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Effects of harvester ant (*Messor* spp.) activity on soil properties and microbial communities in a Negev Desert ecosystem

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Abstract Harvester ants (*Messor* spp.) function as an essential link between aboveground resources and belowground biota such as the microbial community. We examined changes in soil microbial biomass and functional diversity resulting from harvester ant (*Messor* spp.) activity in the Negev Desert, Israel. Abiotic and biotic soil parameters were recorded during two seasons—wet and dry—also representing food availability periods for the ants (low and high seed availability, respectively). Soil samples were collected monthly from the 0- to 10- and 10- to 20-cm soil layers: (1) near the nest entrance, (2) under chaff piles, and (3) at a 2-m radius from the nest entrance (control). Harvester ant activity increased the percentage of organic matter, total soluble nitrogen, and microbial activity in nest-modified soils in comparison to the control soils. Higher CO_2 evolution was recorded in the low-seed season in ant nest soils than in the control soils. During the high-seed season, higher carbon dioxide evolution was recorded only at the nest entrance locations. There were no differences in microbial biomass between the low- and high-seed seasons, but highest microbial biomass was found under chaff in low-seed season and in nest soils in high-seed season. Microbial functional diversity was higher in nest-modified soils than in the control soils. This study suggests that the effect of harvester ant nests on soil fertility is due to increased microbial biomass and microbial activity in ant nest-modified soils.

Keywords Harvester ants · Microbial community · Soil moisture · Soil organic matter · Desert system

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Introduction

Desert ecosystems are patchy environments in which organic matter and nutrients are concentrated mainly under plants and in soil pits produced by animal activity (West and Skujins 1978; Whitford 2002; Pen-Mouratov et al. 2006). Part of these animals' biopedturbations (such as burrowing and nesting) have long-term effects on soil (Whitford and Kay 1999; Whitford 2000), and organisms responsible for it have been defined by Lavelle (2002) and Lawton (1994) as "soil ecosystem engineers". By constructing tunnels and chambers and by foraging on seeds and plant materials, these engineers control food resource availability and energy flow for other soil organisms, creating new niches stimulating a soil food web interaction (Jones et al. 1997; Dauber et al. 2001).

Harvester ants (*Messor* spp.) are one of the most common ant genera in desert environments (Crawford 1981). They build large underground nests visible aboveground as round patches surrounded by chaff piles with prominent entrance holes in the middle. Seeds and other plant materials (green leaves) are gathered into the nest chambers for storage and, later, consumption. The chaff, seed and fruit coating plant debris, is carried outside the nests, where it accumulates in piles in a circle around the nest entrance (MacMahon et al. 2000). Chaff accumulations on the margins of the nests contribute to the organic matter

content of the nest-modified soils and thus to microbial activity (Steinberger et al. 1991).

Numerous studies have described the contribution of harvester ants to different aspects of desert ecosystems, such as increased vegetation cover (Danin and Yom-Tov 1990; Whitford and DiMarco 1995), effect on soil hydrology (Lei 2000; Cammeraat et al. 2002), enhanced nutrient cycling (Wagner and Jones 2006), and effect on soil biota abundance and richness (Wagner et al. 1997; Boulton et al. 2003; Rodriguez-Zaragoza et al. 2007). These papers have focused more on taxonomic composition and less on the functional aspects of the nest microbial community inhabitants of the upper soil layers. The relationship between ant activity and the soil microbial community (bacteria and fungi) is very important in the dry, substrate-poor desert soil environments, as these communities are largely responsible for soil nutrient cycling and energy flow in terrestrial ecosystems (Emmerling et al. 2002; Kirk et al. 2004).

Recent studies on soil biodiversity have focused on the functional aspects of soil microorganisms as a more relevant tool to understand soil functioning than species genetics or taxonomic diversity (Zak et al. 1994; Degens et al. 2000; Emmerling et al. 2002). Microbial functional diversity refers to the ability of the microbial community to utilize a wide range of different substrates (e.g., carbohydrates and amino acids) existing in plant and animal residues in the soil. The proportional abundance of these organic substances changes during decomposition processes (Zak et al. 1994; Lahav and Steinberger 2001).

The method generally used to measure functional aspects of the microbial community is the Biolog, which discriminates soil heterotrophic microbial communities according to their sole-carbon-source utilization profiles (Garland and Mills 1991). However, this method presents several biases, as it provides examination of only the extractable and culturable microflora (Nannipieri et al. 2003). Moreover, evaluation that overlooks the soil matrix in an isolated, reduced-complexity environment does not reflect the soil environment.

In an attempt to overcome such biases, a new method that evaluates microbial catabolic diversity with the use of substrate-induced respiration (SIR) technique in whole soil samples rather than soil extracts was developed by Degens and Harris (1997). On the basis of this time-consuming and laborious method, the MicroResp™ technique was developed (Campbell et al. 2003; Chapman et al. 2007), allowing the rapid assessment of catabolic profiles of whole soil samples using a colorimetric respiration detection system (cresol red) and an automated plate reader.

Since the harvester ant (*Messor* spp.) activity in the Negev Desert is controlled by food availability, foraging activity can be divided into two main periods relative to seed availability: the low seed availability (LSA) period during the wet season (November–March) and the high seed availability (HAS) period which is mainly during the dry season (April–October) (Steinberger et al. 1992).

The objective of this study was to examine the effect of harvester ant (*Messor* spp.) activity during the wet and dry seasons on soil parameters and on microbial biomass and functionality. We also attempted to examine the different consequences of ant activity on these parameters by sampling soil from three areas of the nest: nest entrance, chaff piles, and control.

Materials and methods

Study site

The field study was conducted at the Avdat Farm Research Station in the Negev Desert Highlands, Israel (30°47′ N, 34°46′ E). Elevation is about 600 m above sea level. The area has a temperate desert climate with hot summers (mean maximum, 32°C; mean minimum, 17.7°C in June) and cool winters (mean maximum, 14.8°C; mean minimum, 5.4°C in January). The average annual rainfall is 90 mm (Avdat Station) and occurs in scattered showers only during the winter (November to April). An additional source of moisture in this desert is dew, which falls heavily during the autumn months (September–November) (Evenari et al. 1982). The soils are brown, shallow, rocky desert soils (brown lithosols), as well as loessial and gray desert soils (loessian serozems) (Dan et al. 1972) composed of 24.1% clay, 15.9% silt, and 60% sand. Total organic carbon was 0.31%, N content was 20–30 mg/100 g soil at pH 7.9, and $CaCO_3$ content was 58.4% (Ravikovitch 1981). The vegetation consists of a mixture of perennial shrub communities with a large variety of annuals. Predominant perennials at the research site are *Hammada scoparia*, *Zygophyllum dumosum*, and *Artemisia siberi* (Evenari et al. 1982).

Sampling and analysis

Soil samples from 0- to 10- and 10- to 20-cm depths were collected using a metal core (~200 g each sample) during the study period, between November 2006 and November 2007. The samples were collected monthly in four replicates (four different nests each month, similar in size and activity) from three locations in the nest area: (1) near nest entrance (5-cm radius from nest entrance), (2) under chaff piles, and (3) 3 m outside from the nest entrance as control. The soil samples were placed in plastic bags, transported in a cooler to the laboratory, and stored at 4°C before the biological and chemical analyses were

performed. All soil samples were sieved (mesh size, 2 mm) to remove root fragments and other large organic debris and analyzed:

1. Moisture was analyzed by drying samples at 105°C for 48 h and organic matter content by burning samples at 490°C for 8 h (Steinberger et al. 1990).
2. Total soluble nitrogen (TSN) was determined by chemical extraction and color reactions using a Skalar Autoanalyzer. Dried soil samples were extracted in a 1:10 (*w*/*v*) ratio with 0.01 M calcium chloride solution. The determination of total N content was based on the following reaction: A sample mixed with a borax buffer and excess potassium persulfate solution was added and the mixture placed in an ultraviolet digester. Nitrate was determined by the Griess reaction after oxidation of ammonium and reduction of nitrate to nitrite by cadmium copper redactor. The color was measured at 540 nm (SFAS 1995).
3. Microbial functional diversity and catabolic profiles were detected using the MicroResp™ plate (Campbell et al. 2003). Fifteen different carbon sources of carbohydrates, carboxylic acids, amino acids, and aromatic carboxylic acids (25 µl each) (Table 1) were added to whole soil samples (0.32 g each) in deep-well plates. Carbon dioxide evolution was measured by dye plates—a colorimetric reaction with absorbent alkali with the ability to measure carbon dioxide evolution. The plates were read at 590 nm three times: immediately, after incubation of 6 h, and after 24 h. During that time, the plates were incubated at 27°C in the dark. The results were calculated on the basis of the 16th well (water as substrate), which represents the basal respiration. The carbon source outcomes were divided into carbohydrates, amino acids, carboxylic acids, and aromatic carboxylic acids. The Shannon–Weaver index (H') was used to determine microbial functional diversity:

$$H' = -\sum \mathrm{Pi}\,(\ln \mathrm{Pi})$$

where Pi is the ratio of the activity of a particular substrate and the sum of activities of all substrates (Zak et al. 1994).

4. Carbon dioxide evolution was measured by dye plates—a colorimetric reaction using absorbent alkali with the ability to measure carbon dioxide evolution. Water was added to whole soil samples in deep-well plates covered by the dye plates in order to measure respiration. Glucose was added to determine microbial biomass according to the SIR method (Anderson and Domsch 1978).

Both CO_2 evolution and microbial biomass were used for calculating the competition efficiency of the soil microbial population under environmental conditions. The coefficient (qCO_2) was calculated according to the equation (Anderson and Domsch 1993):

$$qCO_2 = CO_2\,\text{production}/\text{biomass}$$

All the data obtained in the study were subjected to statistical analysis of variance (ANOVA). Differences at the $p < 0.05$ level were considered significant.

Results

Soil chemical properties

Soil moisture was significantly higher ($p < 0.001$) during the wet–LSA season (6.8%) than the dry–HSA season (3.6%) (Table 2). There were no significant differences in soil moisture between the sampling locations or between depths (0–10 and 10–20 cm) at a specific location (Fig. 1a).

Organic matter content in soil during the dry–HSA season was significantly higher ($p < 0.041$) than during the wet–LSA season (Table 2). A similar pattern was found during the two seasons, where organic matter content (Fig. 2a) in soils from nest-entrance and under-chaff accumulations was twofold higher than at the control locations (with the exception that there were no differences in the 10- to 20-cm layer in the wet–LSA season). Differences between the two soil layers were found at the nest entrance location in both seasons (0–10 > 10–20 cm) and for the control location in the wet–LSA season (10–20 > 0–10 cm).

There were no significant differences in TSN values between the two seasons (Table 2), though a consistent

Table 1 A list of carbon substrates used in the MicroResp™ plate divided into four carbon groups

Aromatic carboxylic acids	Carboxylic acids	Carbohydrates	Amino acids
Dihydroxybenzoic 3,4 acid	Citric acid	L-Arabinose	L-Alanine
	L-Malic acid	D-Fructose	Arginine
	Oxalic acid	D-Galactose	L-Cysteine HCl
		N-Acetyl-glucosamine	γ-Amino butyric acid
		Trehalose	L-Lysine
		D-Glucose	

Table 2 ANOVA table of the effect of the two study seasons, wet and dry [low seed availability (LSA) and high seed availability (HSA), respectively], and sampling sites on different soil parameters mentioned below

Parameters	ANOVA results			Mean values	
	LSA × site	HSA × site	LSA × HSA	LSA	HSA
SM	NS	NS	0.0001	6.84	3.63
OM	0.0001	0.0001	0.041	1.92	2.07
TSN	0.0001	0.0001	NS	6.17	6.55
CO_2 evol.	0.0001	0.0001	0.0001	0.08	0.04
MB	0.0001	0.0001	NS	6.99	7.61
qCO_2	0.012	0.0001	0.0001	10.31	8.44
H′ (diversity)	0.0001	0.006	NS	2.36	2.31
c-Aromatic	NS	NS	NS	0.61	0.77
c-Carbox	NS	NS	0.0009	0.18	0.41
c-Carboh	0.0009	0.0001	0.003	0.08	0.15
c-Amino	0.0034	NS	0.024	0.06	0.10

Level of significance, $p<0.05$

Parameters: *SM* Soil moisture, *OM* organic matter, *TSN* total soluble nitrogen, *CO_2 evolution* soil respiration, *MB* microbial biomass, *qCO2* metabolic quotient, *H′* microbial functional diversity, *c-Aromatic* aromatic-carboxylic acid, *c-Carbox* carboxylic acids, *c-Carboh* carbohydrates, and *c-Amino* amino acids, *NS* no significant difference

pattern was found with significant differences ($p < 0.001$) between the sampling locations (Fig. 1c). Almost threefold higher values of TSN were found in soil samples taken from the nest entrance location compared to samples taken from the under-chaff and the control locations in both soil layers (0–10 and 10–20 cm) throughout the research period.

Microbial properties

Carbon dioxide evolution

Soil carbon dioxide evolution values were found to be significantly higher ($p < 0.001$) in the wet–LSA season than in the dry–HSA season (Table 2). During the wet–LSA season, carbon dioxide evolution values in the upper soil layer (0–10 cm) were significantly higher ($p < 0.001$) in soil samples taken from the under-chaff and nest entrance locations than at the control location (Fig. 2a). However, at the same time, in the 10- to 20-cm soil layer, the highest soil carbon dioxide evolution was recorded in soil samples taken from the nest entrance location compared to the under-chaff and the control locations. During the dry–HSA season, there were no significant differences between sampling locations (Fig. 2a), although in the upper soil layer (0–10 cm) twofold higher values of soil carbon dioxide evolution were recorded in soil samples taken from the nest entrance location compared to the under-chaff and the control locations. Differences between soil layers were found at the under-chaff (during the wet–LSA season) and nest entrance locations (during the dry–HAS season).

Microbial biomass

There were no significant differences in microbial biomass between the wet–LSA and dry–HSA seasons (Table 2). There were significant differences among sampling locations during the wet–LSA season in the upper soil layer (0–10 cm), and these values ranked as chaff location >> nest entrance > control location (Fig. 2b). However, the highest microbial biomass values were found during the dry–HSA season in soil samples taken at the nest entrance location compared to the under-chaff and the control locations in the 0- to 10-cm soil layer. For both seasons, there were no significant differences among sampling locations in the 10- to 20-cm soil layer. Significant differences between soil layers (0–10 > 10–20 cm) were found at the nest entrance locations (throughout the study period) and at the under-chaff locations in the wet–LSA season.

qCO_2

Significantly higher qCO_2 values were found in the wet–LSA season than in the dry–HSA season (Table 2). There were significant differences between sampling locations in the 10- to 20-cm soil layer during the dry–HSA season, when qCO_2 values at the nest entrance location were lower than at the under-chaff and the control locations (Fig. 2c). There were differences between the two soil layers (10–20 > 0–10 cm) at control locations in the wet–LSA season and in the control and the under-chaff locations during the dry–HSA season.

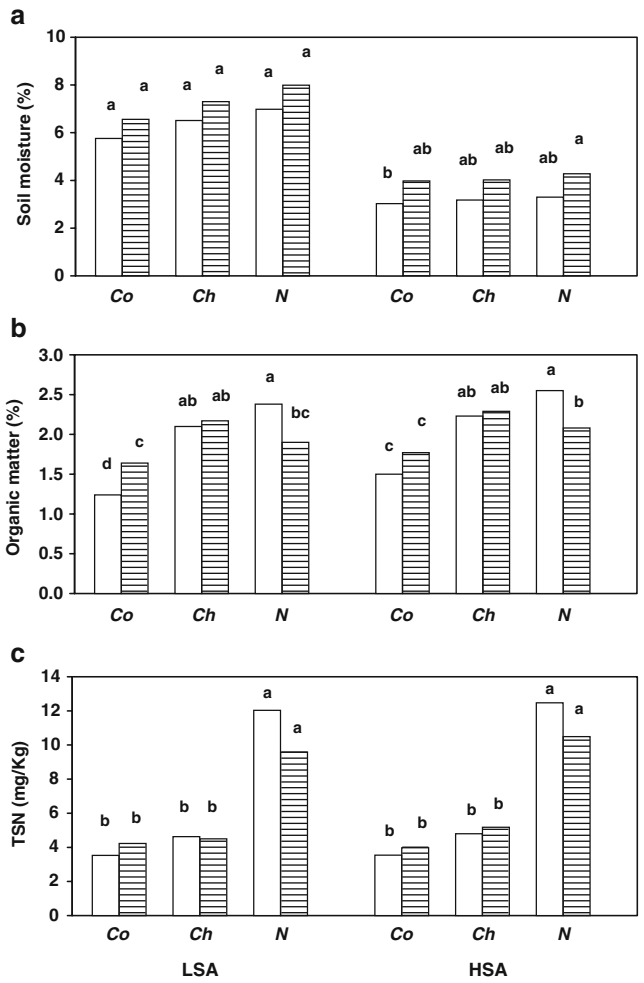

Fig. 1 **a**–**c** Changes in the mean values of soil moisture (**a**), soil organic matter (**b**), and total soluble nitrogen (**c**) in soil samples taken during wet–low seed availability (*LSA*) and dry–high seed availability (*HSA*) seasons, from 0- to 10-cm (*blank columns*) and 10- to 20-cm (*striped columns*) soil layers at three locations: nest entrance (*N*), under chaff (*Ch*), and control (*Co*). The *different letters* represent significant ($p<0.05$) differences between locations within each season (wet–LSA and dry–HSA separately)

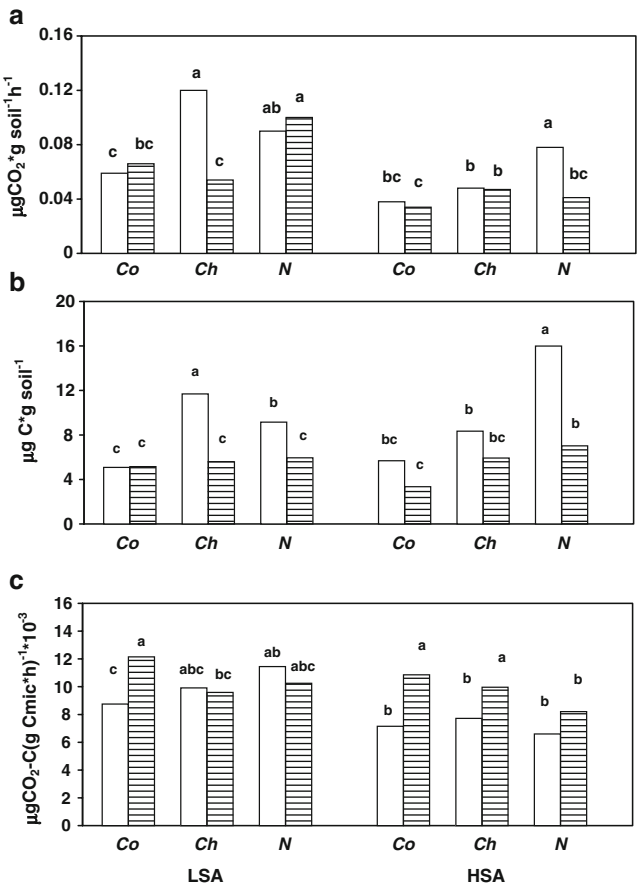

Fig. 2 **a**–**c** Changes in the mean values of soil respiration (**a**), microbial biomass (**b**), and metabolic quotient, qCO_2 (**c**) in soil samples taken during wet–low seed availability (*LSA*) and dry–high seed availability (*HSA*) seasons from 0- to 10-cm (*blank columns*) and 10- to 20-cm (*striped columns*) soil layers at three locations: nest entrance (*N*), under chaff (*Ch*), and control (*Co*). The *different letters* represent significant ($p<0.05$) differences between locations within each season (LSA and HSA separately)

Soil microbial functional diversity (H')

The Shannon index was used to determine microbial functional diversity (*H'*) based on substrate utilization rates in the MicroResp™ plates (Campbell et al. 2003). There were no significant differences between the two seasons, and a consistent pattern was found for differences between sampling locations. Functional diversity values found in soil samples taken from the nest entrance and the under-chaff locations were significantly higher ($p < 0.05$) in comparison to the control location. This pattern was found to be significant in the upper (0–10 cm) soil layer during the wet–LSA season, while it was significant in the deeper (10–20 cm) soil layer in the dry–HSA season (Fig. 3).

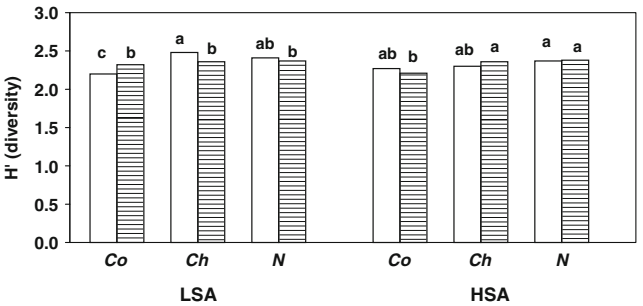

Fig. 3 Changes in the mean value of microbial functional diversity (*H'*) in soil samples taken during wet–low seed availability (*LSA*) and dry–high seed availability (*HSA*) periods from 0- to 10-cm (*blank columns*) and 10- to 20-cm (*striped columns*) soil layers at three locations: nest entrance (*N*), under chaff (*Ch*), and control (*Co*). The *different letters* represent significant ($p<0.05$) differences between locations within each season (LSA and HSA separately)

Significant differences between soil layers were found during the wet–LSA season in the control location (10–20 > 0–10 cm) and the under-chaff location (0–10 > 10–20 cm).

Microbial catabolic profiles

Dividing the 15 substrates composing the microbial functional diversity (*H′*) into four carbon groups (aromatic carboxylic acid, carboxylic acids, carbohydrates, and amino acids) allows the examination of catabolic profiles of the microbial community. Utilization rates of three out of the four carbon groups (carboxylic acid, carbohydrates, and amino acids) were significantly higher ($p < 0.05$) in the dry–HSA season (0.41, 0.15, and 0.10 μgC g soil^{-1} hour^{-1}, respectively) than in the wet–LSA season (0.18, 0.08, and 0.06 μgC g soil^{-1} hour^{-1}, respectively) (Table 2).

Aromatic carboxylic acid Consistent utilization rates were found for aromatic carboxylic acid, with no significant differences between the two seasons (Table 2), sampling locations, and soil layers (Fig. 4a).

Carboxylic acid Utilization rates of carboxylic acids were found to be significantly higher ($p < 0.0009$) in the wet–LSA season than in the dry–HSA season (Table 2). Similar to the consistent utilization pattern of aromatic carboxylic acid, no significant differences in carboxylic acid utilization rates were found between sampling locations (Fig. 4b). Significant differences between soil layers were found at the under-chaff location (0–10 > 10–20 cm) in the wet–LSA season.

Carbohydrates Utilization rates ($p < 0.003$) of carbohydrates obtained during the dry–HSA season were higher than those obtained during the wet–LSA season (Table 2). Throughout the wet–LSA season, similar utilization rates were found at sampling locations in the deeper (10–20 cm) soil layer (Fig. 4c), while significantly higher ($p < 0.001$) utilization rates were found in soil samples taken from under the chaff compared to the control locations in the upper (0–10 cm) soil layer. Moreover, during the dry–HSA season, twofold higher utilization rates of carbohydrates were recorded in soil samples collected at the nest entrance in the upper soil layer (0–10 cm) than at all other sampling locations (Fig. 4c). Significant differences between soil layers (0–10 > 10–20 cm) were found for the under-chaff (during the wet–LSA season) and nest entrance locations (during the dry–HSA season).

Amino acids Utilization rates of amino acids were found to be higher in the dry–HSA season than in the wet–LSA season (Table 2). Similar to the utilization rates of the carbohydrates during the wet–LSA season, significantly higher ($p < 0.05$) utilization rates of amino acids were

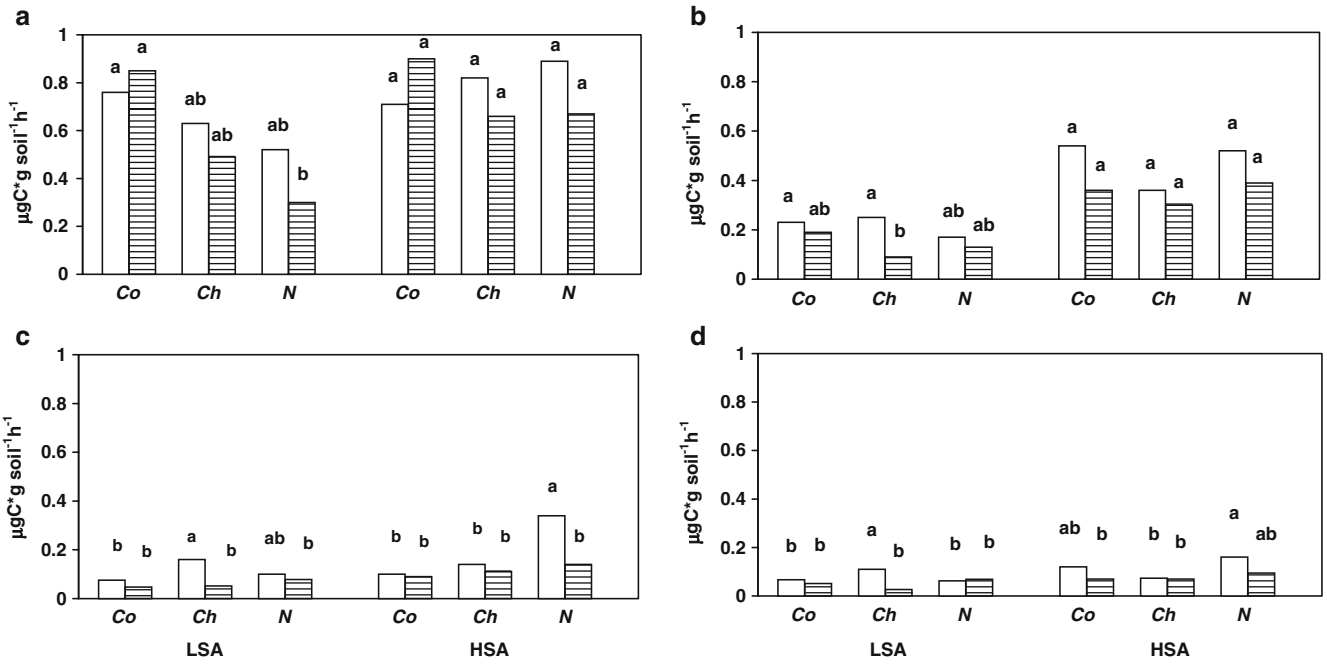

Fig. 4 **a**–**d** Changes in mean values of utilization rates of four carbon groups: aromatic-carboxylic acid (**a**), carboxylic acids (**b**), carbohydrates (**c**), and amino acids (**d**) in soil samples taken during wet–low seed availability (*LSA*) and dry–high seed availability (*HSA*) periods from 0- to 10-cm (*blank columns*) and 10- to 20-cm (*striped columns*) soil layers at three locations: nest entrance (*N*), under chaff (*Ch*), and control (*Co*). The *different letters* represent significant ($p<0.05$) differences between locations within each period (LSA and HSA separately)

observed in soil samples taken under chaff compared to all other locations (Fig. 4d). In contrast, no significant differences were found between sampling locations during the dry–HSA season (Table 2). However, differences in the soil layers in the under-chaff locations (0–10 > 10–20 cm) were found during the wet–LSA season.

Discussion

Harvester ants (*Messor* spp.) collect and retrieve seed and plant material in the vicinity of their nests. In the Negev Desert, they are active and aboveground most of the year, during the dry, HSA season (April–October) (Steinberger et al. 1992). In this season, carbon dioxide evolution and microbial biomass values were higher at the nest entrance site in comparison to the under-chaff and control sites in the upper soil layer (0–10 cm). Such differences between ant-nest soil and no-ant soil were also reported by Dostál et al. (2005), Boulton et al. (2003), Wagner et al. (1997), and Dean and Yeaton (1993). This documents that an ant's nest present favorable environment for microbial activity.

The amount of total soluble N at the nest entrance location was almost three times higher than in the under-chaff and the control locations. This pattern was consistent during the wet–LSA and dry–HAS seasons and indicates that the ant's effect on soil properties is a long-term and ongoing process (Wagner et al. 2004). According to Wagner and Jones (2006), N mineralization rates and N concentrations in ant soil are higher than in no-ant soils due to the higher abundance of organic matter decomposers in the ant nests. Moreover, the abundance and richness of microarthropods and protozoan populations, which control microbial community activity, were found to be higher in ant soils than in no-ant soils (Boulton et al. 2003; Rodriguez-Zaragoza et al. 2007).

Soil moisture (%) during the LSA period was higher than in the HSA period, which is consistent with its separation into two main seasons in the study site: wet (November–March) and dry (April–October) season, respectively. Several studies (Dean and Yeaton 1993; Boulton et al. 2003) have reported lower moisture content in soils collected from ant nests than in the reference soils, while others (Rodriguez-Zaragoza et al. 2007) reported higher soil moisture values at the ant nests than in no-ant soils. In our study, there were no significant differences between nest soils and reference soils. These apparent contradictions can be attributed to differences in hydrological properties of soil and topographic locations of ant nests and their structures (Whitford 2002; Cammeraat et al. 2002).

The contribution of the chaff piles to microbial activity was revealed during the wet–LSA season in which carbon dioxide evolution and microbial biomass values could be ordered as under chaff > nest entrance > control site in the upper soil layer (0–10 cm). According to Kiem and Kandeler (1997), one of the limiting factors for biological activity in soil is the lack of organic substances. Hence, one possible explanation for the high biological activity under the chaff could be due to leaching of organic substances from the chaff piles to the soil below during rain events. This addition of readily decomposable organic substances stimulated the microbial growth and activity (Mondini et al. 2006).

Different catabolic profiles found for soils collected at the nest entrance and under-chaff pile locations compared to those of the control location indicate that the microbial communities at these sites differ in their functions. According to Degens (1999), such differences in catabolic profiles can reflect the composition of organic C added to the soil. Boulton and Amberman (2006), based on a field experiment, suggested that the greater abundance and richness of soil biota (microorganisms, microarthropods, and nematodes) in ant soil is related to the higher concentration of organic matter and moisture in such soils. Dauber and Wolters (2000), who examined soil microbial functional diversity in the mounds of three different ant species, claimed that the differences in the ant effect on the soil microflora is related to feeding strategies (predatory, semipredatory) and nest architecture. In this research, high utilization rates of carbohydrates, which are major components of storage tissues in seeds (Poljakoff-Mayber et al. 1965), were found in the nest entrance soil in comparison to the under-chaff and control soils during the dry–HSA season. This could result from the high concentration of seeds in nest chambers during this period. Our results suggest a bottom-up effect of harvester ant activity on the soil microbial community as elucidated by Jones et al. (1997), Lavelle (2002), and Boulton and Amberman (2006).

One important environmental effect of ant nests present in the desert surroundings is the creation of a special niche in the soil having favorable conditions for microbial activity (Jones and Wagner 2006). The metabolic quotient (qCO_2) is a key index suggested by Anderson and Domsch (1993) to reflect microbial carbon use efficiency. Elevated qCO_2 values indicate that the microbial community operates inefficiently, utilizing carbon mainly for maintenance requirements rather than growth due to environmental stress or disturbance (Wardle and Ghani 1995). In this study, low qCO_2 values were recorded in nest entrance soils compared to under-chaff and control soils during the high seed availability period (the dry season). This difference was recorded only in the 10–20-cm soil layer. Since no differences in soil moisture and microbial biomass were observed between the various sampling locations at the 10-

to 20-cm soil layer, we suggest that supplementary organic matter inputs combined with the better aeration conditions found in nest soils may be the sources for such a difference. It is important to note, however, that differences in the ratio of bacterial-to-fungal biomasses between the investigated soils could also bring on differences in qCO_2 values, as these two microbial groups may utilize and respire C sources with different efficiency (Nannipieri et al. 2003).

We conclude that harvester ant activity has a significant effect on biomass and functional diversity of microflora in the Negev. Nests and chaff piles function as special niches in the desert ecosystem, where favorable conditions contribute to the development of a more active and diverse soil microbial community. In addition, nest areas are enriched with nitrogen throughout the year and contribute to soil fertility in the desert.

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References

Anderson JPE, Domsch KH (1978) Physiological method for quantitative measurement of microbial biomass in soils. Soil Biol Biochem 10:215–221 doi:10.1016/0038-0717(78)90099-8

Anderson TH, Domsch KH (1993) The metabolic quotient for CO_2 (qCO_2) as a specific activity parameter to assess the effects of environmental conditions, such as pH, on the microbial biomass of forest soils. Soil Biol Biochem 25:393–395 doi:10.1016/0038-0717(93)90140-7

Boulton AM, Amberman KD (2006) How ant nests increase soil biota richness and abundance: a field experiment. Biodivers Conserv 15:69–82 doi:10.1007/s10531-004-2177-7

Boulton AM, Jaffee BA, Scow KM (2003) Effects of a common harvester ant (*Messor andrei*) on richness and abundance of soil biota. Appl Soil Ecol 23:257–265 doi:10.1016/S0929-1393(03)00046-5

Cammeraat LH, Willott SJ, Compton SG, Incoll LD (2002) The effects of ants' nests on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. Geoderma 105:1–20 doi:10.1016/S0016-7061(01)00085-4

Campbell CD, Chapman SJ, Cameron CM, Davidson MS, Potts JM (2003) A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. Appl Environ Microbiol 69:3593–3599 doi:10.1128/AEM.69.6.3593-3599.2003

Chapman SJ, Campbell CD, Artz RRE (2007) Assessing CLPPs using MicroReSp (TM)—a comparison with biolog and multi-SIR. J Soils Sediments 7:406–410 doi:10.1065/jss2007.10.259

Crawford CS (1981) Biology of desert invertebrates. Springer, Berlin

Dan J, Yaalon DH, Koyumdji H, Raz Z (1972) The soil association map of Israel (1:1,000,000). Isr J Earth Sci 2:29–49

Danin A, Yom-Tov Y (1990) Ant nests as primary habitats of *Silybum marianum* (Compositae). Plant Syst Evol 169:209–217 doi:10.1007/BF00937675

Dauber J, Wolters V (2000) Microbial activity and functional diversity in the mounds of three different ant species. Soil Biol Biochem 32:93–99 doi:10.1016/S0038-0717(99)00135-2

Dauber J, Schroeter D, Wolters V (2001) Species specific effects of ants on microbial activity and N-availability in the soil of an old-field. Eur J Soil Biol 37:259–261 doi:10.1016/S1164-5563(01)01094-9

Dean WRJ, Yeaton RI (1993) The effects of harvester ant *Messor capensis* nest mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. J Arid Environ 25:249–260 doi:10.1006/jare.1993.1059

Degens BP (1999) Catabolic response profiles differ between microorganisms grown in soils. Soil Biol Biochem 31:475–477 doi:10.1016/S0038-0717(98)00133-3

Degens BP, Harris JA (1997) Development of a physiological approach to measuring the catabolic diversity of soil microbial communities. Soil Biol Biochem 29:1309–1320 doi:10.1016/S0038-0717(97)00076-X

Degens BP, Schipper LA, Sparling GP, Vojvodic-Vukovic M (2000) Decreases in organic C reserves in soils can reduce the catabolic diversity of soil microbial communities. Soil Biol Biochem 32:189–196 doi:10.1016/S0038-0717(99)00141-8

Dostál P, Březnová M, Kozlìčková V, Herben T, Kovář P (2005) Ant-induced soil modification and its effect on plant below-ground biomass. Pedobiologia (Jena) 49:127–137 doi:10.1016/j.pedobi.2004.09.004

Emmerling C, Schloter M, Hartmann A, Kandeler E (2002) Functional diversity of soil organisms—a review of recent research activities in Germany. J Plant Nutr Soil Sci 165:408–420 doi:10.1002/1522-2624(200208)165:4<408::AID-JPLN408>3.0.CO;2-3

Evenari M, Rogel A, Masig D, Nesslar U (1982) Runoff farming in the Negev Desert of Israel. 7th Progress Report. Hebrew University and Blaustein Desert Research Institute, Jerusalem, Sede Boker

Garland JL, Mills AL (1991) Classification and characterization of heterotrophic microbial communities on a basis of patterns of community-level sole-carbon-source utilization. Appl Environ Microbiol 57:2351–2359

Jones JB, Wagner D (2006) Microhabitat-specific controls on soil respiration and denitrification in the Mojave Desert: the role of harvester ant nests and vegetation. West N Am Nat 66:426–433 doi:10.3398/1527-0904(2006)66[426:MCOSRA]2.0.CO;2

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Kiem R, Kandeler E (1997) Stabilization of aggregates by the microbial biomass as affected by soil texture and type. Appl Soil Ecol 5:221–230 doi:10.1016/S0929-1393(96)00132-1

Kirk JL, Beaudette LA, Hart M, Moutoglis P, Khironomos JN, Lee H et al (2004) Methods of studying soil microbial diversity. J Microbiol Methods 58:169–188 doi:10.1016/j.mimet.2004.04.006

Lahav I, Steinberger Y (2001) Soil bacterial functional diversity in a potato field. Eur J Soil Biol 37:59–67 doi:10.1016/S1164-5563(01)01063-9

Lavelle P (2002) Functional domains in soils. Ecol Res 17:441–450 doi:10.1046/j.1440-1703.2002.00509.x

Lawton JH (1994) What do species do in ecosystems? Oikos 71:367–374 doi:10.2307/3545824

Lei SA (2000) Ecological impacts of seed harvester ants on soil attributes in a Larrea-dominated shrubland. West N Am Nat 60:439–444

MacMahon JA, Mull JF, Crist TO (2000) Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Annu Rev Ecol Syst 31:265–291 doi:10.1146/annurev.ecolsys.31.1.265

Mondini C, Cayuela ML, Sanchez-Monedero MA, Roig A, Brookes PC (2006) Soil microbial biomass activation by trace amounts of

readily available substrate. Biol Fertil Soils 42:542–549 doi:10.1007/s00374-005-0049-2

Nannipieri P, Ascher J, Ceccherini MT, Landi L, Pietramellara G, Renella G (2003) Microbial diversity and soil functions. Eur J Soil Sci 54:655–670 doi:10.1046/j.1351-0754.2003.0556.x

Pen-Mouratov S, Rakhimbaev M, Steinberger Y (2006) Spatio-temporal effect on soil respiration in fine-scale patches in a desert ecosystem. Pedosphere 16:1–9 doi:10.1016/S1002-0160(06)60019-2

Poljakoff-Mayber A, Mayer AM, Koller D (1965) Plant physiology. Am Oved, Tel Aviv, Israel

Ravikovitch S (1981) The soils of Israel: formation, nature and properties, 1st edn. Hakibbutz Hameuchad, Tel Aviv, (in Hebrew)

Rodriguez-Zaragoza S, Whitford WG, Steinberger Y (2007) Effects of temporally persistent ant nests on soil protozoan communities and the abundance of morphological types of amoeba. Appl Soil Ecol 37:81–87 doi:10.1016/j.apsoil.2007.04.002

SFAS (1995) Manual—San Plus Analyzer. Skalar Analytical, The Netherlands

Steinberger Y, Shmida A, Whitford WG (1990) Decomposition along a rainfall gradient in the Judean Desert, Israel. Oecologia 82:322–324 doi:10.1007/BF00317478

Steinberger Y, Leschner H, Shmida A (1991) Chaff piles of harvester ant (*Messor* spp.) nests in a desert ecosystem. Insectes Sociaux 38:241–250 doi:10.1007/BF01314910

Steinberger Y, Leschner H, Shmida A (1992) Activity pattern of harvester ants (*Messor* spp.) in the Negev Desert ecosystem. J Arid Environ 23:169–176

Wagner D, Jones JB (2006) The impact of harvester ants on decomposition, N mineralization, litter quality, and the availability of N to plants in the Mojave Desert. Soil Biol Biochem 38:2593–2601 doi:10.1016/j.soilbio.2006.02.024

Wagner D, Brown MJF, Gordon DM (1997) Harvester ant nests, soil biota and soil chemistry. Oecologia 112:232–236 doi:10.1007/s004420050305

Wagner D, Jones JB, Gordon DM (2004) Development of harvester ant colonies alters soil chemistry. Soil Biol Biochem 36:797–804 doi:10.1016/j.soilbio.2004.01.009

Wardle DA, Ghani A (1995) A critique of the microbial metabolic quotient (qCO_2) as a bioindicator of disturbance and ecosystem development. Soil Biol Biochem 27:1601–1610 doi:10.1016/0038-0717(95)00093-T

West NE, Skujins J (1978) Nitrogen in desert ecosystems, US/IBP no. 9. Dowden, Hutchinson & Ross, Stroudsburg, PA

Whitford WG (2000) Keystone arthropods as webmasters in desert ecosystems. In: Coleman DC, Hendrix PF (eds) Invertebrates as webmasters in ecosystems. CABI, NY, pp 25–41

Whitford WG (2002) Ecology of desert systems. Academic, London

Whitford WG, DiMarco R (1995) Variability in soils and vegetation associated with harvester ants (*Pogonomyrmex rugosus*) nests on a Chihuahuan Desert watershed. Biol Fertil Soils 20:169–173 doi:10.1007/BF00336554

Whitford WG, Kay FR (1999) Biopedturbation by mammals in deserts: a review. J Arid Environ 41:203–230 doi:10.1006/jare.1998.0482

Zak JC, Willig MR, Moorhead DL, Wildman HG (1994) Functional diversity of microbial communities: a quantitative approach. Soil Biol Biochem 26:1101–1108 doi:10.1016/0038-0717(94)90131-7