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Faunalpedturbation effects on soil microarthropods in the Negev Desert

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ABSTRACT

Soil microarthropod communities in seed-harvester ant-nest (*Messor* spp.) soils and pits excavated by porcupines (*Hystrix indica*) were examined on a hill-slope catena in the Negev Desert to test the hypothesis that animal-produced soil disturbances increase abundance and diversity of soil biota. There were significantly fewer arthropods and lower taxonomic diversity of soil microarthropods at the top and mid-slope locations, with no consistent patterns of abundance between cool-wet and hot-dry seasons. Some prostigmatids, cryptostigmatids, and other arthropods in ant-nest, porcupine-pit, and undisturbed soils were more abundant in wet than dry seasons at some locations but more abundant in the hot-dry season at other locations and sample sites. Seven prostigmatid mite families that were relatively abundant in undisturbed soils were absent or of low abundance in ant-nest modified and porcupine-pit soils at mid- and low-slope catena locations. The data result in rejection of the hypothesis. However, the significant effects of topographic position on the catena on soil microarthropod communities emphasize the importance of examining broad spatial patterns and temporal variation before making generalizations about the effects of ecological engineers on arid ecosystem structure and function.

1. Introduction

Faunal pedturbation (soil modification by animal activity) has been reported to increase soil nutrients, increase water infiltration rates, increase plant biomass production, and to change species composition of the plant communities that develop on the modified soils (Whitford and Kay, 1999; Whitford, 2000). Faunal pedturbations are frequently cited as examples of ecological engineering (Jones et al., 1997). Most studies of the effects of faunal pedturbations have been limited both spatially (single site) and temporally (single sample date). A study of the effects of seed harvester ant (*Pogonomyrmex rugosus*) nests on soil nutrients and annual plant communities on a Chihuahuan Desert watershed found that soil nutrients and annual plant production increased in nest-modified soils on low-slope locations on the watershed but not on the steeper erosional surfaces (Whitford and DiMarco, 1995). A recent study of the effects of long-lived ant nests on a desert watershed reported different effects on annuals associated with *P. rugosus* nests at different locations on a low-slope catena and differences at the same locations in other seasons (Whitford et al., 2008). Therefore, the effects of faunal pedturbations appear to vary among topographic locations on watersheds or catenas but more studies are required in order to understand the response patterns if such patterns really exist. It is possible that there are no general patterns of responses to faunal pedturbations related to topographic position. Soil nutrient concentrations vary temporally with organic matter inputs, soil water content, annual plant growth, and activities of soil microflora, micro and mesofauna (Tongway and Whitford, 2002). It is, therefore, probable that the effects of faunal pedturbations will vary among seasons and among years. As with patterns of spatial variability, temporal variation in the effects of faunal pedturbations require considerably more data before patterns can be discerned.

The frequently reported effects of faunal pedturbations on soil nutrients and plant communities suggest that these soil modifications have affected processes mediated by soil microflora and micro-mesofauna. In arid ecosystems, certain taxa of soil microarthropods (mesofauna) were found to affect nitrogen immobilization–mineralization rates, rates of decomposition, and the abundance of free-living nematodes (Santos and Whitford, 1981; Santos et al., 1981; Parker et al., 1984). One study reported higher density and abundance of soil mesofauna in soils modified by the nests of seed harvester ants *Messor* spp. (Boulton et al., 2003). In arid ecosystems, microarthropod abundance and diversity increase with increased amounts of plant litter (Santos et al., 1978). This suggests that faunal pedturbations that result in concentration of plant litter should result in increased abundance of microarthropods and in differences in composition of the microarthropod community.

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In the Negev Desert, the Indian crested porcupine, *Hystrix indica*, and seed harvesting ants, *Messor* spp., are sympatric agents of soil disturbance. *H. indica* digs large, discrete, elongated pits in the soil when foraging for below-ground plant storage organs (Shachak et al., 1991). Pits produced by *H. indica* serve as traps for wind and water transported plant litter and seeds (Alkon, 1999). *Messor* spp. ants transport soil from depths of 2 m or greater and deposit the soil near the nest entrance (Steinberger et al., 1992). They also transport seed husks, awns, and other plant debris from the nest and deposit that material in chaff piles around the nest entrance. Because these animals produce disturbances that result in organic material accumulations and which may affect water infiltration and soil porosity, we hypothesized that perturbations produced by these taxa would result in increased abundance and diversity of soil microarthropods. We also hypothesized that the effects of these perturbations would be greater in run-on locations on a catena than on upper-slope, run-off locations.

2. Materials and methods

2.1. Study sites

The study site was located at the M. Evenari Runoff Research Farm (30°47′, 34°36′E) Avdat, a watershed of the highland Negev Desert, Israel. The area has a temperate desert climate, with cool winters (5–14 °C range in January) and hot, dry summers (18–23 °C in June). The elevation of this site is approximately 600 m above sea level, with a multi-annual average rainfall of 89.5 mm (Avdat Station), ranging from 24.0 mm in an extreme drought year to 183.3 mm in a wet year (Evenari et al., 1982a,b). The rainy season usually begins in October and ends at the end of April, with most of the rainfall occurring in scattered showers between December and February. An additional moisture source comes from approximately 35 mm of dew, which occurs heavily during an average of 210 nights in late summer and autumn. The annual evaporation rate is 2615.3 mm (Evenari et al., 1982a). Soils at the study site are composed of aeolian loess deposits. The loess soils are alkaline and exhibit low salinity in the upper layer, which increases with depth, as well as a horizon of gypsum accumulation (Dan et al., 1973).

The study site is a hill-slope catena consisting of four distinct areas that differ in run-off, run-on characteristics. The catena consists of hill top, mid-slope, low-slope, and run-on basin. The soil microarthropod communities of harvester ant (*Messor* spp.) nest-modified soils and of porcupine (*H. indica*) pits were examined in this catenary sequence. Seed harvester ants of the genus *Messor* include: *Messor arenarius* (Fab.), *Messor ebeninus* (Sant.), and *Messor rugosus* (Andr.), and differ from each other in size and diet (Steinberger et al., 1992).

2.2. Soil sampling

Ant nests and porcupine diggings were studied at the four locations on the Avdat catena: the top of the hill, mid-slope on the hill, low slope on the hill, and the basin. An 8-cm diameter corer was used to take soil samples from four ant *Messor* spp. nests, four porcupine (*H. indica*) digs, and four reference soils (bare soil) at each location, on six dates that span the cool-wet season (November, January, March) and the hot-dry season (May, July, September) from July 2004 to May 2006.

The samples were always taken from a new dig or nest. The dig/nest were identified as new by the fact that a new ant nest had a new entrance within a nest mound and porcupine digs do not last more than two weeks, since they become covered with sand and ephemeral plants, due to the wind regime.

The samples were placed in plastic bags and kept in an insulated box until arrival at the Soil Ecology Laboratory of Bar-Ilan University. The soil samples were sieved (2 mm mesh size) and stored at 4 °C until biological and chemical analysis.

2.3. Laboratory analysis

Soil moisture was measured gravimetrically for each fresh soil sample by drying in an oven at 105 °C for 24 h. Total organic carbon in soils was measured for each soil sample by the method of Rowell (1994).

At each sampling period, 100 g soil was placed in a modified Tullgren funnel to extract microarthropods (Santos et al., 1978), prior to chemical analysis. The total number of microarthropods was counted and representatives of the different microarthropods were mounted on slides in Hoyer's medium. Mites were identified to family using the keys in Krantz (1978) and some cryptostigmatid mites were identified to genus using reference collections made by J.A. Wallwork.

2.4. Statistical analysis

All data were subjected to analysis of variance using an SAS model (two-way ANOVA, (SAS Inst, 1988)). Differences obtained at a level of $p < 0.05$ were considered significant. Duncan's and Tukey's multiple range tests were used to evaluate differences between separate means (Sokal and Rohlf, 1969). Taxonomic diversity of microarthropods of ant nest, porcupine pit, and reference soils at the four topographic locations on the catena was calculated by the Shannon–Weaver diversity index *H*. $H = -\Sigma p_i \ln p_i$, where p_i is the proportion of the *i*th taxon (Shannon and Weaver, 1949).

3. Results

3.1. Soil water content and organic carbon

There were no differences in soil moisture among the catenary locations or animal modified soils and reference soils during the period of the study. Soil water content of 11.3–12.0% in January 2005 and of 4.5–7.4% in March 2005 was higher ($p < 0.05$) than on all other sampling periods in which soil water content varied between 0.5 and 3.0%. There were no differences in percent of organic carbon among catenary positions, undisturbed ant nests and porcupine-pit soils. Percent of organic carbon varied between 2% and 4% for the 2005–2006 sample dates and between 0.2 and 1.0% for the 2004 sample dates.

3.2. Temporal and spatial patterns

The abundances of prostigmatids, cryptostigmatids, astigmatids, and other arthropods were significantly different among different sample months ($p < 0.0001$).

The temporal differences were primarily the result of lower abundances during the hot-dry season sample dates than during the cool-wet season sample dates. Therefore, the data on abundance were summarized for these seasons. There were significant month–location–sample site interactions for the abundances of prostigmatid mites ($p < 0.02$), cryptostigmatid mites ($p < 0.02$), and other arthropods ($p < 0.0002$) that resulted from large differences in abundance at the mid-slope and top catena locations in the hot-dry and cool-wet seasons (Table 1). Total numbers of microarthropods were higher in undisturbed soils than in ant-nest soils and porcupine-pit soils at the top of the catena but not at any of the other topographic positions. Prostigmatids and cryptostigmatids were more abundant during the cool-wet season at the mid-slope, low-slope, and basin locations but not at the top of the catena (Table 1).

The wet and dry season differences were not consistent across topographic locations and sample sites (Table 2). Prostigmatid

Table 1
Total densities (number per 100 grams dry soil) of microarthropods in harvester-ant (*Messor* spp.) nest soils, porcupine (*Hystrix indica*) pit soils, and undisturbed soils from the topographic positions sampled on a Negev Desert hill-slope catena.

Position/Sample Site	Prostig.	Crypto.	Astigm.	Others
Basin – ant nest	7.2	2.7	0	0.8
Basin – porcupine	3.9	2.2	0	1.8
Basin – undisturbed	2.9	3.0	0.4	1.5
Low slope – ant nest	7.3	3.7	0.5	0.2
Low slope – porcupine	6.1	2.4	0.2	0.8
Low slope – undisturbed	8.9	2.6	0	4.8
Mid-slope – ant nest	10.6	8.1	0	1.0
Mid-slope – porcupine	6.5	3.5	0.2	1.2
Mid-slope – undisturbed	6.9	3.7	0	1.5
Hill top – ant nest	2.1	0	0	1.5
Hill top – porcupine	2.0	1.5	0	0.7
Hill top – undisturbed	10.2	2.8	0.6	2.1

Prostig., Prostigmata; Crypto., Cryptostigmata; Astigm., Astigmata; others, other arthropods (Collembola, Psocoptera, insect larvae, pseudoscorpions).

mites were more abundant in ant-nest and porcupine-pit soils in the cool-wet season than in the hot-dry season in the basin but there were no seasonal differences in prostigmatid abundance in undisturbed soils. There were fewer cryptostigmatids in porcupine pits in the cool wet season than in the dry season in the basin. The abundance of prostigmatids was higher in the wet season ant-nest soils than in the dry season at that location and sample site. Prostigmatid and cryptostigmatid mites were more abundant in ant-nest soils in the wet season at mid-slope than during the dry season at that location and sample site. In contrast, prostigmatids were absent in ant-nest soils in the cool-wet season at the top of the catena (Table 2). Abundance of other arthropods (Collembolans, Psocopterans, and insect larvae) were higher in the hot-dry season than in the cool-wet season in undisturbed soils in the basin, and ant-nest and porcupine-pit soils at the top of the catena.

There were few seasonal differences in taxonomic richness between years and between animal-modified soils and undisturbed soils. There were no differences in taxonomic richness in the hot-dry seasons 2004 and 2005 for prostigmatids, cryptostigmatids, and other arthropods in ant-nest, porcupine-pit, and undisturbed soils. Taxonomic richness of prostigmatids was higher in ant-nest modified soils in the 04/05 wet season than in the 05/06 wet season but there were no differences in richness of cryptostigmatids and other arthropods (Table 3). The taxonomic richness of soil mesofauna in the cool-wet seasons was not different between years in porcupine-pit and undisturbed soils (Table 3).

Table 2
Average numbers of microarthropods per 100 g dry soil summed for the wet (W) and dry (D) seasons of the study.

Position/Sample Site	PrD	PrW	CrD	CrW	AsD	AsW	OtD	OtW
Basin – ant nest	1.2	6.8	1.2	2.6	0	0	0.6	1.1
Basin – porcupine pits	2.3	4.3	1.3	0.5	0.3	0.3	0.5	1.6
Basin – undisturbed	2.6	2.6	1.0	3.3	0.3	0	2.4	0.9
Low slope – ant nests	1.7	7.4	1.1	3.9	0	0	0.3	0.7
Low slope – porcupine	3.3	4.0	1.8	1.3	0	0	1.2	0.3
Low slope – undisturbed	5.5	5.2	2.4	0.6	0	0	1.3	4.8
Mid-slope – ant nest	3.9	11.6	0.5	10.1	0	0	1.8	0
Mid-slope – porcupine	5.7	4.1	3.0	2.0	0	0	0.3	1.6
Mid-slope – undisturbed	4.0	5.1	3.6	1.6	0	0.7	0	4.2
Top – ant nest	3.0	0	0	0	0	0	3.0	0
Top – porcupine pits	1.4	1.4	0.6	1.4	0	0	1.4	0
Top – undisturbed	6.3	6.8	1.6	2.1	0	0	2.2	2.2
Basin sums	6.1	13.7	3.5	6.4	0.6	0.3	3.5	3.6
Low slope sums	10.5	16.6	5.3	5.8	0.0	0.0	2.8	5.8
Mid slope sums	13.8	20.8	7.1	13.7	0.0	0.7	2.1	5.8
Top sums	10.7	8.2	2.2	3.5	0.0	0.0	6.6	2.2

Pr, Prostigmata; Cr, Cryptostigmata; As, Astigmata; Ot, other arthropods.

Table 3
Seasonal patterns of average number and range of operational taxonomic units (OTU) (families plus some genera) summarized for all locations on a Negev Desert hill-slope catena.

Season	Prostigmata	Cryptostigmata.	Astigma	Other Taxa
Ant nests				
Hot-dry 04	2.3 (0–6)	1.0 (0–2)	0	0.7 (0–1)
Hot-dry 05	2.0 (1–3)	1.3 (1–2)	0	0.7 (0–1)
Cool-wet 04/05	8.0 (6–12)	1.3 (1–2)	0.3 (0–1)	1.3 (1–3)
Cool-wet 05/06	3.3 (1–7)	1.3 (1–2)	0	1.6 (2–3)
Porcupine excavations				
Hot-dry 04	1.3 (1–2)	1.0 (1–2)	0	0.7 (0–1)
Hot-dry	4.0 (3–5)	2.3 (2–3)	0	1.0 (0–2)
Cool-wet 04/05	4.3 (2–7)	1.8 (1–2)	0	1.6 (1–2)
Cool-wet 05/06	4.0 (3–5)	1.3 (1–2)	0	0.8 (1–2)
Undisturbed soil				
Hot-dry 04	2.0 (0–4)	2.3 (1–4)	0.3 (0–1)	2.0 (2)
Hot-dry	4.0 (3–5)	1.3 (0–3)	0.3 (0–1)	2.0 (1–3)
Cool-wet 04/05	7.1 (4–12)	1.0 (1–4)	0.3 (0–1)	2.3 (2–3)
Cool-wet 05/06	5.2 (2–11)	1.0 (1–3)	0	2.0 (2)

Hot-dry season, May, July, September sample dates; cool-wet season, November, January, March sample dates.

3.3. *Taxonomic composition and diversity*

The taxonomic diversity of the microarthropod communities in undisturbed soils was similar at all locations on the hill-slope catena except for the mid-slope position (Table 4). The taxonomic diversities of microarthropods of ant-nest soils and porcupine-pit soils at the top of the catena were considerably lower than the diversity in undisturbed soils at that topographic position. The differences in taxonomic diversity of microarthropods from ant-nest soils, porcupine-pit soils, and undisturbed soils on the lower slope and basin were not significant.

Two prostigmatids (raphignathids and stigmaeids) occurred at all locations except in ant-nest soils at the top of the catena. Oribatid mites (Cryptostigmata) were recovered from animal-modified soils and undisturbed soils at all locations on the catena. The dominant oribatids, *Cosmochthonius* spp., *Haplocthonius* spp., and *Cosptoceles* spp. were of equal or greater abundance in the disturbed soils of the lower slope and basin than in undisturbed soils of those topographic locations (Table 4). Seven prostigmatid mite families that were relatively abundant in undisturbed soils were absent or of low abundance in ant-nest soils and porcupine-pit soils at the top of the catena. No prostigmatid mites were recovered from ant-nest or porcupine-pit soils at the top of the catena.

Other mesoarthropods (Collembolans, Psocopterans, and insect larvae) were relatively abundant in undisturbed soils at all locations on the catena, absent or in low abundance in ant-nest soils and porcupine-pit soils at top, mid-slope, and low locations. These arthropods were relatively abundant in both undisturbed and ant- or porcupine-modified soils in the catena basin.

4. Discussion

The results of this study did not support the hypothesis that soils disturbed by animals (ants, *Messor* spp., and porcupines, *H. indica*) would support a more abundant and diverse microarthropod assemblage. Since ant-nest modified and porcupine-pit soils supported lower abundance and diversity of microarthropods than undisturbed soil at the upper locations on the catena, the hypothesized response of soil microarthropods to faunal pedturbation is not only rejected, but also the trajectory of the response is reversed.

Table 4
Total numbers of individuals of each taxon identified in this study during the two years of the study and at the various sampling sites.

Taxon	TC	TA	TP	MC	MA	MP	LC	LA	LP	BC	BA	BP
Prostigmata												
Tydeidae	25			6	2	4	2	4	4	1		4
Paratydeidae												1
Nanorchestidae	2			3	4	1	2	3	5	6	5	3
Pyemotidae												1
Tarsonemidae	8							1	4		2	3
Raphignathidae	3			3	3	3	7	3	3	2	2	1
Stigmaeidae	9			2	2	1	6	2	4	5	4	3
Bdellidae							2	1				1
Cunaxidae					1							
Scutacaridae	1				2			1		3		2
Erythraeidae							1					
Cheyletidae	2				1	1		2	1			1
Tarsocheylidae					1	1		2	1			1
Teneriffidae					1						8	
Eupodidae	1											
Nematalycidae								3	1		1	1
Trombidiidae	1											1
Cryptostigmata												
Joshuella spp.	1											
Aphelacaridae		1		1	5		2	2	2	1	1	2
Cosmochthonius spp.	4	2		5	5	2	2	8	4	9	7	7
Oribatula spp.					1				1	1		1
Oppidae												1
Haplochthonius spp.	3			4	2		2		3	1	8	6
Galumnidae					1							
Cosptocheles spp.			1			2	2		2		1	1
Passolozetes spp.							1	2		1	1	
Astigmata												
Acaridae	1			4	3							1
Rhodacaridae											1	
Other arthropods												
Collembola	8			55	9		12	5		1	5	7
Psocoptera				1			2		3		5	3
Insect larvae	3		1	4			4	1	4	4	8	8
Pseudoscorpionidae	1				1		1					
Number of taxa	16	2	2	11	17	8	15	15	15	12	15	23
Diversity index H'	2.2	0.7	0.7	1.4	2.3	1.8	2.3	2.2	2.3	1.9	2.3	2.7

Sample site codes: C, undisturbed soil; A, ant-nest modified soil; P, porcupine-pit soils; T, top of catena; M, mid-slope of catena; L, low-slope of catena; B, catena basin.

Significant reductions in abundance and diversity in faunal perturbed soils were primarily but not solely on the upper slopes of the catena. These results provide evidence of negative effects of ecological engineers on the structure and function of Negev Desert ecosystems. The spatial differences in the effects of faunal perturbations on soil microarthropods emphasize that conclusions about 'ecological engineers' (Jones et al., 1997) must be tempered by consideration of spatial and temporal variability. Abundance and diversity of soil microarthropods have been found to be related to soil moisture and soil organic matter (Cepeda-Pizarro and Whitford, 1989a, b). The absence of differences in soil moisture and soil organic carbon among catenary positions, and between faunal-disturbed and undisturbed soils, contributes to the absence of differences in diversity and abundance during some seasons and at several catenary positions. The lack of differences in soil organic carbon and water content among perturbed and undisturbed soils may be related to the type of disturbance and/or the age of the disturbance. Nests of seed-harvesting ants that have been documented to increase soil organic matter and water infiltration, persist for more than 5 years (MacMahon et al., 2000). The ages of the *Messor* spp. nests sampled in this study are unknown and were judged to be relatively new (established one or two years prior to this study based on the size and activity of the colonies). If the *Messor* spp. nests are relatively young, the accumulation of organic carbon in the nest soils from the decomposition of the chaff accumulations would not have sufficient time to develop, and this is consistent with the data.

Soil cores collected from recent porcupine excavations represent subsoils from 5 to 10 cm below the surface of undisturbed soil. Microarthropods are most abundant and diverse in the upper 5–10 cm of soil (Wallwork, 1982; Silva et al., 1989). Porcupine pits on the lower slopes and basin partly in-fill with run-off transported soil. Loose soil excavated by porcupines enhances soil erosion and transport (Alkon, 1999), thereby contributing material for in-filling down-slope pits. Pits partially filled with eroded topsoil provide suitable habitat for a number of species of microarthropods.

In arid regions, the abundance and diversity of cryptostigmatid mites have been shown to be a function of soil organic matter or soil organic carbon (Wallwork, 1982; Wallwork et al., 1986). While some important differences in abundance and diversity of cryptostigmatids were found in this study, there were no differences during most seasons and locations on the catena. The increase in soil organic carbon in the November–March period probably resulted from the growth of roots of winter ephemeral plants. Decomposition of these roots may have provided the organic matter substrate for fungi that support populations of cryptostigmatid mites in the undisturbed soils and ant-nest modified soils. The reduced diversity and abundance of cryptostigmatids in porcupine pit samples are probably because pit samples were mineral soils from depths of 8 to 20 cm.

The taxonomic composition of the microarthropod fauna on the hill-slope catena in the Negev is similar to that of a Chihuahuan Desert watershed, with prostigmatid mites as the most abundant and diverse group of soil microarthropods and with cryptostigmatid mites as the second most abundant and diverse group (Cepeda-Pizarro and Whitford, 1989a, b). The most abundant prostigmatid mites on the Negev hill-slope catena (Raphignathidae) are not included among the most abundant taxa on the Chihuahuan Desert watershed. However, the other abundant taxa, Tydeidae, Nanorchestidae, and Stigmaeidae, are the dominant prostigmatid mites in both deserts.

The lower abundance and diversity or lack of difference in abundance and diversity of microarthropods in ant-nest soils, porcupine-dig soils, and reference soils on this desert catena suggest that significantly higher soil microarthropod abundance and diversity reported in ant-modified soils (Boulton et al., 2003) and in earthworm-modified soils (Loranger et al., 1998) may be attributed to the more mesic soil conditions of these studies. The most significant factor affecting the abundance and diversity of microarthropods in this study was the season in which soil moisture was high due to seasonal rainfall. Studies of microarthropod communities in the Chihuahuan Desert of North America have documented the dependence of microarthropod abundance and diversity on rainfall, and subsequent increased soil water content (Steinberger et al., 1984; MacKay et al., 1986; Cepeda-Pizarro and Whitford, 1989a; Whitford and Sobhy, 1999). The importance of soil water content for the abundance and diversity of soil microarthropods has been reported for the Negev Desert (Steinberger, 1990) and in an experimental irrigation study in Greece (Tsiafouli et al., 2005).

In arid regions, animal-disturbed soils may have a positive effect on water infiltration. However some disturbed soil has been found to lose stored water more rapidly than undisturbed soils (Mun and Whitford, 1990). Differences in water evaporation from animal modified patches of soil could negate the effects of increased infiltration and contribute to the absence of differences in soil water content of animal modified and undisturbed soil.

In conclusion, this study documented lower abundance and diversity of soil microathropods in ant-nest modified soils and porcupine-foraging pits relative to undisturbed soil at some locations and during some time periods. Based on the extensive literature on the effects of nests of seed-harvesting ants on soil properties (MacMahon et al., 2000; Whitford, 2000), higher abundance and diversity of soil biota would be expected in *Messor* spp.-nest modified soils in comparison to undisturbed soils. While the reduced abundance and diversity of microarthropods may result from the characteristics of loess soil when modified by the activity of harvester ants or from the unique habitat requirements of Negev Desert microarthropods, the importance of topographic position relative to run-off and run-on processes is paramount. The significant effects of topographic position on the soil microarthropod communities in *Messor* spp.-nest modified soils and in porcupine pits emphasize the importance of examining broad spatial and temporal variation before making generalizations about the effects of ecological engineers on the structure and function of arid ecosystems.

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