Microbial Ecology

Seasonal Changes in Free-Living Amoeba Species in the Root Canopy of *Zygophyllum dumosum* in the Negev Desert, Israel

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Abstract

The influence of seasonality and *Zygophyllum dumosum* root canopy on the species diversity of free-living amoebae at two soil depths (0–10 and 10–20 cm) was studied in a Negev Desert ecosystem in Israel. Free-living amoebae were extracted and identified after cultivation in non-nutritive agar plates. A total of 90 amoeba species were identified in the soil during the study period, with the most common genera present being *Hartmannella, Platyamoeba, Vahlkampfia, Acanthamoeba*, and *Echinamoeba*. Differences between the control soil and the soil under *Z. dumosum* were found mainly during the dry seasons, when 97% similarity was found between the two soil layers, which could be due to the effect of the shrub on the soil microenvironment. The amoeba community exhibited more species diversity in spring (reaching a value of 34 species) than in the winter (18 species) or summer and autumn (20 species), since the community has a time lag for becoming stabilized after the dry summer and autumn. This is one of the first studies on the amoeba population in the Negev Desert and elucidates the importance and the need for taking trophic and functional groups into consideration in order to understand biomineralization processes.

Introduction

A common feature of desert ecosystems is low soil moisture availability, extreme temperature, and high radiation. In the Negev Desert, water availability, which is one of the most important triggers for biological activity, is unpredictable in time, amount, and frequency and is limited to the rainy seasons, which occur during very short periods and produce runoffs and floods [7]. Dew formation is an additional source of water and allows biological activity during the long dry season. This moisture source has a short-term effect with high effectiveness for biotic activity [7, 9].

In such harsh environments, perennial desert plants form ''fertile islands'' greater in biological activity than the spaces devoid of vegetation [13, 14, 23, 28]. Moreover, below ground vegetation growth in the rhizosphere provides suitable niches for soil biotic activity inducing nutrient turnover. Campbell et al. [2] elucidated that the plant rhizosphere increases biotic activity and may sustain higher diversity during the growth season. In his study, Tilman [27] asserted that species richness is also a community attribute related to stability, productivity and the trophic structure of food webs.

Perennial slow-growing and long-living shrubs, such as *Zygophyllum dumosum*, which is well-known as an arido-active shrub, dominate the scattered vegetation of the Negev Desert Highlands [7, 9]. Their success is due mainly to their physiological adaptation and to the development of two functional root systems that become active at different depths and times [11]. These plants can thus utilize the high water variability [6, 19] producing strong effects on the microbial/fungal ratio throughout seasons [11, 24, 25, 28].

Nutrient availability in both layers is mainly due to root exudes and litter decomposition mediated by the underground food webs.

Protozoa are one of the links between the microflora and mesofauna in the soil food web. Prey preferences have been described for several groups of soil protozoa covering all groups of microorganisms. Because of this important feeding feature, protozoan species richness may change spatially and temporally in response to sea-

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sonal changes and food source availability [8]. However, the effects of major ecological processes such as competition, succession or predation play an important role in population dynamics and diversity [18, 26, 29]. Free-living amoebae are one of the main groups known to be microbial grazers in soil, since they move easily through the pore spaces. They may feed selectively on bacteria, fungi, algae, yeasts, other protozoa, and microbial multicellular organisms such as rotifers or nematodes [16, 20]. However, despite their importance in the soil nutrient cycle, very little is known about the effect of seasonal changes on the species diversity of amoebae inhabiting desert soil systems. Even less is known about the implications of the *Z. dumosum* rooting pattern on the biodiversity of soil amoebae.

The aim of this study was to elucidate seasonality and the effects of *Z. dumosum*'s canopy soil on the species diversity of free-living amoebae in a desert soil ecosystem. Based on the above knowledge, we hypothesized that species diversity would be strongly affected by seasonal changes, moisture availability and plant root canopy.

Materials and Methods

Study Site. The study site is located at the M. Evenari Runoff Study Farm (30 47′, 34 36′ E) Avdat, in the Negev Desert, Israel. This site is ~600 m above sea level, with a multiannual average rainfall of 90 mm (Avdat Station). This area consists of loess plain rocky slopes with shallow, saline gray lithogenic calcareous soils. The soil is alkaline (pH 7.8) with a deep fine-textured loessial sierozem [5] containing low amounts of organic carbon (0.47%) and high amounts of carbonate (40%). The climate is Mediterranean, with mild rainy winters (5–14°C in January) and hot summers (18–32°C in June). The rainy season usually begins in October and ends in late April, with most of the rainfall occurring in scattered showers between December and February. An additional moisture source comes from dew deposition, which accounts for ~35 mm a year and occurs heavily during 210 nights in late summer and autumn. The annual evaporation rate is 2615.3 mm a year [7].

Soil Sampling. Soil samples were taken during the four seasons of 2001: winter (February), spring (May), summer (August), and autumn (November). Four *Z. dumosum* shrubs were randomly selected at the study site and canopy soil samples were collected at layers of 0 to 10 cm, and 10 to 20 cm. Four soil cores at similar depths were also taken from the interspaces between the shrubs as control samples.

The soil samples collected were placed in individual plastic bags and were protected from overheating by placing them in an insulated container during collection and transport from the field to the laboratory. At the laboratory, the soil samples were kept in cold storage (4°C) until processed. Subsamples from each depth were analyzed for moisture and free-living amoeba populations.

Identification of free-living amoebae was accomplished after cultivation in nonnutritive agar plates. Neither live nor dead bacteria were added to the medium, in order to avoid the overgrowth of bacterial-feeder amoebae over those that feed on different sources such as yeasts, fungi, algae, protozoa, and/or other organisms. Soil extract was prepared by suspending 200 g soil collected at the study site in 1000 mL tap water. It was left at 4°C for 7 days, then filtered and autoclaved for 15 min at 121°C and 1.1 kg cm^{-2} pressure. A 1:5 dilution of soil extract in sterilized tap water was used to avoid toxicity to any organisms, as explained by Bamforth [1]. The initial cultivation was performed by homogenizing a 1-g soil sample in 10 mL soil extract to a final dilution of 1:10. Homogenates were then left untouched for 30 min for particle sedimentation, and the supernatant was gently transferred onto bacteria-free nonnutritive agar plates. Cysts and trophozoite individuals that remained attached to the bigger soil particles after homogenization may be lost for cultivation in the sedimentation step.

Amoebae were allowed to settle on the agar for 2 h before withdrawal of the excess water, avoiding ciliate and flagellate growth. Cultivates were identified under a binocular microscope after 15 days of incubation at 26°C. The strains were identified by using a phase contrast microscope, following the morphological Keys for Gymnamoebae and Protozoa [15–17]. Flagellation tests were carried out for determining the genus of the Vahlkampfiidae family and measures of 50 cysts and trophozoites were registered. Strains that did not correspond to any morphological description were registered as "sp."

Amoebae species were recorded as presence–absence for each replicate and the isolation frequency matrix of species and genus was used for data analysis.

Statistical Analysis. Data matrixes of the total number of species were analyzed by two-way ANOVA ($p = 0.05$) with the different seasons serving as one factor and the different soil depths as the other. In this case, depths were treated as independent from each other, since there is no experimental evidence of protozoan migration in soil [10]. Sørensen's Similitude Index was used for exploring the relation between the study sites due to species similarities. This analysis was carried out using PCord software ver. 4.0 for Windows (MJM Software Design, Gleneden Beach, OR).

Results

Soil moisture content was found to be significantly different ($p < 0.001$) between seasons, without any significant difference between samples, reaching the highest

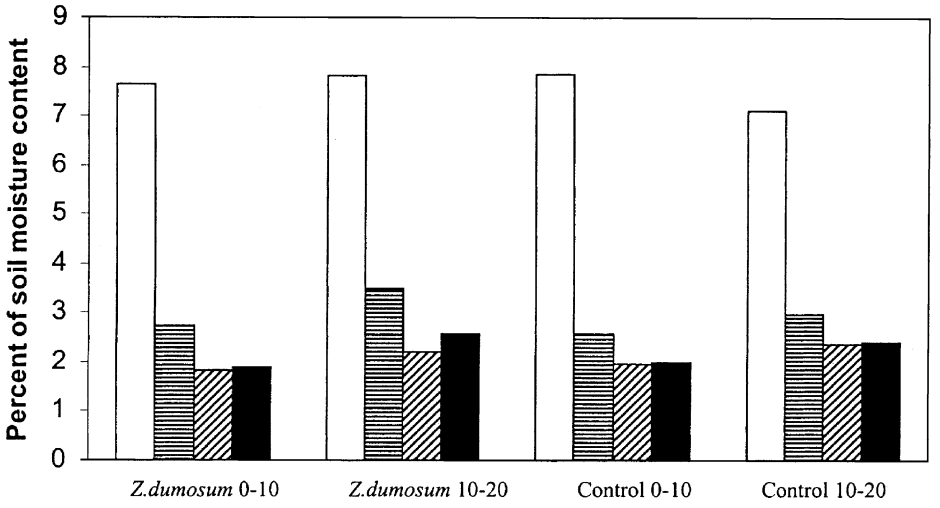

Figure 1. Soil moisture content during winter (□), spring (▤), summer (▨), and autumn (■), 2001, in Negev Desert soil.

moisture value in winter (8%) and the lowest (1.2%) in summer (Fig. 1). Soil moisture content found to be significantly correlated with the number of genera only at the 10–20 cm layer under *Z. dumosum* ($r = 0.61$). However, no correlation was found between soil moisture content and the number of species.

A total of 90 amoeba species were identified in the soil layer under *Z. dumosum* during the sampling period. These 90 species belong to 32 genera and 18 families (Table 1). Based on the description by Page [15, 16] and Patterson [17], 55 species were identified, fitting the characteristics for species determination. An additional 35 strains could be identified only to the level of genus, since they did not fulfill morphological characteristics of any species reported in the available keys. The rank of species curve was found to fit the lognormal distribution ($\chi^2 = 3.97$; $df = 6$; $p > 0.5$) [12].

The most common genera were *Hartmannella, Platyamoeba, Vahlkampfia, Acanthamoeba*, and *Echinamoeba*, since 70% of the isolations from the control soils and 50% from the *Z. dumosum* root canopy belonged to these taxa. The strains belonging to these genera were consistently present in most of the soil samples, while the remaining 27 genera accounted for 30% and 50% of the isolations, respectively.

The species followed the same pattern as the genera, with rare species accounting for 47% of the isolations. The species with the highest number of isolations were *Vahlkampfia aberdonica* (57%), *Hartmannella vermiformis* (53%), *H. cantabrigiensis* (53%), *Platyamoeba stenopodia* (52%), and *P. placida* (47%). However, they accounted for only 5% of the total number of identified species. In contradistinction, 66% of the species were found only 1 to 10 times during the study period.

There were no significant differences ($p = 0.5$) in the number of species neither in rhizospheric and nonrhizospheric soil samples nor between the two layers (0–10 cm and 10–20 cm) during the spring. However, the genus composition of the amoeba community exhibited significant differences ($p < 0.01$) under *Z. dumosum* and the control samples in summer, autumn, and winter (Fig. 2a). These differences in genus presence were also significant between the two corresponding layers ($p < 0.01$) during the same seasons.

A close analysis of the microenvironment provided by the plant demonstrated that the number of genera remains very constant throughout the year (Fig. 2a) and the species number is more stable under *Z. dumosum* than in the control soil. The total number of genera in the surface layer under the shrub (0–10 cm) was found to be similar throughout the year. In the deep layer (10–20 cm), the number of genera reached its maximum in spring, accounting for 17 genera, decreasing to a minimum of 14 genera toward autumn (Fig. 2a). The number of genera found in the control soil samples was significantly ($p < 0.05$) lower during the winter, summer, and autumn seasons than in the root canopy sample taken under *Z. dumosum*. However, a similar number of genera were obtained from the control soil and under the *Z. dumosum* shrub during the spring sampling.

The number of amoeba species found in the control soil samples in the winter season reached a mean value of 18 species and increased significantly to 34 species in spring in both layers (Fig. 2b). Toward the summer and autumn seasons, the number of species decreased to ~20 species in both depths (Fig. 2a).

The pattern of richness varied by site ($p < 0.001$) and season. More species were found in the *Z. dumosum* canopy soil at both depths than in bare soil. The deeper soil under *Z. dumosum* contained fewer species in winter, which was opposite of the more shallow depth. Generally, fewer species occurred in bare soil than in soil with

Table 1. List of amoebae in the *Z. dumosum* (Zd) root canopy and in control soils (Cs)

				Zygophyllum dumosum								*Control*							
				0–10 cm				*0–20 cm*				*0–10 cm*				*0–20 cm*			
Class	*Family*	*Species*	*Feeding habits*	*W*	*SP*	*S*	*A*	*W*	*SP*	*S*	*A*	*W*	*SP*	*S*	*A*	*W*	*SP*	*S*	*A*
Filosea																			
	Arachnulidae	*Arachnulla* sp.	F					1			1								
	Nucleariidae	*Nuclearia*sp.	F-A		2	1			1		2						1		
Granuloreticulosa																			
	Biomyxidae	*Biomyxa* sp.	P		1	1									2				
		B. vagans	P							1									
		Gymnophris sp.	P										1				1		
Heterolobosea																			
	Acrasidae	*Acrasis* sp.	Y	1															
	Guttulinidopsidae	*Rosculus ithacus*	B										3						1
	Vahlkampfiidae	*Naegleria gruberi*	B	2	2		2	1					1			1	1		
		Naegleria sp.	B			1	1		2	2	2				2				
		Paratetramitus jugosus	B		2		1		3	4			1	4		1	3	4	1
		Tetramitus rostratus	B	1				2	2							2			
		Vahlkampfia aberdonica	B	4	4	4	3	4	4	4	3	3	4	4	3	4	3	4	2
		V. avara	B	3	3	4	1		2	4	1	1		3			1	2	3
		V. debilis	B	3	2	2	1	2	3	2	2		1		1	2	2	1	1
		V. enterica	B	3	4		2	3	4	1	2	2	2	1	1	3	2	1	
		V. erythaenusa	B					1	1								1		
		V. froschi	B						1										
		V. hartmanni	B														1		
		V. inornata	B						1										
		V. lacustris	B			1	2	4		2			1					1	1
		Vahlkampfia sp1	B	2				1	2	1		3	1	1		3	1		
		Vahlkampfia sp2	B	2															
		Vahlkampfiidae sp3	B										1						
		Vahlkampfiidae sp4	B										1						
		Vahlkampfiidae sp5	B						1	2									
Lobosea																			
	Acanthamoebidae	*Acanthamoeba castellanii*	O		1	1							1						
		A. culbertsoni	O	2	1	3	2			1	2	1	3	2	2			3	
		A. hatchetti	O							1	2		3					1	
		A. lenticulata	O	1	1	2	2		1	2	2		1	2	2			2	
		A. palestinensis	O																
		A. polyphaga	O	1	1	2	1			2	3		1	1	3			4	
		Acanthamoeba sp1	O	2	2	2	1		1	2	4		4	3	2		1		1
		A. traingularis	O	1							1				1				
		Acanthamoeba sp. GII	O		2			2							1		1		
		Acanthamoeba sp. GIII	O		3		3			1	2	2							
	Amoebidae	*Amoeba diminutiva*	B					1											
		Amoeba sp	B				1		2		1								
	Hartmannellidae	*Cashia limacoides*	B-Y			1	2								1		1		
	Paramoebidae	*Dactylamoeba* sp.	P-A	2															
	Thecamoebidae	*Dermamoeba minor*	F							1									
	Echinamoebidae	*Echinamoeba exundans*	B		3	2	4		4		3	1	3		3	1	2	2	2
		E. silvestris	B	1	3	2	3	1	4		3	2	4	1	1		3	4	
		Echinamoeba sp1	B	2								2				1			
	Echinamoebidae	*Filamoeba nolandi*	B		1	1	1		1	1				1		1			1
		Filamoeba sp.	B	1		1													
	Hyalodiscidae	*Flamella* sp.	P			2								1					1
	Gephyramoebidae	*Gephyramoeba* sp.	P				1		2								1		
	Hartmannellidae	*Hartmannella cantabrigiensis*	B	2	3	4	3	4	3	4	3	2	4	4	4	3	2	4	4
		Hartmannella sp.	B					2				3	1						
		Hartmannella spg	B			1				2				2				2	1
		Hartmannella sps	B	2		1			1							3			
		H. vermiformis	B	4	4	4	3	4	3	4	4	4	3	4	3	4	4	3	3
	Leptomyxidae	*Leptomyxa reticulata*	P					1											
		Leptomyxa sp1	P				1												
		Leptomyxa sp2	P				1												

(Continues)

Table 1. Continued

				Zygophyllum dumosum								*Control*							
				0–10 cm				*0–20 cm*				*0–10 cm*				*0–20 cm*			
Class	*Family*	*Species*	*Feeding habits*	*W*	*SP*	*S*	*A*	*W*	*SP*	*S*	*A*	*W*	*SP*	*S*	*A*	*W*	*SP*	*S*	*A*
	Paramoebidae	*Mayorella cantabrigiensis*	P-A		1														
		M. cultura	B		2	1	2	4	1		2		2		1	2			
		M. microeruca	B		2			1	1										
		M. penardi	P-A			1			1										
		Mayorella sp.	B	2	3	1		1	2			2					1		
	Vannellidae	*Platyamoeba placida*	B	3	3	4	4	4	3	4	4	1	3	4	4	1	2	1	3
		Platyamoeba sp1	B	2	1			2					1						
		Platyamoeba sp2	B		1	2			2	1	2			1					
		Platyamoeba sp4	B			1				1	1			1			1	3	1
		P. stenopodia	B	4	3	4	3	4	3	4	4	2	3	3	3	4	3	4	1
	Amoebidae	*Polychaos timidum*	P-A		3		1		3	2			1				2		1
		Polychaos sp.	P-A														1		
	Leptomyxidae	*Rhizamoeba autraliensis*	P	4	1							3				2			
		Rhizamoeba sp.	P			1				3			1	1		2			
	Hartmannellidae	*Saccamoeba stagnicola*	A-B		3				2	1	2		2				2		
		S. limax	B	1															
		Saccamoeba sp.	B			2	1			1	1								
	Thecamoebidae	*Sappinia diploidea*	F	3															
		S. pedata	F																1
		Thecamoeba quadrilineata	B		2	2				1	2		1						1
		T. similis	P		4	1	1		1		1								
		Thecamoeba sp.	B		1	1													
		T. striata	P			2													
	Vannellidae	*Vannella cirrifera*	B	1															
		V. lata	B	1					1								1		
		V. mira	B					1						1					
		V. platypodia	B	1		2	1		1	2	2	2	1		2		2		2
		Vannella sp.	B	1		2			1	1				1				1	1
	Vexilliferidae	*Vexillifera telma*	B														1		
		V. variabilis	B	1	1								1				3		
	Testacea-Lobosea																		
	Cochliopodiidae	*Cochliopodium bilimbosum*	Y		2	2			2	2	1					1	2		
		C. minus	Y	3	4		2	1	1			2	2			1	1		
		G. obscura	Y-B							2									
		Gocevia sp.	Y-B							1									

The values are the total frequency of isolation in the four repetitions from samples taken in winter (W), spring (SP), summer (S), and autumn (A) 2001 at Avdat, Negev Highlands, Israel. Feeding behavior of species were determined by their main source of food as bacteria (B), filamentous fungi (F), yeasts (Y), algae (A), protozoa (P), and omnivorous (O).

plants. Bare soil contained most species in the surface layer in spring compared to greater depths or other seasons (Fig. 2b).

Winter samples from control and root canopy sites were found to be completely different from the other seasons, as assessed by the Sørensen analysis (Fig. 3). Samples from the other three seasons formed two clusters. The spring samples exhibited the maximum similarity between the control and root canopy sites (87% similarity at the 10 cm depth and 80% similarity at the 20 cm depth). These similarities between above- and below-layers of root canopy and control sites are mainly due to soil moisture. The second cluster is the result of plant microniche contribution. During summer and autumn, the sites exhibited higher similarity between the sites (Fig. 3), being the highest in the control site in summer (100% similarity), and the root canopy site in autumn (96% similarity).

Discussion

The soil amoeba community in the Negev Desert can be considered to be highly diversified. A total of 90 species was found during the study period in the soil samples taken from the Negev Desert soil. These numbers are significantly ($p < 0.05$) higher than the 60 species reported by Rodriguez-Zaragoza and Garcia [19] in the Tehuacan Desert of Mexico. This difference may be explained, at least partially, by the more coarse taxonomic identification used in other studies. The species diversity and population dynamics of soil protozoa have been the main focus in very few studies [4]. The scarcity of soil

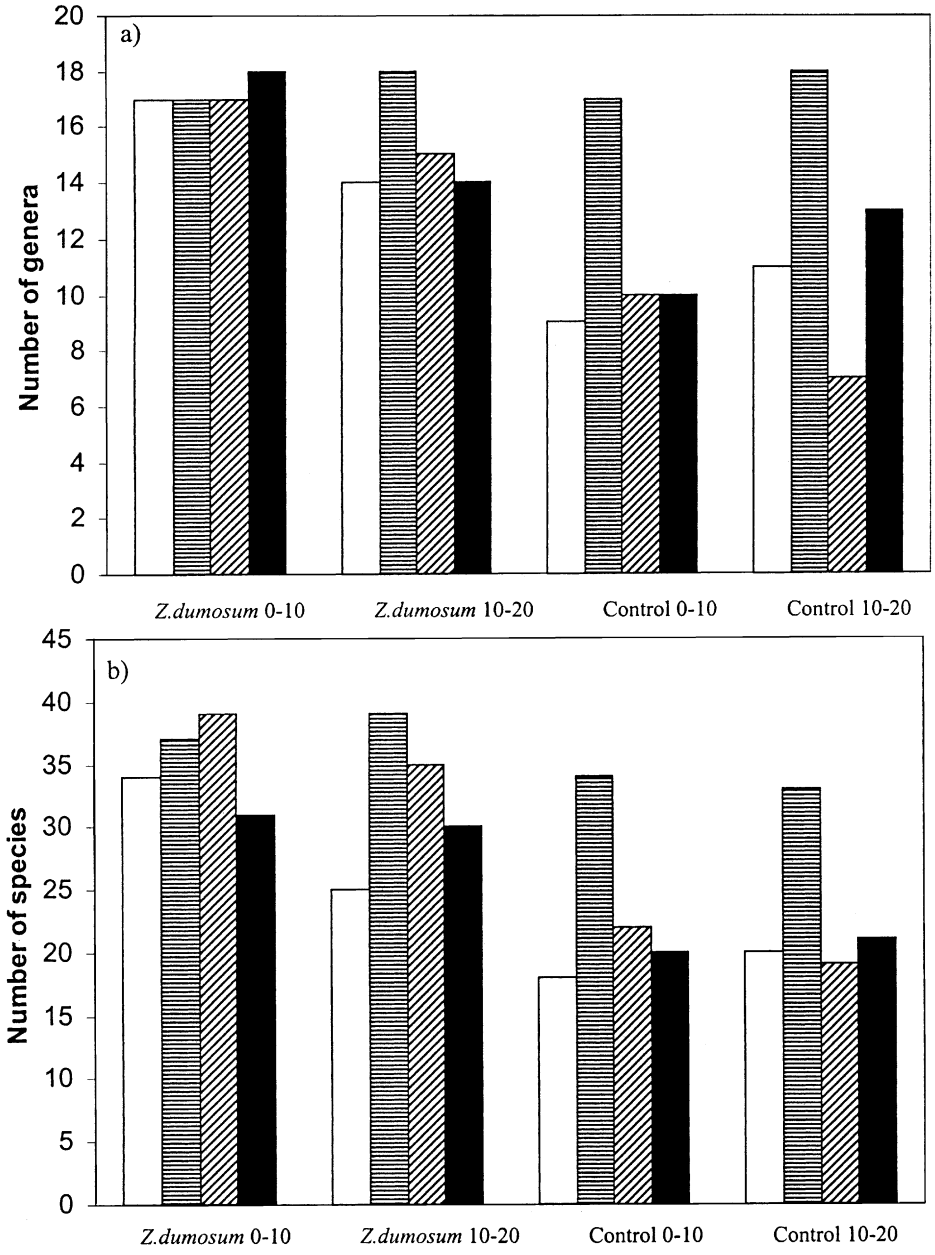

Figure 2. Number of genera (a) and species (b) present in soil under *Z. dumosum* was very stable in the 10-cm layer under the shrub and variable in the control soils throughout the year. The seasons are shown, from left to right, as winter (□), spring (▤), summer (▨), and autumn (■).

amoeba species reported in the literature is also due to the rarity of such studies, which may mislead one to think that this group is poorly represented in soil. In fact, their abundance in soil is usually high.

The highest number of species in spring corresponds to a well-timed system where above- and below-ground production is relatively high, allowing the amoeba community to fulfill its biological functions. Since amoebae demonstrate prey preferences, allowing their classification into trophic groups, they may appear along with their preferred prey such as bacteria, fungi, algae, yeasts, protozoa, or other organisms of comparable size.

The community of all of these groups fed upon by amoebae is separated in space and time [21], appearing in soil on a successive basis. This may explain why the amoeba community is more diverse in spring, when the microfauna soil population is already established and has reached large populations [22].

The utilization of bacteria-free, nonnutritive agar plates may be another possible explanation for the high number of species found in this study. Addition of bacteria exerts a strong selective pressure against nonbacterial feeders, which may be overgrown by the voracious species grouped in genera such as *Acanthamoeba, Rosculus*, or *Vahlkampfia*. This may also explain why these genera are so widely reported in the literature. Furthermore, the extension of time for observing amoebae after seeding facilitated the detection of the slow-growing species.

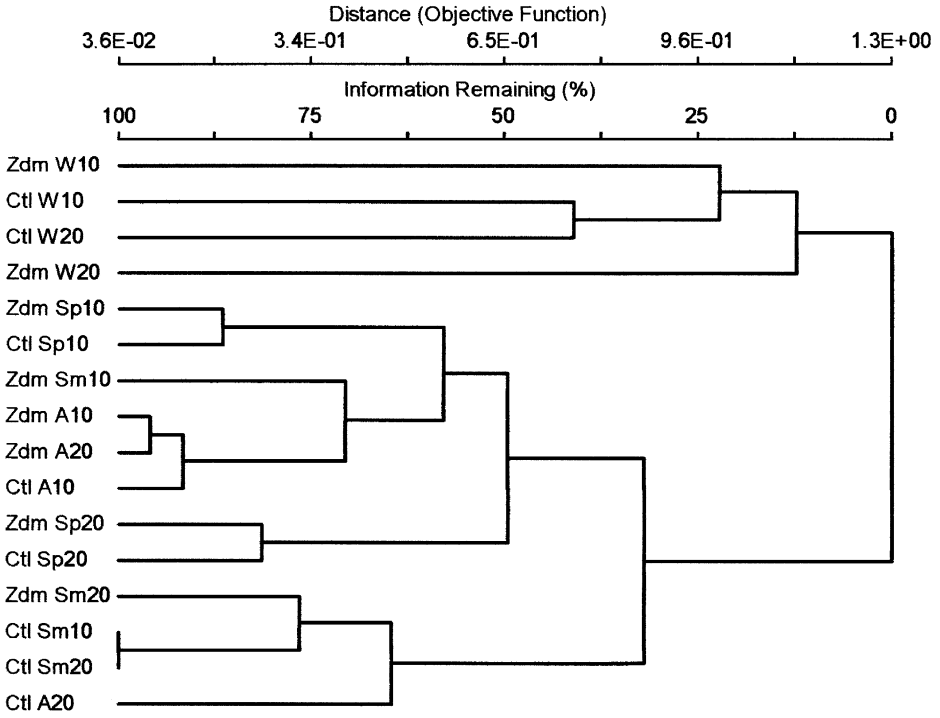

Figure 3. Sørensen's similitude index based on species presence–absence in the soil samples collected at different locations. The dendrogram was chained by the group average method. The site code is referred by site, season and depth as follows: Sites are referred as Zdm = *Z. dumosum* and Ctl = Control site; W = winter, Sp = spring, Sm = summer, A = autumn; soil depths are referred as 0 to 10 and 10 to 20 cm layer following the site and season.

Vahlkampfia, Hartmannella, Echinamoeba, Platyamoeba, Mayorella, Acanthamoeba, and *Vannella* were the most common genera in this study (from the most to the least frequent). All of them are reported as the most common genera from many stressed and unstressed environments, as discussed by Rodriguez-Zaragoza [20] and Côuteaux and Darbyshire [4]. The genus *Acanthamoeba* is found most frequently in those stressed environments. However, in desert soil its frequency is lower than that of *Mayorella*, which is a non-cyst-forming genus. The presence of these different genera is therefore due to other factors in addition to water availability.

Among the species isolated in the Negev, 35 strains could not be assigned to a known or described species as reported in the literature. Keys for identification of naked amoebae are scarce and descriptions of new species from marine, freshwater, or soil environments are scattered. The study of the diversity of soil protozoa, especially naked amoebae, is woefully incomplete and needs to be addressed in the near future for better understanding of the functional groups and their relationship with the soil nutrient cycle.

Variations of genera and species in winter and spring may be attributed to the community's time lag for becoming stabilized after the dry summer and autumn. These dynamics are related to the general tendency observed for the establishment of microfauna communities in soils after wetting. Although amoebae appear 1 or 2 days after wetting, their populations become stabilized after several days [3]. The same is observed with mesofauna communities: they appear later after the first wetting events, but they also become stabilized after one to several weeks. This suggests that the soil community forms a continuum that is nonsynchronous with the beginning of the rains, but depends on them to start and lasts while the soil water reservoir enables them to stay active, which happens during spring. This explains the higher species richness, the gradient changes in species composition in the deep layer of control soil, and the similarity observed for these seasons after Sørensen analysis.

By summer, with a large increase in temperature and evaporation of soil water, activity is restricted to deeper soils and plant surroundings. During these seasons, plant canopies provide a more suitable environment for microbial activity than the control soils. This may explain why microenvironments rather than depths, as observed during winter and spring, aggregated soil samples from summer and autumn. During autumn, dew formation may momentarily alleviate water stress for microbial communities near the wet surfaces, which may allow more genera of amoebae to appear under *Z. dumosum*.

Differences between the control soil and soil under *Z. dumosum* are due to the effect of the shrub on the soil microenvironment. Litter production and root exudes are the key factors sustaining the soil microbial food web [24]. Microbial activity is higher in these "hot spots," also depending on the kind of plant exudes. This productivity is higher when plants are actively growing, normally during the rainy season. However, whenever a plant moves into the nongrowing or resting stage, the microbial consortium activity in its roots also diminishes

and arrests. The two different rooting patterns of *Z. dumosum* [7] also produce different spatial distributions of microbiota. Thus, fungi heavily colonize the roots at the surface, while bacteria colonize the deep roots [28]. This different microbial community may lead to the differences observed in the amoeba community, since the different species grow after feeding on their prey. Based on this logic, we expected to find less species diversity in the control soil than that found in the present study.

The effect of the shrub on the amoeba community was substantial, since diversity is greater under *Z. dumosum* than in control soil, especially during the dry seasons. Although the proportion of species and genera present in both depths under *Zygophyllum* are similar, there are differences in the total quantity and composition of species. These differences can be explained by the physiological stage of the roots, since protozoa can be considered nonmigrating soil organisms [10].

This study is one of the first studies on soil amoebae in the Negev Desert and elucidates the importance of the temporal and spatial contribution to the soil amoeba community. The importance of plant cover and its root canopy has been elucidated as a mediator of the amoeba community and plays an important role in nutrient cycling. A more detailed study to help understand this community and its trophic interaction with nitrogen turnover is essential, especially in desert ecosystems that are inherently nitrogen-limited.

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