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Spatiotemporal Variations of Soil Microarthropod Communities in the Negev Desert

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ABSTRACT

Desert ecosystems are characterized by sparse vegetation that affects both abiotic parameters and soil biota along the soil profile. This study was conducted in 2010–2011 in a loess plain in the northern Negev Desert highlands, Israel, to test two main hypotheses: 1) the abundance and diversity of microarthropods would vary seasonally in the top 30-cm soil layer, but would be relatively stable at soil depths between 30 and 50 cm and 2) soil microarthropods would be more abundant in soils under shrubs with large litter accumulations than under shrubs with less litter or bare soil. Soil samples were collected each season from the 0–50 cm profile at 10-cm intervals under the canopies of *Hammada scoparia* and *Zygophyllum dumosum* and from the bare interspaces between them. Soil moisture and soil organic carbon in the top 30-cm layers varied seasonally, but there was little variation in the soil layers deeper than 30 cm. Soil mites were most abundant in the top 30-cm soil layer in autumn and winter, with the highest number of families found in winter. There were no differences in soil microarthropod abundance attributable to the presence or absence of shrubs of either species. The microarthropod communities of the microhabitats studied consisted of Acari, Psocoptera, and Collembola. The Acari were mostly identified to the family level and were dominated by Oribatida (55%) and Prostigmata (41%) in all seasons and microhabitats, while the psocopterans were most abundant in summer. These results are opposite to those obtained in other studies in similar xeric environments. Moreover, our findings were not in line with our hypothesis that a better microhabitat played a major role in microarthropod community composition, diversity, and density.

Key Words: microhabitat, seasonality, shrub, soil depth, soil mites, soil moisture, soil organic carbon

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INTRODUCTION

Soil microarthropods are an important component of any terrestrial ecosystem due to their crucial role as regulators of key processes, such as plant litter decomposition and mineralization (Wallwork, 1970; Kaczmarek *et al.*, 1995; Kampichler and Bruckner, 2009), soil formation (Persson, 1989), and nutrient cycling (Powers *et al.*, 1998). In arid and semiarid ecosystems, microarthropods are more abundant and diverse under shrubs or in the rhizosphere of desert grasses (Santos *et al.*, 1978). In arid environments, plant litter is trapped and accumulates under shrub canopies, resulting in islands of relatively large amounts of organic matter and nutrients (Charley and West, 1975; Garner and Steinberger, 1989) that increase soil microbial biomass and activity (Berg and Steinberger, 2010).

Most studies on soil microarthropod communities were conducted in temperate and tropic environments and were confined to the topsoil (30 cm or less), which gives a partial picture of the soil microarthropod communities (André *et al.*, 2002). Moreover, in arid environments, studies were focused on the upper 10–15 cm soil layer under shrubs or grasses because most biological activity is concentrated in those layers (Santos *et al.*, 1978; Wallwork *et al.*, 1985). A study on microarthropods associated with the roots of two shrubs, with sampling up to 13 m depth in several habitats, found that the abundance and diversity of soil microarthropods vary with the abundance of roots at different depths (Silva *et al.*, 1989). The significance of plant root presence is its contribution to organic matter levels in the soil (Kinsbursky and Steinberger, 1989; Wichern *et al.*, 2007). According to Evenari *et al.* (1982), the root systems of shrubs growing on loessial plains in the Negev Desert are able to penetrate to 30–50 cm depths, having a great effect on soil biotic composition, functions, and trophic interactions (Steinberger *et al.*, 1995; Shmueli *et al.*, 2007).

The morphology of shrubs affects both the thermal

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and hydrological characteristics of the soil by shading and reducing the evaporation of dew and rainfall (Whitford, 2002). Desert plants have developed different physiological and behavioral adaptations to the extreme environmental conditions in their habitats (Evenari *et al.*, 1982; Rodriguez-Zaragoza *et al.*, 2008). These ecophysiological adaptations of plants have a great effect on abiotic conditions, *e.g.*, soil organic matter and nutrients beneath the shrub canopies, and, as a result, they influence the activity of soil biota (Schlesinger and Pilmanis, 1998; Thompson *et al.*, 2006).

In the Negev Desert highlands, two of the most common perennial shrubs, *Zygophyllum dumosum* and *Hammada scoparia*, are characterized by different morphologies and physiologies that have an effect on the variation in soil moisture and nutrients with soil depth. *Z. dumosum* is a semi-deciduous shrub, 30–100 cm in height, which sheds its leaflets during the dry period and continues photosynthesis by the fleshy petiole, which stays green and active (Evenari *et al.*, 1982). Its mean total litter production is about 433 g per shrub per year (Steinberger, 1991). *H. scoparia* is a leafless dwarf shrub, 30–50 cm in height, with photosynthetic jointed stems. Its dense stems capture windblown litter, producing an environment that increases the density of annual plants (Sarig *et al.*, 1994) and, therefore, contributing to higher accumulation of organic matter in the soil beneath *H. scoparia*. Its low and dense structure also causes reduced soil temperature and lowered evaporation rate of soil moisture.

The microarthropod community in desert environments, especially in a dry environment such as the Negev Desert, was hardly studied in the past, and our study provides more information on those small, obscure animals, not only in the soil upper layer but up to the 0.5-m deep layer in such an ecosystem. Therefore, the current study was initiated in order to expand our knowledge on the effect of desert shrubs on the vertical distribution of microarthropods in the loessial plains of the Negev Desert, and to elucidate abiotic variables and microarthropod community interactions under the canopies of *Z. dumosum* and *H. scoparia*, and in the bare interspaces between them, during the year.

Since the upper 30-cm soil layer is subject to seasonal fluctuations in temperature and evaporation, soil biotic populations inhabiting that layer vary as environmental conditions change (Elkins and Whitford, 1982; Steinberger *et al.*, 1995). The distribution of resources in dry environments varies both spatially and temporally (Noy-Meir, 1985), and has a significant effect on soil biotic composition, activity, and distribution (Steinberger *et al.*, 1995). The temporal patterns of soil organism abundance in arid environments are determined by soil water potential and temperature (Whitford, 1989). Since the soil environment at depths greater than 30 cm exhibits little variation annually, the soil biota of deeper soils should exhibit little seasonal variation in abundance (Whitford, 2002). We tested this hypothesis by examining the soil microarthropod communities at 10-cm intervals from the surface to a 50-cm depth. Moreover, the morphological and physiological differences between *Z. dumosum* and *H. scoparia* have been found to affect the vertical abundance and diversity of soil biota, *e.g.*, nematodes and microbial communities (Pen-Mouratov *et al.*, 2003; Yu and Steinberger, 2011). Therefore, we hypothesized that the abundance and diversity of soil microarthropods would be higher in the deeper soil layers underneath the plant canopy of *H. scoparia* than *Z. dumosum* due to its better microhabitat (Berg and Steinberger, 2010). The effects of soil depth and shrub species on the abundance and community structure of soil microarthropods in a desert ecosystem were studied.

MATERIALS AND METHODS

Study site

A field study was conducted in 2010–2011 at the M. Evenari Runoff Research Farm at Avdat (30°47′ N, 34°46′ E) in a loess plain in the northern Negev Desert highlands, Israel. The elevation of the study site is about 600 m above sea level. These highlands have a temperate desert climate, *i.e.*, mild, rainy winters (4.4–14.8 °C in January) and hot, dry summers (18.6–32.6 °C in August). The multiannual mean rainfall is about 90 mm, most of which occurs in scattered showers between December and March. Dew formation occurs on an average of 195 nights per year (primarily from September to November), with water of 35 mm per year on average (Evenari *et al.*, 1982). The annual evaporation is 2 615 mm. This area (over a 1 000 ha) consists of loess plains and rocky slopes with shallow, saline, gray lithogenic, calcareous soils. The soil at the study site is a deep, fine-textured loessial sierozem. The perennial plant cover of the run-on areas at the base of hillslopes is low ($< 8\%$), and the aridoactive shrubs (Evenari *et al.*, 1975), *H. scoparia* and *Z. dumosum*, are the dominant perennial vegetation in these areas. The abundance of a variety of annual plants varies with the amount of rain (Evenari *et al.*, 1982).

Soil sampling and analysis

Soil samples were collected at the mid-point of each season under the canopies of four *Z. dumosum* shrubs and four *H. scoparia* shrubs, and from the bare interspaces between them as a control using an auger (5-cm diameter). The shrubs were first selected at random for sampling, with a minimum distance of 10 m between them, and the same four shrubs were sampled in each season. Control samples were taken from four bare soil interspace areas between the shrubs, with a minimum distance of 4 m from the nearest shrub. Each season, the samples were collected at the same time, after sunrise, because of the vertical movement of the microarthropods during the day (Steinberger and Wallwork, 1985).

Under each shrub and in each bare interspace, independent samples were collected from each of the five depths, 0–10, 10–20, 20–30, 30–40, and 40–50 cm, and placed in individual polyethylene bags, resulting in a total of 20 soil samples collected from each microhabitat every season. Prior to sampling, the litter layer was removed. The soil samples were stored at 4 °C in the laboratory for use in biological and physico-chemical analyses. A total of 240 soil samples were collected during four seasons on the following dates: October 3, 2010 (autumn), January 2, 2011 (winter), April 3, 2011 (spring), and August 7, 2011 (summer).

Subsamples from each replicate were analyzed for soil moisture (SM) and soil organic carbon (SOC), as follows. The SM content was determined gravimetrically by drying the soil samples at 105 °C for 48 h and measuring the mass loss. The SOC content was determined by oxidation with dichromate in the presence of H_2SO_4 (Rowell, 1994).

Microarthropod extraction and identification

We took a subsample of 100 g fresh soil from each of the 240 samples for microarthropod extraction within 48 h of field collection. Each subsample (one for each depth) was placed separately in modified Berlese-Tullgren funnels under standard light bulbs (40 W) for 48 h. The microarthropods were collected from the funnels and then counted and identified. A representative from each taxonomic unit was mounted on a slide and identified under a light microscope to the lowest taxon possible based on available keys. Mites of the order Mesostigmata, the suborders Prostigmata and Endeostigmata, and the cohort Astigmata were identified to the family level using keys by Krantz and Walter (2009). The suborder Oribatida was identified to the genus level. Psocoptera and Collembola were recorded at the order level. Microarthropod feeding habits were assigned to each family based on feeding behavior reported in literature (Krantz and Walter, 2009). Feeding behaviors were divided into five groups: predators, algivores, fungivores, macrophytophages, and detritivores. Unfortunately, the ecological data published on many soil microarthropods are incomplete so feeding habits were based on documented "most probable" feeding behavior. When no such information was available, feeding habits were deduced based on closely related families.

Data analysis

Abundance (individuals m^{-2}), taxonomic richness (TR), which represents the number of identified taxa in each sample (Gotelli and Colwell, 2001), two diversity indices, Shannon index (H') ($H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of individuals in the ith taxon) and evenness (J') ($J' = H'/\ln S$, where S is the number of total taxa), and relative abundance were all calculated for the different seasons and microhabitats. Soil parameters and microarthropod abundance were initially analyzed for normality, after which repeated measures of analysis of variance (ANOVA) were used to determine seasonal and microhabitat effects. Duncan's multiple range tests were used to evaluate differences among means. All data were subjected to ANOVA using the SAS system. Ordination techniques were used to determine the contribution of the environmental variables to microarthropod community composition (Lepš and Šmilauer, 2003). Redundancy analysis (RDA) was conducted using CANOCO for Windows 4.5 in order to evaluate differences between separate means. The Monte Carlo test with 499 unrestricted permutations was used to evaluate the significance of a given environmental factor and its relevance to results obtained during the study period (ter Braak, 1995). All statistical tests were conducted at a significance level of $P < 0.05$.

RESULTS

Soil abiotic characteristics

During the dry period (spring through autumn), there was no significant difference in soil moisture content at soil depths greater than 30 cm, with soil moisture ranging between 25 and 40 g kg^{-1} (Fig. 1, Table I). During the wet winter season, the top 10-cm soil layer had the highest moisture content recorded, but with no statistically significant differences between the bare interspaces (control) and shrubs. Soils of the up-

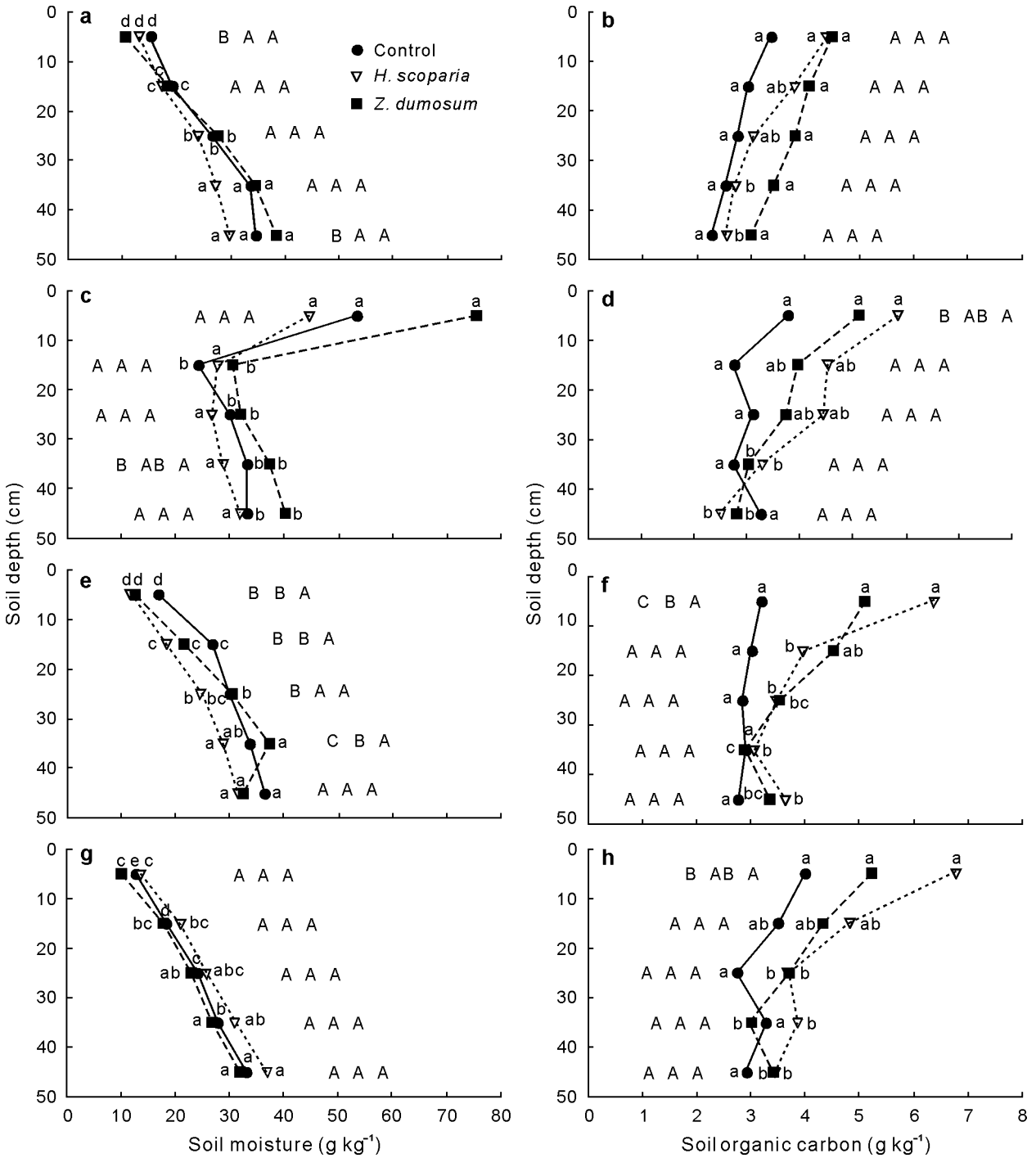

Fig. 1 Changes in the mean values ($n = 4$) of soil moisture and organic carbon in soil samples collected from the vicinity of shrubs (*Z. dumosum* and *H. scoparia*) and in the bare interspaces between the shrubs (control) during the seasons autumn 2010 (a and b), winter 2011 (c and d), spring 2011 (e and f), and summer 2011 (g and h). Different lowercase letter(s) represent significant differences ($P < 0.05$) between the five depths and different uppercase letter(s) represent significant differences ($P < 0.05$) between the three microhabitats.

per 10-cm layer dried rapidly in spring and remained low in moisture content (between 10 and 20 g kg^{-1}) in summer and autumn.

Soil organic carbon was relatively stable at depths greater than 30 cm in soil samples in every season. There were increases in soil organic carbon in soil samples taken from the upper 10-cm layer under shrubs in spring and summer. In the autumn samples, there were no differences in soil organic carbon between soil depths or shrub species (Fig. 1).

Soil microarthropods

Abundance and community composition. During our study, we recorded a total of 19 families of mites, including 1 of Mesostigmata, 9 of Prostigmata, 2 of Endeostigmata, 1 of Astigmata, and 6 of Oribatida, plus representatives of Psocoptera and Collembola (Table II).

TABLE I

Results of analysis using repeated measures of analysis of variance (ANOVA) on soil moisture and soil organic carbon in 0–30 and 30–50 cm soil profiles with seasons, microhabitats, and the interaction between them

Soil parameter	0–30 cm					
	Season		Microhabitat		Season × microhabitat	
	F value	P value	F value	P value	F value	P value
Soil moisture	18.07	$< 0.000\,1$	2.15	NS[a)]	1.73	NS
Soil organic carbon	2.10	NS	10.45	$< 0.000\,1$	0.62	NS
Soil parameter	30–50 cm					
	Season		Microhabitat		Season × microhabitat	
	F value	P value	F value	P value	F value	P value
Soil moisture	1.37	NS	2.31	0.004 9	2.71	0.037 0
Soil organic carbon	1.52	NS	1.81	NS	1.47	NS

[a)] Not significant.

TABLE II

Mean relative abundance of each taxonomic group of soil microarthropods from all three different microhabitats, shrubs (*H. scoparia* and *Z. dumosum*) and the bare interspaces between shrubs (control), during the four seasons

Taxonomic group	Feeding habit(s)[a)]	Control	*H. scoparia*	*Z. dumosum*
Acari		0.913	0.895	0.873
Mesostigmata		0.012	0.001	0.010
Rhodacaridae	P	0.012	0.001	0.010
Prostigmata		0.401	0.401	0.318
Bdellidae	P	–	0.038	0.022
Cunaxidae	P, F	0.018	0.030	0.010
Paratydeidae	P	0.008	0.008	0.012
Raphignathidae	P	0.040	0.092	0.010
Scutacaridae	F	–	0.006	0.005
Stigmaeidae	P	0.252	0.172	0.161
Stigmocheylidae	P*	0.007	0.003	0.009
Tarsonemidae	F, M	0.037	0.005	0.015
Tydeidae	P, A, F	0.026	0.047	0.059
Unidentified		0.014	–	0.014
Endeostigmata		0.009	0.025	0.007
Nanorchestidae	A*, F, M	0.009	0.015	0.007
Terpnacaridae	F	–	0.010	–
Oribatida		0.514	0.481	0.532
Aphelacarus sp.	A, F	0.112	0.024	0.122
Cosmochthonius sp.	A	0.031	0.008	0.049
Haplochthonius sp.	A*	0.224	0.282	0.221
Oppia sp.	P, A, F	0.002	0.015	0.005
Zygoribatula sp.	P, A, F, D	–	0.010	–
Sphaerochthonius sp.	A*	0.003	0.004	0.005
Immature		0.139	0.136	0.129
Astigmata		0.004	–	0.022
Acaridae	P, A, F	0.004	–	0.022
Hexapoda		0.087	0.105	0.126
Psocoptera		0.072	0.081	0.105
Collembola		0.015	0.024	0.021

[a)] P = predators; A = algivores; F = fungivores; M = macrophytophages; D = detritivores. The subscript * denotes the deduced feeding habit based on the feeding behavior of closely related taxon.

Soil Acari were significantly more abundant in the top 30-cm layers than in the layers between 30 and 50 cm. Soil Acari were more abundant in autumn and winter samples in the top 30-cm layers, but there were no seasonal differences in soil Acari abundance in the layers between 30 and 50 cm (Fig. 2). There were no significant seasonal differences in the abundance of soil Acari between the different microhabitats (control, *H. scoparia*, and *Z. dumosum*). The differences in soil Acari abundance between seasons and depths were primarily due to the abundance patterns of the prostigmatid mites. The dominant suborders of Acari were Prostigmata, which accounted for 41% of the total Acari, and Oribatida, which accounted for 55% of the total Acari. Oribatid mites were more abundant in the top 30-cm soil layers than in the 30–50-cm soil layers, but did not differ in abundance between sampling seasons or microhabitats (Fig. 2). These mites were more abundant than prostigmatid mites in all microhabitats. The total number of oribatid mites exceeded the total number of prostigmatid mites by approximately 10 000 individuals m^{-2}, yielding a ratio between them of 0.78 in the upper (0–30 cm) soil layers and 0.74 for the deeper (30–50 cm) layers.

The mesostigmatid and astigmatid mites exhibited seasonal differences in abundance, but no differences between soil depths or microhabitats (Table III). There were few mites of the suborder Astigmata and these were limited to the upper 30-cm soil layers. The astigmatid mites were found in winter in the control and *H.*

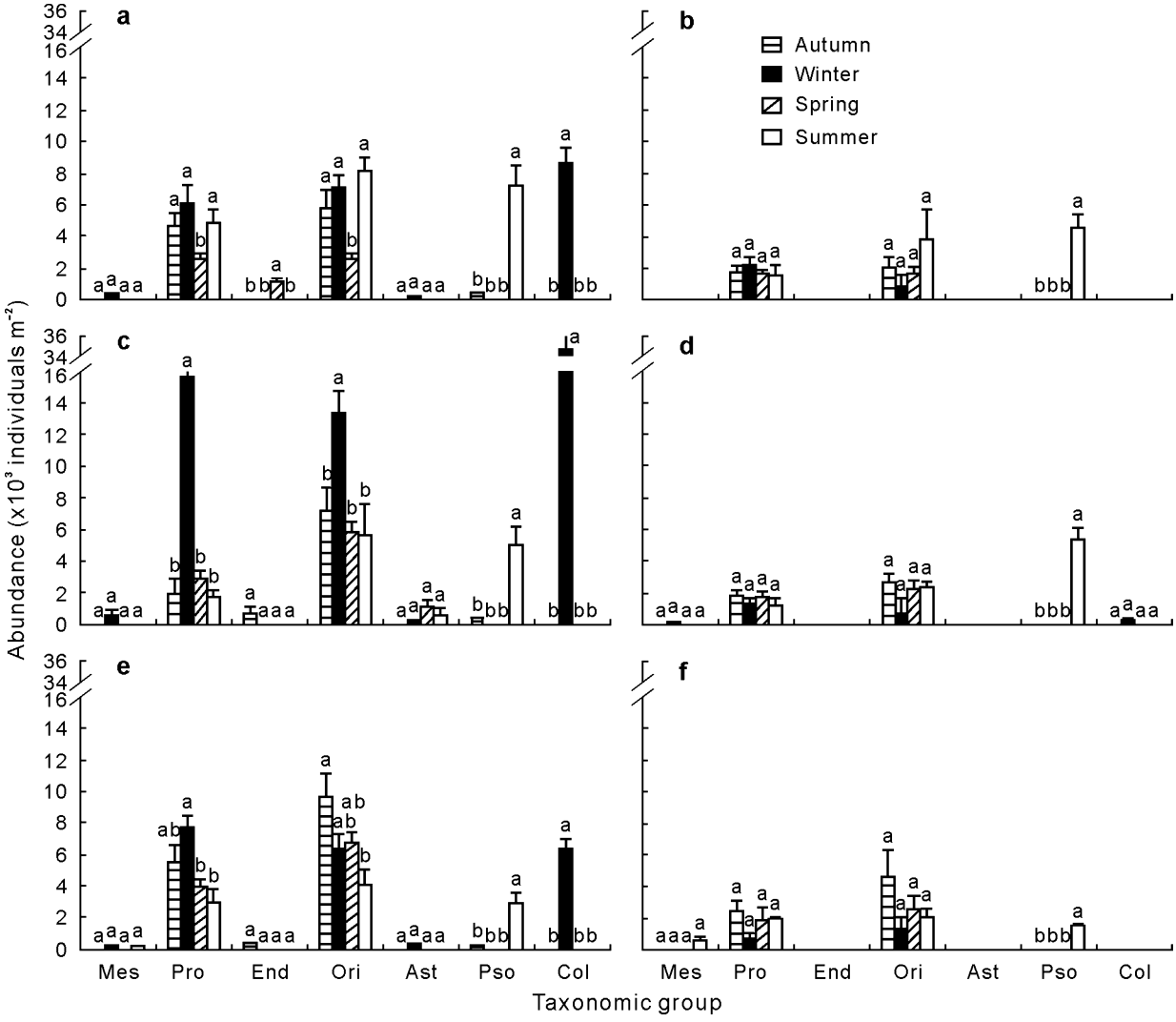

Fig. 2 Changes in mean abundance of each taxonomic group of soil microarthropods found in the three different microhabitats, shrubs (*H. scoparia* (a and b) and *Z. dumosum* (c and d)) and the bare interspaces between shrubs (control) (e and f), during the four sampling seasons in 0–30 (a, c, and e) and 30–50 cm (b, d, and f) soil profiles. Mes = Mesostigmata; Pro = Prostigmata; End = Endeostigmata; Ori = Oribatida; Ast = Astigmata; Pso = Psocoptera; Col = Collembola. Values are means with standard deviations shown by the vertical bars ($n = 4$). Bars with the same letter(s) are not significantly different ($P < 0.05$) between the four seasons.

TABLE III

Results of analysis using repeated measures of analysis of variance (ANOVA) on the abundances (total numbers of individuals collected) of different taxonomic groups of soil microarthropods of three different microhabitats, shrubs (*H. scoparia* and *Z. dumosum*) and the bare interspaces between shrubs (control), during the four seasons in 0–30 and 30–50 cm soil profiles

Taxonomic group	0–30 cm						
	Total number of individuals collected	Season		Microhabitat		Season × microhabitat	
		F value	*P* value	*F* value	*P* value	*F* value	*P* value
Acari	6 026	3.56	0.025 1	0.37	NS[a)]	0.83	NS
Prostigmata	2 467	6.51	0.000 8	0.08	NS	2.68	0.043 7
Endeostigmata	62	1.35	NS	0.21	NS	1.81	NS
Oribatida	3 352	0.92	NS	0.52	NS	1.39	NS
Mesostigmata	66	4.61	0.030 2	0.78	NS	1.16	NS
Astigmata	79	2.11	NS	1.64	NS	1.89	NS
Hexapoda	2 621	2.06	NS	1.65	NS	1.29	NS
Psocoptera	624	43.57	< 0.000 1	2.97	NS	2.16	NS
Collembola	1 997	3.17	0.020 8	1.03	NS	1.98	NS
Total	8 647	2.33	0.048 3	1.04	NS	1.94	NS
Taxonomic group	30–50 cm						
	Total number of individuals collected	Season		Microhabitat		Season × microhabitat	
		F value	*P* value	*F* value	*P* value	*F* value	*P* value
Acari	2 164	1.59	NS	1.60	NS	1.62	NS
Prostigmata	1 020	1.31	NS	0.58	NS	1.45	NS
Endeostigmata	0	–	–	–	–	–	–
Oribatida	1 094	4.07	0.030 2	0.70	NS	2.30	NS
Mesostigmata	37	1.26	NS	1.10	NS	0.70	NS
Astigmata	13	1.30	NS	2.01	NS	1.50	NS
Hexapoda	482	11.23	< 0.000 1	2.40	NS	2.84	0.047 3
Psocoptera	482	28.30	< 0.000 1	1.86	NS	2.20	NS
Collembola	0	–	–	–	–	–	–
Total	2 646	4.73	0.000 9	2.10	NS	1.89	NS

[a)] Not significant.

scoparia soils, and in winter, spring, and summer in the *Z. dumosum* soils. There were no differences in endeostigmatid mites between seasons, soil depths, or microhabitats. Psocopterans were the most abundant hexapods and exhibited significant differences in abundance between both seasons (most abundant in the summer samples) and microhabitat (most abundant under shrubs). Springtails (Collembola) were abundant in winter, but not in other seasons. Springtails were 4 times more abundant in *Z. dumosum* soils than *H. scoparia* and control soils.

Trophic structure. Most of the prostigmatid families are predators, but mites such as tydeids and cunaxids feed on fungi in addition to preying on nematodes (Walter *et al.*, 1988; Walter and Proctor, 2013). The endeostigmatid mites have been reported to feed on algae and fungi (Walter, 1988). Most of the oribatid mites feed on fungi and algae (Krantz and Walter, 2009), with *Oppia* sp. (Oppiidae) and *Zygoribatula* sp. (Oribatulidae) known to prey on nematodes (Mueller *et al.*, 1990; Schneider *et al.*, 2004). Mites of the families Stigmaeidae (36.1%) and Tydeidae (22.5%) were the dominant prostigmatid mites. Stigmaeid mites were found in all samples during summer at all depths and microhabitats. They were also found in 51% of the samples in other seasons. *Haplochthonius* sp. was the dominant oribatid mites and was found in 88.3% of the samples.

There were no obvious variations in distribution patterns of Acari of different feeding habits with soil depths or microhabitats (Table II), while there was a seasonal effect on their abundance (Fig. 3). We found 6 families of obligatory predators, 2 of obligatory fungivores, and 3 of obligatory algivores (Table II). Mites of the other families recorded in this study were not restricted to a single resource and can prey on nematodes, and feed on fungi, algae, or dead plant material. Redundancy analysis revealed that algivores, fungivores, and predators preferred winter, detritivores preferred spring, and macrophytophages preferred autumn (Fig. 3). Two fungivore families, Scutacaridae (Prostigmata) and Terpnacaridae (Endeostigmata),

were found only in the three upper soil layers (0–30 cm) under the canopies of the two shrubs. *Sphaerochthonius* sp. (Oribatida) was found only during winter in the two upper soil layers (0–20 cm) under *Z. dumosum*.

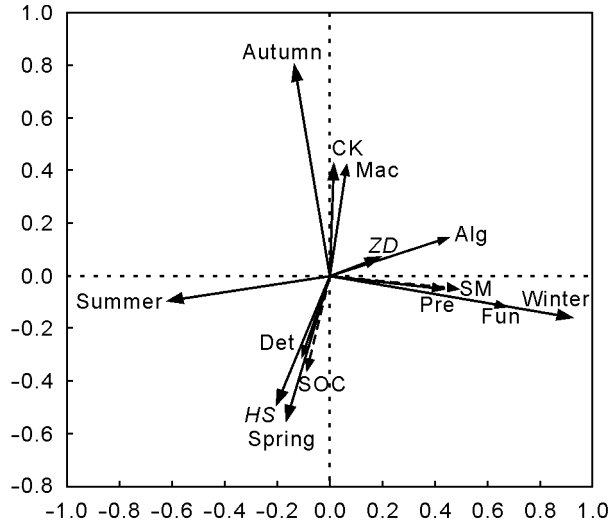

Fig. 3 Redundancy analysis of microhabitats, shrubs (*H. scoparia* and *Z. dumosum*) and the bare interspaces between shrubs (control), and seasons with the groups exhibiting different Acari feeding habits and soil parameters. *HS* = *H. scoparia*; *ZD* = *Z. dumosum*, CK = control; Pre = predators; Alg = algivores, Fun = fungivores; Mac = macrophytophages; Det = detritivores; SM = soil moisture; SOC = soil organic carbon.

Taxonomic richness and diversity. There was a decreasing trend in the taxonomic richness of soil microarthropods (Table IV) in the deeper layers (30–50 cm) compared to the top (0–30 cm) layers. The highest number of taxa was recorded in the three upper layers (0–30 cm) during winter in all three microhabitats. In the subphylum Hexapoda, collembolans were only found in the two upper layers (0–20 cm), while psocopterans were found in nearly equal numbers at all depths and microhabitats. The diversity as demonstrated by the Shannon index results varied with seasons in the different microhabitats. The lowest values of Shannon index was found under *Z. dumosum* during summer, while during winter it was the highest. As shown by the taxonomic richness, the highest diversity in all three microhabitats was also found during winter. The values of evenness were remarkably high, with no significant variations between the microhabitats.

DISCUSSION

The soil biota in general, and microarthropods in particular, are known to play an important role in decomposition processes and nutrient cycling in terrestrial ecosystems (Petersen and Luxton, 1982). Microarthropods also play a crucial role in the context of soil biodiversity (André *et al.*, 2002). Their abundance is influenced by several abiotic factors, such as soil moisture, temperature (Steinberger and Wallwork, 1985), and organic matter content (Loots and Ryke, 1967). Water and organic matter are known to be major factors that limit soil biotic distribution in xeric environments (Whitford, 2002). The results of this study confirm the seasonal stability of soil moisture and organic carbon in soil below 30-cm depth and the mites being more abundant in the upper 30-cm soil layers than the layers below 30 cm. Seasonal variations in both soil moisture and organic carbon in the top 30-cm soil layer were reflected in the variations in abundance of soil mites and collembolans. The highest densities of microarthropods were in the top 10-cm soil in winter from all three habitats studied. This was due to higher soil moisture in this layer, the result of a rain event earlier in the sampling week. The lowest densities were recorded in deeper soil layers below 30 cm in winter,

TABLE IV

Taxonomic richness (TR), Shannon index (H'), and evenness (J') of the Acari community of three different microhabitats, shrubs (*H. scoparia* and *Z. dumosum*) and the bare interspaces between shrubs (control), during the four seasons in 0–30 and 30–50 cm soil profiles

Index	Microhabitat	Autumn		Winter		Spring		Summer	
		0–30 cm	30–50 cm	0–30 cm	30–50 cm	0–30 cm	30–50 cm	0–30 cm	30–50 cm
TR	Control	5.7b[a)]	4.0c	6.7b	3.5cd	4.3c	3.0cd	4.3c	4.0c
	H. scoparia	4.3c	2.0d	6.0b	4.0c	3.3cd	4.5c	4.3c	4.5c
	Z. dumosum	3.0cd	3.0cd	9.3a	3.5cd	4.0c	4.0c	3.7cd	2.5d
H'	Control	1.3b	1.1bc	1.4b	1.2b	1.2b	0.9c	1.1bc	0.9c
	H. scoparia	1.1bc	0.7c	1.2b	1.2b	1.1bc	1.3b	0.9c	1.0c
	Z. dumosum	0.9c	0.9c	1.6a	1.1bc	1.2b	1.2b	0.8c	0.5d
J'	Control	0.7b	0.8a	0.8ab	0.9a	0.8ab	0.9a	0.8ab	0.8ab
	H. scoparia	0.8ab	1.0a	0.8ab	0.9a	1.0a	0.9a	0.6b	0.7b
	Z. dumosum	0.8ab	0.9a	0.7b	0.9a	0.9a	0.9a	0.7b	0.6b

[a)] Values followed by the same letter(s) are not significantly different at $P < 0.05$ within each index.

possibly reflecting vertical movement toward the wetter surface. During the other seasons, microarthropods were more abundant in the deeper soil layers, apparently because they prefer the higher moisture level and/or more moderate temperature in those layers in comparison to the top 10-cm soil layer (Steinberger and Wallwork, 1985). The seasonal patterns of microarthropod abundance may be more related to soil temperature than to soil moisture since soil moisture in the upper 30 cm was relatively high during the cool winter rainy season, but fluctuated a little during spring, summer, and autumn. Experimental studies in the Chihuahuan Desert reported that soil microarthropods responded more directly to temperature than to variation in soil moisture (MacKay *et al.*, 1986). Soil temperature has also been shown to be the most important driver for vertical migration of desert microarthropods (Mackay *et al.*, 1987). In deserts, soil temperatures at depths below 30 cm change very slowly (Whitford, 2002), which, combined with the relative stability of soil moisture and soil organic carbon, accounts for the relative stability of the microarthropod populations at soil depths greater than 30 cm.

In the dry seasons in the Negev Desert, dew formation is the main trigger of soil biotic activity, but it is limited to the very top soil layer. Studies on vertical movement of microarthropods, population dynamics of nematodes, and changes in microbial community activity and density through diurnal sampling in the upper 30-cm soil layer in the Negev Desert by Steinberger and Wallwork (1985) and Steinberger *et al.* (1988), during the dry period, suggest that the summer season abundance of microarthropods might, in part, result from direct and indirect effects of dew formation.

Our data did not support the hypothesis that soil microarthropod community abundance and diversity would be greater under the shrub *H. scoparia* in comparison to *Z. dumosum* due to dissimilarity in annual plant abundance. Such distinctions raise questions regarding the influence of the divergence in their ecophysiological adaptation on the microarthropod community composition in general. The most surprising result of this study was the absence of significant differences in the abundance of soil mites between the bare interspace soil and soil under shrubs (Table II). This result was probably caused by the fact that in most of the samples, there were no significant differences in soil moisture between the three habitats. Moreover, it was higher in some soil samples from the bare interspaces. To our surprise, the same trend was found for the soil organic carbon results in most of the samples. Combined together, these two parameters suggest that the soil conditions under the canopy of the shrubs and in the bare interspaces were not very different during the study period. Most microarthropod studies conducted in arid regions report relationships between plant litter accumulation and abundance and diversity of microarthropods, with large differences in abundance and diversity of soil microarthropods between the shrub species and bare interspace soils (Santos *et al.*, 1978; Franco *et al.*, 1979; Wallwork *et al.*, 1985; Cepeda-Pizarro and Whitford, 1989; Noble *et al.*, 1996). This pattern of abundance and diversity has been considered to be a function of differences in resource concentrations in these habitats. The significant seasonal differences in the abundance of oribatid mites and psocopterans in the soils under *Z. dumosum* can be due to the wide canopy of this shrub that modifies soil temperature by shading and also reduces the evaporation rate of rainfall and dew.

Taxonomic richness was found to be strongly related to seasons, with the highest number of families in the cool winter rainy season (Table IV). The abiotic conditions determine the activity of the different feeding groups. Predators were found to prefer the winter season, when the populations of fungivores and algivores had their highest numbers. There appears to be a relationship between spring soil moisture and temperature as well as soil organic carbon and the abundance of detritivores.

The pattern of the oribatid mites being more abundant than the prostigmatid mites in this study was not related to the organic carbon content of the soils. The relationship of the ratio of the oribatid mites to the prostigmatid mites (less than 1) with soil organic matter content was first described by Loots and Ryke (1967). Oribatid mites dominated the soil Acari communities in Chihuahuan Desert habitats, where soil organic matter content was greater than 20 g kg^{-1} (Wallwork *et al.*, 1985). In the Australian scrublands, prostigmatid mites were dominant at all sites, ranging from 92.7% of the microarthropods in soil under a cryptogamic crust to 63.8% of the microarthropods in an *Acacia aneura* shrubland (Noble *et al.*, 1996). Soils under *A. aneura*, which has a sparse canopy, have a low organic carbon content, thereby supporting a hypothesis that oribatid mites dominate the soil Acari communities in soils with relatively high organic matter content (Loots and Ryke, 1967). Prostigmatid mites were dominant in other studies in the Negev Desert, where soil samples were collected from under upland shrubs with soil organic carbon being generally less than 10 g kg^{-1} (Steinberger and Wallwork, 1985; Steinberger, 1990). The data from the present study differed from

other reports where the presence of oribatid mites was related to relatively high soil organic matter. Soil organic matter in arid systems depends upon litter and organic debris production by shrubs such as *H. scoparia* and *Z. dumosum*. Litter production by these shrubs exhibits a lag based on the rainfall of the previous year.

The diversity of prostigmatid mite families recorded in this study (9 families) is much lower than those recorded in a North American desert (21 families) (Elkins and Whitford, 1982; Cepeda-Pizarro and Whitford, 1989) and a Australian desert (19 families) (Noble *et al.*, 1996). The low diversity of prostigmatid mite families in the Negev Desert may be the result of competition with the more abundant oribatid mites. The diversity of oribatid mite families was nearly the same in the Negev Desert, the North American desert (Elkins and Whitford, 1982; Cepeda-Pizarro and Whitford, 1989), and the Australian desert (Noble *et al.*, 1996), suggesting that the oribatid mite families have adapted to arid environments. The dominant prostigmatid mite family in a variety of habitats in the Chihuahuan Desert of North American (Elkins and Whitford, 1982; Cepeda-Pizarro and Whitford, 1989) and at most sites of the Australian desert (Noble *et al.*, 1996) was Tydeidae. Mites of the family Stigmaeidae were abundant (24% of the total mites) only in soils with a cover of annual grasses, but represented less than 2% of the total mites in all the other locations and habitats sampled in Australia (Noble *et al.*, 1996). Stigmaeid mites occurred in a few habitats in the Chihuahuan Desert of North America and never accounted for more than 1% of the Acari fauna. Comparisons of dominant families of mites in arid regions of different continents are problematic because the species of those families have evolved with very different selective pressures in each location.

CONCLUSIONS

The spatial and temporal variations of soil microarthropods under desert shrubs were studied in order to evaluate the vertical distribution of their density and diversity throughout the seasons. The data obtained elucidated the strong relationship between the microarthropod community and depths and seasons. The microarthropod community was found to be dominated by oribatid mites. These results are opposite to those obtained in other studies in similar xeric environments. Moreover, our data were not found to be in line with our hypothesis that a better microhabitat played a major role in microarthropod community composition, diversity, and density. Therefore, desert shrub litter, which plays an important role in enhancing organic matter, should be strongly affected by previous total yearly rainfall and its distribution. In order to be able to determine such a relationship, a long-term study should be initiated.

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