ± 0.02	1543.7956	< 0.0001*
Phosphorous (mg/kg)	15.37 ± 1.89	22.66 ± 1.40	55.4824	< 0.0001*
Field capacity (%)	18.33 ± 1.17	15.71 ± 0.72	21.1470	< 0.0001*
Moisture (%)	0.89 ± 0.05	0.29 ± 0.04	1113.7799	< 0.0001*
Fine particle fraction (%)	14.06 ± 0.63	9.79 ± 0.59	160.0367	< 0.0001*
pH	7.58 ± 0.22	7.81 ± 0.12	6.1542	0.0207*
Electric conductivity (dSm/m)	86.26 ± 6.09	91.83 ± 5.06	5.1606	0.0668

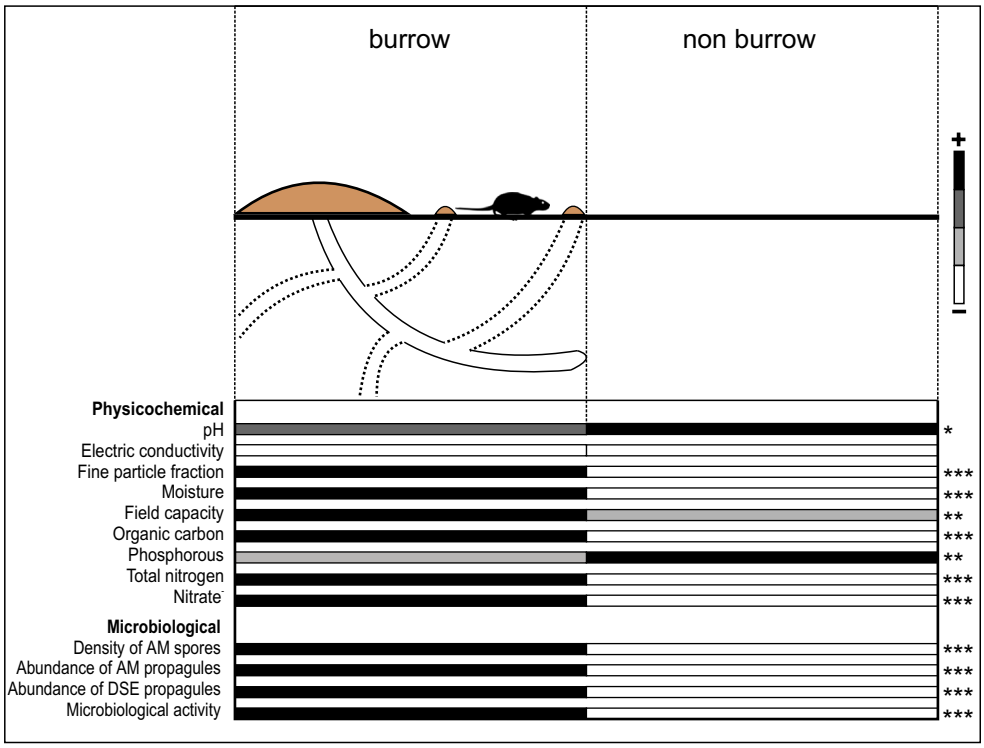

Fig. 3 Schematic representation of the physicochemical and microbiological variables analyzed in this study in *Ctenomys* burrow and non-burrow soils. Different colors show significant differences between the measured parameters. Asterisks indicate level of statistical significance from Tukey's post hoc tests (ns non-significant; $p > 0.05$, $*p < 0.05$; $**p < 0.01$; $***p < 0.0001$)

[66]. Therefore, the higher abundance of DSE fungi in burrow soils could be explained because tuco-tucos disperse in their scats not only the DSE from ingested roots, but also DSE-like coprophilous fungi.

In general, we observed very low values of AM spore density, both in burrow and non-burrow soils, with respect to the other evaluated propagules. Low AM sporulation rates in desert biomes have been reported by other authors (e.g. [30, 60, 62, 67–69]) and, also, the existence of huge fluctuations in sporulation depending on the season and the availability of water [70]. Although a patchy distribution of AM spores was found in this study (e.g., higher spore densities in burrows soils), our results suggest that the main source of AM propagules are mycorrhizal root fragments and mycelia that are either introduced into the burrow along with the plant fragments cached for food or contained in the excreted rodent feces.

Respiration rates in burrows were up to seven times higher than in non-burrow soil samples. This increased microorganism activity agrees with previous reports of higher abundance of soil biota (including fungi and bacteria) within the burrow environment of subterranean rodents [23, 71, 72]. An active soil, microbial community is involved in the breakdown of organic matter and consequent release of nutrients, which is a direct indicator of general soil fertility [73]. Taking into account that microorganisms are more active in burrows because of the addition of organic matter, then, a faster decomposition into nutrients available for plants should be expected, leading to an enrichment in soil nutrients compared to non-burrow soils. In concordance with this prediction, we found higher levels of organic carbon, total nitrogen, and nitrates in burrow soils. In contrast, the level of available phosphorus was lower. A possible explanation could be that the higher microbial activity in burrow soils results in a higher sequestering of P [74]. In addition, the presence of fine particles in a greater proportion in the burrows soil reduces the amount of available P, due to their capacity to adsorb this element [75, 76]. Therefore, in non-burrow soils, where microbial abundance and activity can be extremely low, the available P remains mostly in the soil matrix. Differences in nutrient concentration between burrow soils of subterranean rodents and surrounding soil have been found in almost all studies performed (e.g. [17, 18, 26]), though not always as an enhancement when considering specific nutrients [25, 77].

We also found significant soil textural differences between burrow and non-burrow soils. In burrows, soils were finer grained and with higher field capacity and moisture compared to non-burrow soils. When the tuco-tucos construct their multiple entrance burrow systems, they contribute to soil mixing by transporting deep soil layers to the surface. Soil mixing by burrowing mammals is an important pedogenic process [78] and, generally, increases soil porosity (resulting in increased water infiltration), redistributes soil nutrients, and provides a low-bulk density rooting environment for plants (reviewed in [17]).

Our results provide a general insight on the effect of the burrowing activities of the tuco-tucos in a desert shrub landscape. One general conclusion is that food haulage, the

deposition of excretions, and soil mixing by burrowing create patches of soil that differ both in their microbiological and physicochemical properties from those of the surrounding landscape. These patches contain soil enriched with organic matter, soil microorganisms that decompose it into nutrients available for plants, fungal propagules that can establish mutualistic relations with their roots, and greater retention of water. These improved edaphic properties may condition soil such that, when the burrow is abandoned, it can act as "island of opportunity" for plant establishment [79]. Turning back to Darwin's last published work, we can cite Desmet and Cowling [23] when saying "The role that burrowing rodents play is essentially one of a large earthworm."

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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