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Original article

Soil microbial activity and free-living nematode community in the upper soil layer of the anticline erosional cirque, Makhtesh Ramon, Israel

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ABSTRACT

The physical–chemical peculiarity of soil rock formations is one of the leading factors determining diversity and abundance of soil biota. The main aim of the present research was to study soil microbial and free-living nematode abundance and diversity on different soil rock formations (basalt, sandstone, limestone, granite and gypsum) of the Makhtesh Ramon erosional cirque. The obtained results showed the strong effect of soil features of different soil formations on microbial biomass and respiration as well as on the soil free-living nematode communities and its trophic and species composition. The Sorenson-Czenkanowski similarity index indicated significant differences between soil properties as well as between soil biota in observed soil formations. The qCO_2, which is known to increase according to the level of environmental stress, reached maximal values in the sandstone soil formation. The values of ecological indices such as Simpson's dominance index, maturity index and modification and species richness pointed to a specific ecological condition in the studied soil formations dependent on low content of an essential soil matter as soil moisture, organic matter and cations.

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1. Introduction

The Makhtesh (Hebrew for crater) Ramon is located in southern Israel in the Negev Desert area. Structurally, the area is an anticline with a central eroded valley, mostly drained by a single river, Nahal Ramon. Makhtesh Ramon exposes numerous geological features: a large variety of rock types with superb assemblages of macro- and micro-fossils from the Triassic (~220 million years BP) up to the upper Cretaceous (~70 million years BP [18]. Evolution of the present exposure of Makhtesh Ramon is the result of post-Eocene erosion and structural modification [20]. Physical–chemical weathering resulted in the formation of soil horizons on the truncated surfaces of bedrocks with different compositions [26].

The abundance and species of soil organisms are dependent on the type and physical characteristics of the soil [10]. Many studies have been published in which changes in soil microbial parameters and soil free-living nematodes gave an

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early warning of decreasing soil quality (e.g. [14,45]). Parameters that describe the amount, activities, and diversity of soil microorganisms are also used as biological indicators of soil quality and health [33], integrating the chemical and physical properties of the ecosystem. Soil microorganisms are usually studied and monitored at the process and biomass levels. The process level includes overall activities of the soil microorganisms, especially respiration [33]. An additional important soil biota component which plays a major role as regulator of energy and nutrient flow is the nematode population [39]. According to Bongers and Ferris [5], the soil free-living nematodes are among the most numerous groups of multi-cellular animals participating in fundamental ecological processes in soil, such as decomposition and nutrient cycling [7]. Since they are sensitive to ecosystem disturbances [39,45], they can be used as stable indicators for understanding processes in the soils of different ecosystems, including semi-arid and arid desert zones [22].

There are numerous publications about the geological and geomorphological mapping, physical and geochemical features of sediments, distribution and behavior of separated chemical elements in the different types of rocks (e.g. [3,25]), whereas the number of publications about the biological component of the soil erosion basin related to geomorphological formation seems to be limited [38]. To fill this gap, the present study was targeted to:

1. Determine the spatial distribution of soil microbial and nematode populations in the different types of soil formations (basalt, sandstone, limestone, granite and gypsum) taking place in the main types of rocks of the erosion basin.
2. Determine the spatial distribution and trophic diversity of the nematode population in each type of soil formation in the main types of rocks.

2. Materials and methods

2.1. Location and geo-climatic conditions

Makhtesh Ramon (40 km long, ~9 km wide, 400 m deep), located within the Ramon Reserve National Park, southern Israel, is composed of many geological formations and large varieties of exposed rocks of various compositions [20]. Altitudes vary from 1020 m on the western rim to 420 m a.s.l. in the east near the outlet of Nahal (river) Ramon, which drains 90% of the Makhtesh area. Nahal Ramon is an ephemeral stream, 39 km long, which drains the central and western parts of the Makhtesh. Nahal Holit-Qamai drains the eastern part of Makhtesh Ramon. Nahal Neqarot, which flows east of the Ramon anticline, serves as the erosional base level of the Makhtesh valley [25].

The area is characterized by an arid to extremely arid climate. Mean multi-annual rainfall is 85 mm at the northern rim of the Makhtesh and 56 mm at the bottom, most of it coming from the west and northwest [20]. Mean daily temperature in July is 34 °C, and in January 12.5 °C; mean annual temperature is 17–19 °C [24]. Most of Makhtesh Ramon has a bare surface. The studied soils are immature, being actually non-lithified products of the initial stage of the weathering of parent rocks and, therefore, they partly inherit their structure. The thickness of soil does not exceed 20–30 cm. Due to arid climatic conditions, the processes of physical weathering prevail. Therefore the physical-weathered material contained no material finer than 30 μm [9]. The soils developed on Cretaceous basalts consist mainly of sand fractions mixed with approximately the same content of gravel and a minor amount of silt. The physical weathering of the friable Jurassic sandstones results in the accumulation of fine and medium sand with a strongly subordinated role of silt fractions. Coarse-grained soil developing on the Cretaceous granite consists mainly of coarse friable sand and fine gravel constitutes crystals of feldspar and quartz, almost without a fine matrix. The products of weathering on the Triassic gypsum strata along with the fine-grained composition partly preserve the structure of the parent rocks expressed as very thin blade-shape particles of granule size.

Vegetation cover is scarce and confined mainly to the stream channels. Trees are rare, and only two species, *Tamarix nilotica* and *Acacia raddiana*, are represented [26].

2.2. Sampling

Soil samples ($n = 25$) were taken from the 0 to 10 cm layer at five sampling sites having different types of rocks, stretching about 1000 m^2 each (Fig. 1). Five individual replicates of the soil samples were randomly collected from every site in the early hours at the end of the rainy season (in April 2004). Every soil sample consisted of five pseudo-replicates. Soil samples were collected at a distance from plants in the open area at: the lower Cretaceous basalt, belonging to the magmatic formation (station 1); the Jurassic marine limestone (sedimentary rocks, station 2); the Jurassic near-shore sandstone (sedimentary rocks, station 3); the Cretaceous granite, belonging to the magmatic formation (station 4), and the Triassic gypsum, belonging to the sedimentary formation (station 5).

Each soil sample (1 kg weight) was collected and placed in an individual plastic bag, which was then sealed. The samples were kept in insulated boxes for transport to the laboratory, where they were kept at 4 °C until biological and chemical analyses were performed. Before laboratory analysis, the soil samples were sieved through a 2 mm mesh sieve in order to remove organic remains.

2.3. Laboratory analysis

All collected samples of different types of soil formations were subjected to the following analyses:

1. *Soil moisture* was determined gravimetrically (105 °C, 48 h).
2. *Organic matter* was determined by oxidization with dichromate in the presence of H_2SO_4, without application of external heat [28].
3. *pH* was determined in H_2O (soil:solution ratio 1:2.5) with a potentiometric glass electrode.
4. *Soil salinity* was determined in soil extracts and expressed as electrical conductivity (μS m^{-1}).
5. *Total soluble nitrogen* (TSN) in soil was determined automatically [15] with a Skalar Autoanalyzer System [29].

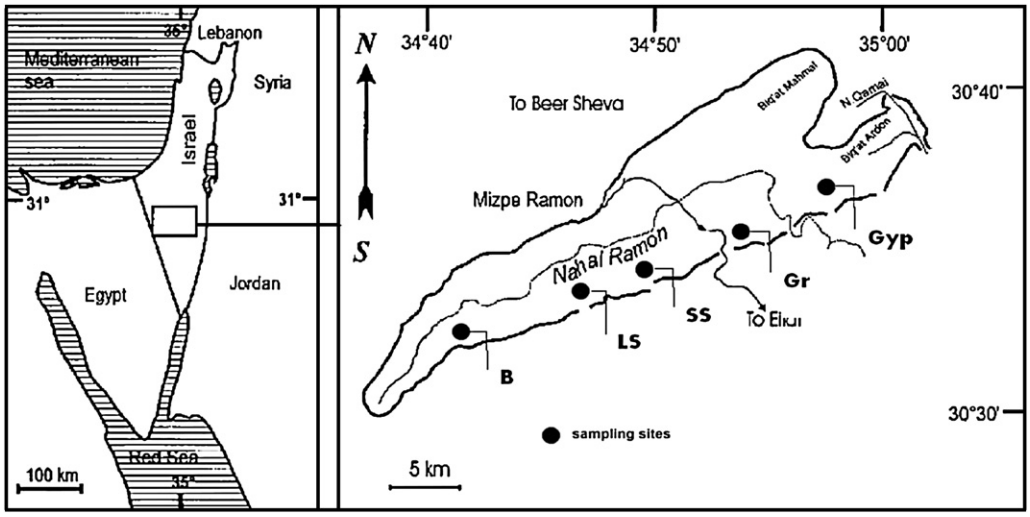

Fig. 1 – Location map of the Makhtesh Ramon Crater and sampling site. B – basalt soil formation; LS – limestone soil formation; SS – sandstone soil formation; Gr – granite soil formation; Gyp – gypsum soil formation.

6. *Soluble cations* (Ca^{2+}, K^+, Na^+) were determined using an atomic absorption spectrometer [27].
7. *Soil microbial biomass* (C_{mic}) was determined using a chloroform fumigation incubation (CFI) assay, according to Jenkinson and Powlson [13]. Five-gram soil samples were adjusted to 40% water-holding capacity and fumigated in a $CHCl_3$-saturated atmosphere in a desiccator for 24 h. The fumigated and corresponding non-fumigated (control) samples were then transferred to 0.5-L glass jars and incubated for 10 days at 25 °C in the dark. CO_2 concentration was measured in the head space of the glass jars using a Gas Chromatograph (GC), and C_{mic} was calculated as:

$$C_{mic} = [(CO_2 - C \text{ from fumigated soil}) - (CO_2 - C \text{ from control sample})]/kc$$

A kc of 0.41 was used, as proposed by Anderson and Domsch [2].
8. *CO_2 basal respiration* (BR) was evaluated by determining CO_2 using a SHIMADZU C-R6A Gas Chromatograph [34]. Similar to the soil microbial biomass analysis, the samples for CO_2 respiration analysis were incubated for 10 days at 25 °C in the dark.
9. *Nematode communities* were extracted from 100 g soil samples using the Baermann funnel procedure [6]. The recovered organisms were counted and preserved in formalin [36], and identified according to order, family, and genus level (if possible), using a compound microscope.

2.4. Ecological indices, parameters and statistical analysis

2.4.1. Microbial parameters

(1) Metabolic quotient (qCO_2) was calculated as the ratio between CO_2 production and microbial biomass [1]. The qCO_2 is a specific parameter for evaluating the effects of environmental conditions on the soil microbial biomass; (2) microbial coefficient, known as substrate availability, was determined as % of C_{mic}/C_{org} ratio [12].

2.4.2. Characteristics of nematode communities

Characteristics of nematode communities were described by means of indices: (1) Absolute abundance of individuals 100 g^{-1} dry soil. (2) Abundance of omnivore–predator (OP), plant-parasitic (PP), fungal-feeding (FF) and bacterial-feeding (BF) nematodes (trophic structure) [22]. (3) Trophic diversity, $T = 1/\sum p_i^2$, in which p_i is the proportion of the i-th trophic group [11]. (4) Simpson's dominant index, $\lambda = \sum p_i^2$ [32]. (5) Shannon index, $H' = \exp(-\sum p_i[\ln p_i])$, where p is the proportion of individuals in the i-th taxon [31]. (6) Maturity indices (MI), $MI = \sum v_i \rho_i$, where v_i, is the c–p value assigned by Bongers [4] of the i-th genus in the nematode and ρ_i, the proportion of the genus in the nematode community. The c–p indices, which according to Bongers [4] describe nematode life strategies and their sensitivity to environmental distribution, with values ranging from 1 to 5 (from tolerant-to-disturbance colonizers to sensitive-to-disturbance persisters), were found to divide the genus/family belonging to the different trophic groups into three distinct groups. The first group consists of all the bacterivore- and fungi-feeders (with c–p values of 1 and 2), known to be more abiotic-dependent. They, therefore, developed a colonizer strategy. The second group consists of the OP (with c–p values of 4 and 5), which developed a persister strategy. The third group consists of plant-parasites, including 50% colonizers, 20% persisters and the remaining 30% having a c–p value of 3, as intermediaries. (7) Maturity index modification ($\sum$MI) includes both PP and free-living nematodes [42]. (8) Species richness, $SR = (S - 1)/\ln(N)$, where S is the number of taxa and N is the number of individuals identified [44]; and (9) Sorenson-Czenkanowski similarity index, $ISC = 2\sum\min(x_i, y_i)/(\sum x_i + \sum y_i)$, where min is the minimum value for the number of individuals of the most abundant species in the two compared sites, x_i is total number of individuals in the first site, y_i is total number of individuals in the second site [17].

All data obtained were subjected to statistical analysis of variance using the SAS statistical software package (ANOVA, Duncan's multiple range tests and Pearson correlation coefficient) and were used to evaluate differences between separate

means. Differences with $p < 0.05$ were considered statistically significant.

3. Results

3.1. Soil properties

Soil moisture (SM) and organic matter (OM) analyses. Soil moisture values were found to be significantly different ($p < 0.0001$) for the five different types of soil formations, with maximal values observed for the gypsum soil formation and minimal values for the sandstone soil formation (Table 1). Soil organic matter and pH were not significantly different between different types of soil formations (Table 1).

Electrical conductivity (EC). The values of soil electrical conductivity were lowest in the basalt and granite soil formations and highest for the gypsum soil formation ($p < 0.0001$) (Table 1). A positive correlation was found between EC and SM ($r = 0.52$, $p < 0.01$), between EC and OM ($r = 0.35$, $p < 0.01$), between EC and Ca^{2+} ($r = 0.97$, $p < 0.01$), and between EC and Na^{+} ($r = 0.44$, $p < 0.01$), while a negative correlation was observed between EC and pH ($r = -0.36$, $p < 0.01$).

Ca, Na, K. All cations exhibited significant differences between the different types of soil formations ($p < 0.01$) (Table 1). The values of K^{+} were minimal for the sandstone soil formation and not significantly different for the other sampling sites (Table 1). Ca^{2+} and Na^{+} values were maximal for the gypsum soil formation (Table 1).

3.2. Microbial biomass and basal respiration

Soil microbial biomass was significantly different between sites ($p < 0.01$), reaching a maximum of 65.4 mg C_{mic} g^{-1} for limestone and a minimum of 4.4 mg C_{mic} g^{-1} for the sandstone soil formation (Fig. 2), while values of the other three soils ranged from 16 to 51 mg C_{mic} g^{-1}.

Soil CO_2 evolution exhibited a trend similar to the microbial biomass, with a range between 54 and 177 CO_2-C_{mic} 100 g^{-1} ($p < 0.0001$) (Fig. 2). The maximum value was observed for the gypsum soil formation (Fig. 2).

The qCO_2 coefficient was maximal (19.8 mg CO_2-C (gC_{mic} $h)^{-1}$) in the sandstone soil formation and exhibited no difference between other soil formations (1.4–4.5 mg CO_2-C (gC_{mic} $h)^{-1}$), while the CO_2 evaluation showed minimal (1.6%) values in the sandstone and maximal values (6.1%) in the basalt soil formation (Fig. 2).

The difference in the microbial coefficient C_{mic}/C_{org} value was non-significant between the soil formations observed (Fig. 2).

A positive correlation was found between soil properties (SM, OM, EC, and Ca^{2+}) and basal respiration (Table 2). Microbial biomass also had a positive correlation with SM and K^{+} (Table 3). The qCO_2 of the soil microbial community was correlated with SM (Table 2).

3.3. Nematode communities

The mean total number of nematodes in the soil samples taken at the different sampling sites ranged from 8 to 43 individuals 100 g^{-1} dry soil, with no significant difference between the observed soil formations (Fig. 3). Soil nematode diversity was found to decrease from 12 genera in the limestone and granite soil formations to 1 genus in the basalt soil formation (Table 3). No correlation was found between the total number of nematodes and soil properties (Table 2).

3.4. Nematode trophic groups

A total of 19 genera were found in the various types of soil formations, including nine bacterivores, four fungivores, five omnivores–predators and only one genus belonging to the plant-parasite trophic group (Table 3). The bacteria-feeders (BF) exhibited a similar trend to that of the total number of nematodes, while the other trophic groups had different patterns of density in the observed soil formations (Fig. 3).

The BF were the most abundant trophic group, with a mean relative abundance varying between 74 and 100% except for the gypsum soil formation, where the mean relative abundance was 8% (Fig. 3, Table 3).

Wilsonema was the most widespread genus among the bacterivores, followed by the *Acrobeles* and *Chiloplacus* genera (Table 3).

The fungi-feeding (FF) trophic group ranged between 0 and 7 individuals per 100 g dry soil ($p < 0.0001$) (Fig. 3, Table 3), reaching maximal values for the gypsum soil formation (86%), and was not found at all in the basalt and sandstone soil formations (Table 3).

The genus *Ditylenchus*, followed by the genus *Aphelenchus*, was the most dominant genera among the fungivores (Table 3).

Table 1 – Main ecophysiological characteristics of soil samples from different types of soil formations of Makhtesh Ramon Crater (mean ± standard deviation, $n = 5$)

Type of soil	SM (%)	OM (%)	pH	EC ($\mu S\,m^{-1}$)	Ca^{2+} ($mg\,kg^{-1}$)	Na^{+} ($mg\,kg^{-1}$)	K^{+} ($mg\,kg^{-1}$)
Basalt	12.0 ± 1.6^{b}	0.10 ± 0.04^{a}	8.2 ± 0.08^{a}	0.8 ± 0.1^{c}	51 ± 1.0^{c}	296 ± 27^{bc}	23.6 ± 4.5^{a}
Limestone	8.6 ± 1.2^{c}	0.14 ± 0.02^{a}	8.2 ± 0.04^{a}	0.9 ± 0.2^{bc}	72 ± 19^{c}	300 ± 51^{bc}	21.6 ± 3.7^{a}
Sandstone	1.6 ± 1.1^{e}	0.24 ± 0.23^{a}	8.1 ± 0.21^{a}	1.9 ± 1.3^{b}	513 ± 500^{b}	226 ± 48^{c}	11.8 ± 5.0^{b}
Granite	4.0 ± 0.01^{d}	0.09 ± 0.05^{a}	8.1 ± 0.11^{a}	0.8 ± 0.2^{c}	78 ± 20^{c}	252 ± 58^{bc}	18.8 ± 7.0^{a}
Gypsum	15.6 ± 2.5^{a}	0.24 ± 0.10^{a}	8.1 ± 0.01^{a}	6.4 ± 0.3^{a}	1449 ± 57^{a}	335 ± 20^{b}	18.8 ± 2.2^{a}

SM, soil moisture; OM, organic matter; EC, electrical conductivity; cations: Ca^{2+}, K^{+}, Na^{+}. Significant differences ($p < 0.05$) between sampling terraces are indicated by different letters.

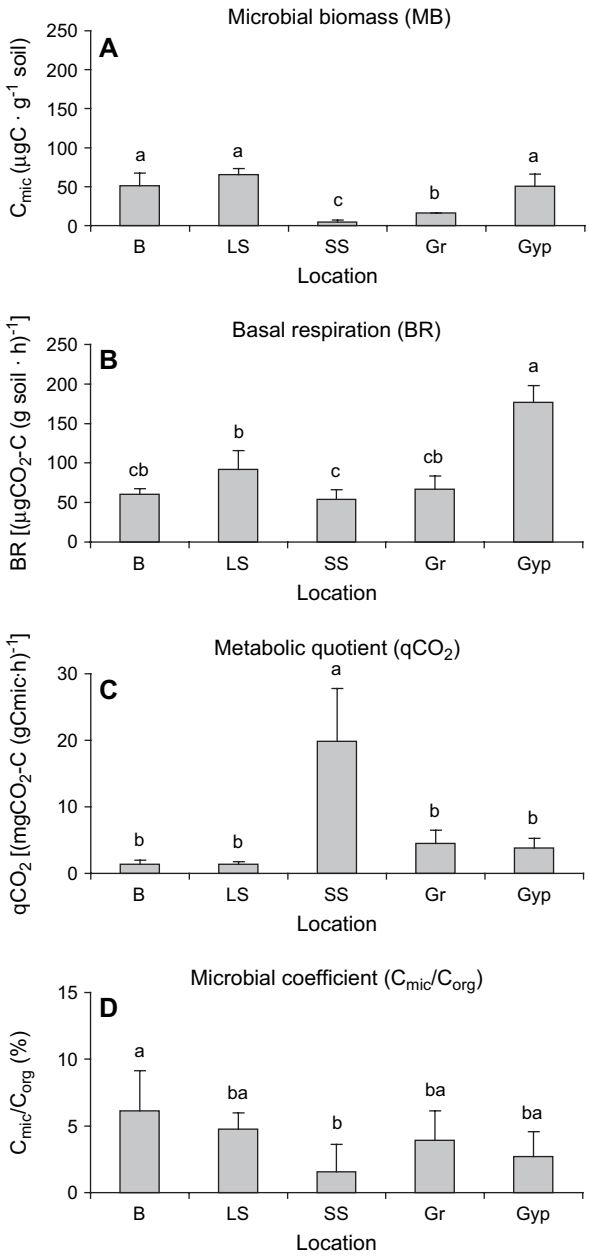

Fig. 2 – (A) Soil microbial biomass; (B) soil basal respiration; (C) metabolic quotient (qCO_2); and (D) microbial coefficient (C_{mic}/C_{org}) of the different soil formations of the Makhtesh Ramon erosion cirque. B – basalt soil formation; LS – limestone soil formation; SS – sandstone soil formation; Gr – granite soil formation; Gyp – gypsum soil formation.

The plant-parasite (PP) feeding group was represented by only one *Xiphinema* genus (amounting to 1% compared with other trophic groups) in the granite soil formation (Table 3).

The omnivore–predator (OP) trophic group ranged between 0 and 8 individuals per 100 g dry soil (Fig. 3), reaching maximal values (eight individuals per 100 g dry soil) in the limestone soil samples, and no presence in the basalt soil formation (Table 3).

Mesodorylaimus was the most dominant genus of the omnivore–predator trophic group (Table 3).

Table 2 – Correlation coefficient between observed parameters

Index	SM	OM	EC	pH	Ca^{2+}	Na^{+}	K^{+}
MR	0.44*	0.37*	0.67***	NS	0.67***	NS	NS
MB	0.66***	NS	NS	NS	NS	NS	0.39*
qCO_2	−0.51**	NS	NS	NS	NS	−0.42*	
TNEM	NS	NS	NS	NS	NS	NS	NS
Trophic structure							
BF	−0.50**	NS	−0.83***	NS	−0.85***	NS	NS
FF	−0.59***	NS	0.87***	NS	0.85***	NS	NS
PP	NS	NS	NS	NS	NS	NS	NS
OP	NS	NS	NS	NS	NS	NS	NS
Ecological indices							
T	NS	NS	NS	NS	0.45**	NS	NS
λ	0.45**	NS	NS	NS	NS	NS	NS
H′	NS	NS	NS	NS	NS	NS	NS
MI	NS	NS	NS	NS	NS	NS	NS
MMI	NS	NS	NS	NS	NS	NS	NS
SR	−0.54**	0.39*	NS	NS	NS	−0.40*	−0.42*

*, **, ***Correlation coefficient significant at $p < 0.05$, 0.01 and more than 0.001, respectively.
(1) SM, soil moisture; OM, organic matter; EC, electrical conductivity; cations: Ca^{2+}, K^{+}, Na^{+}.
Indices are: (2) MR, microbial respiration; (3) MB, microbial biomass; (4) TNEM, total number of nematodes (100 g^{-1} dry soil); (5) trophic structure: BF, bacterial-feeding; FF, fungal-feeding; PP, plant-parasitic; OP, omnivores–predators. (6) Ecological indices: *T*, trophic diversity; λ, dominant index; *H′*, Shannon index; MI, maturity index; MMI, modified maturity index; SR, richness.

The BF trophic group exhibited a significant correlation only with SM, EC, and Ca^{2+} (Table 2). The FF trophic group was negatively correlated with SM and positively correlated with EC and Ca^{2+}, without any correlation with other soil properties (Table 2). The PP trophic group as well as the OP trophic group did not exhibit any correlation with the observed soil properties (Table 2).

3.5. *Ecological indices and statistical analysis*

In the present study, the soil free-living nematode population belonging to the colonizers (*c–p* values of 1–2), known as abiotic-dependent, was the most common group, represented by 100, 81, 86, 94 and 94% in the basalt, limestone, sandstone, and granite soil formations, respectively. The remaining 19, 14, 6, and 6% of the total soil free-living nematode population in the limestone, sandstone, granite, and gypsum soil formations, respectively, were found to belong to the *c–p* 4–5 strategy group (Table 3).

Trophic diversity (*T*). The mean values of the *T* index ranged between 0 and 0.32 with no differences between soil formations (Fig. 4A).

Dominance. Genus dominance (λ) mean values decreased from 1 for the basalt to 0.5 for granite and 0.5 for sandstone soil formations ($p < 0.05$) (Fig. 4B).

Shannon index. The Shannon index (*H′*) values ranged from 0 for basalt to 1.6 for gypsum soil formations (Fig. 4C).

Maturity index. The maturity index and its modification had similar values for all soil formations (Fig. 4D and E). The means

Table 3 – The mean relative abundance (%) of soil nematodes on the different types of soil formations

Trophic groups/ genus/family[a]	c–p[b]	Type of soil formation[c]				
		B	LS	SS	Gr	Gyp
Bacterivores		**100**	**74**	**86**	**79**	**8**
Acrobeles	2	0	9	21	15	5
Acrobeloides	2	0	1	8	2	0
Cephalobus	2	0	5	0	7	0
Cervidellus	2	0	4	5	0	0
Chiloplacus	2	0	7	21	6	0
Eucephalobus	2	0	0	0	0	3
Panagrobelus	1	0	0	0	3	0
Panagrolaimus	1	0	0	0	5	0
Wilsonema	2	100	48	31	41	0
NG[d]		**1**	**6**	**4**	**7**	**2**
Fungivores		**0**	**7**	**0**	**15**	**86**
Aphelenchoides	2	0	0	0	2	0
Aphelenchus	2	0	7	0	13	0
Ditylenchus	2	0	0	0	0	69
Nothotylenchus	2	0	0	0	0	17
NG		**0**	**1**	**0**	**2**	**2**
Plant-parasites		**0**	**0**	**0**	**1**	**0**
Xiphinema	5	0	0	0	1	0
NG		**0**	**0**	**0**	**1**	**0**
Omnivores–predators		**0**	**19**	**14**	**5**	**6**
Discolaimus	4	0	2	0	0	0
Dorylaimus	4	0	2	0	0	6
Eudorylaimus	4	0	7	0	0	0
Mesodorylaimus	4	0	6	14	4	0
Nygolaimus	5	0	2	0	1	0
NG		**0**	**5**	**1**	**2**	**1**

a By classification Yeates and King [44].
b c–p Value as defined by Bongers [4].
c B, basalt; LS, limestone; SS, sandstone; Gr, granite; Gyp, gypsum.
d NG, total number of genera.

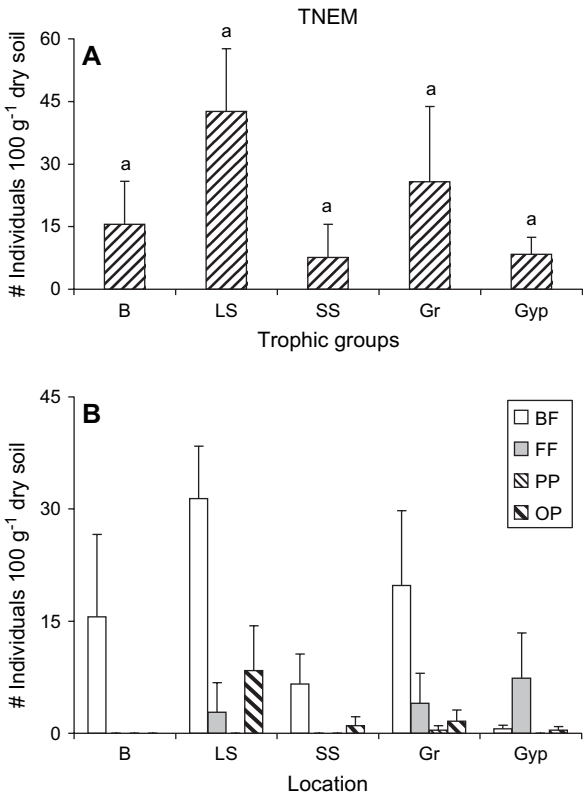

Fig. 3 – Distribution of the total number of nematodes (A) and nematode trophic groups (B) in the different soil formations of the Makhtesh Ramon erosion cirque. BF, bacterial-feeding; FF, fungal-feeding; PP, plant-parasitic; OP, omnivore–predator. B – basalt soil formation; LS – limestone soil formation; SS – sandstone soil formation; Gr – granite soil formation; Gyp – gypsum soil formation.

of MI and ∑MI were significantly different between observed soil formations ($p < 0.05$), reaching a maximum in the sandstone and limestone (2.2, in both cases) and a minimum in the basalt, granite and gypsum (~2) soil formations.

Richness. The mean of the SR index ranged between 0 and 1 and was significantly different between the observed soil formations ($p < 0.05$). The SR values were maximal in the sandstone soil formation and minimal in the basalt and gypsum soil formations (Fig. 4F).

A correlation was found between the trophic diversity index and Ca^{2+} (Table 2). The dominance index was correlated with SM (Table 2). The richness index was correlated with SM, OM, Na^{+}, and K^{+} (Table 2).

Sorenson-Czenkanowski similarity index. The ISC values indicated that gypsum soil formation was the lowest, similar to the basalt and limestone soil formations, while the basalt soil formation was the most similar to limestone soil formation (Table 4). The ISC index showed different values between basal respiration, microbial biomass and nematode communities (Table 4).

4. Discussion

The physical–chemical characteristics of the study area indicate a divergence process development that took place between the observed soil formation types. Most of the soil properties observed in the current investigation had different values in the different soil formations, thereby actively participating in creating an individual micro-environment for every type of soil formation. Soil moisture, which is one of the most important environmental factors affecting soil microorganism populations [23], was strongly dependent on the type of soil formation, with maximal values in the gypsum and minimal values in the sandstone soil ormation. Soil moisture values of the sandstone soil formation were found to be in agreement with data observed in other studies performed in the Negev Desert area (loess plain) during dry periods of the year [16], while soil moisture values of the other soil formations were similar to data observed in the same area but during a wet period [23].

The biomass and basal respiration as well as the trophic structure of soil free-living nematodes were found to be controlled by SM in the different soil formations. Moreover, microbial biomass and basal respiration were positively

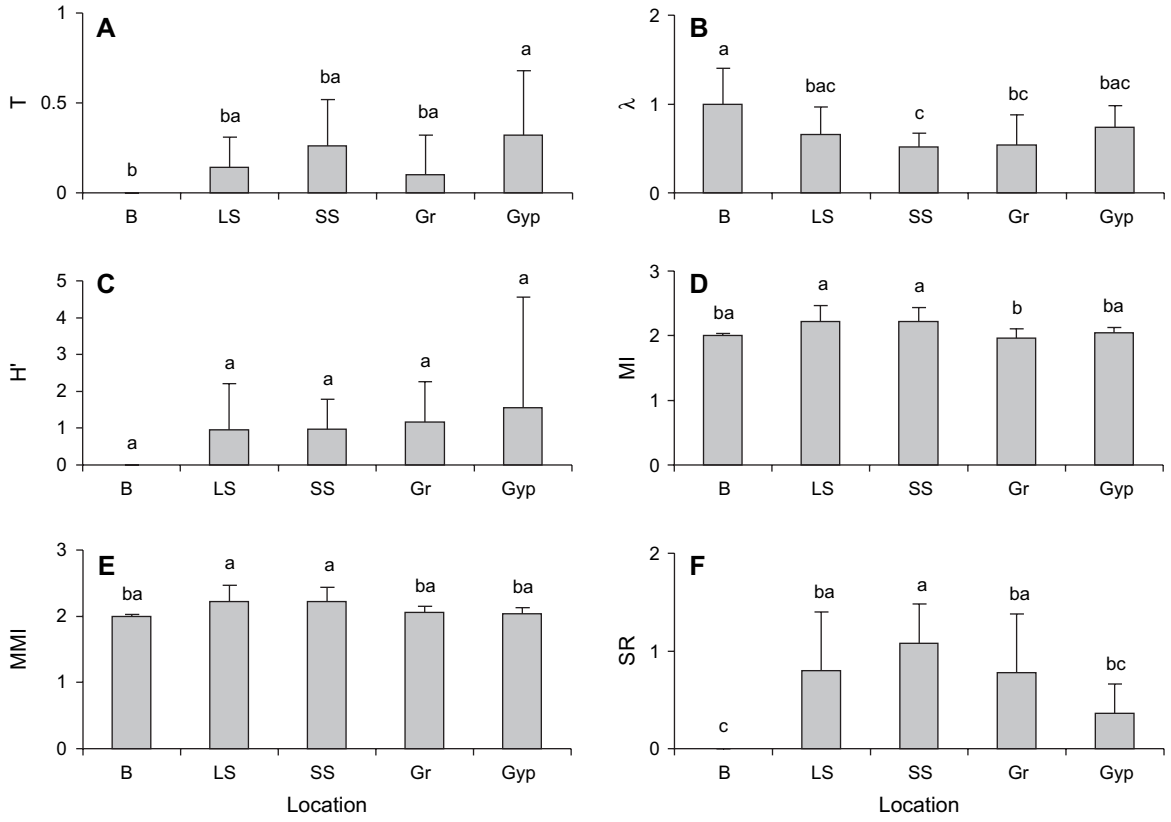

Fig. 4 – Variation in ecological indices of soil free-living nematodes in soil sample taken from the different soil formations of the Makhtesh Ramon erosion cirque. (A) *T*, trophic diversity; (B) dominant, λ, genus dominance; (C) H', Shannon index; (D) MI, maturity index; (E) $\sum$MI, modification index modification; (F) SR, specific richness. B – basalt soil formation; LS – limestone soil formation; SS – sandstone soil formation; Gr – granite soil formation; Gyp – gypsum soil formation.

correlated with SM, while the bacteria-feeding and fungal-feeding trophic nematode groups were negatively correlated with the latter. The microbial metabolic activity and trophic structure of nematodes were also found to be affected by the EC and Ca^{2+}. Basal respiration and fungi-feeding nematodes were positively correlated with the above-mentioned soil properties, whereas the bacterial-feeding trophic groups were negatively correlated. Furthermore, a high concentration of calcium in the soil formations may be the significant factor that negatively affects soil organisms [37]. Thus, the high calcium concentration in the sandstone together with the lowest soil water availability leads to increasing stress on microorganisms. This effect on the sandstone is confirmed by the highest values of qCO_2, whose increase indicates the level of environmental stress [2].

Microbial biomass in observed soil formations was lower than in other parts of the Negev Desert [30]. Also, nematode density was significantly lower than that found in different areas of the Negev Desert [35] and both the Chihuahuan Desert [41] and the Mojave Desert [8]. However, nematode density was similar to that observed under *A. raddiana* and inter-tree areas under the most unfavorable conditions in the Negev Desert during the dry period [22].

The low nematode density indicates that the environment of the erosional cirque is one of the most unfavorable and extreme places for the development of a free-living nematode community in an Israeli desert. Moreover, the high degree of variation in the total number of nematodes between sampling replicates of separate soil formations can be explained by "clumping" as a result of the aggregation of individuals in response to the specific nature of the habitat [21]. The aggregation of the nematodes in this case can be due to unfavorable environmental conditions [19].

The species diversity of nematodes, similar to the trophic groups, was found to be dependent on the physical–chemical

Table 4 – Sorenson-Czenkanowski similarity index

Comparison	SP	BR	MB	NC
B:LS	0.96	0.81	0.88	0.78
B:SS	0.52	0.94	**0.29**	**0.27**
B:Gr	0.89	0.85	0.48	0.57
B:Gyp	**0.35**	**0.55**	0.99	**0.00**
LS:SS	0.55	0.76	**0.24**	0.47
LS:Gr	0.92	0.96	**0.39**	0.69
LS:Gyp	**0.36**	0.72	0.89	**0.06**
SS:Gr	0.58	0.80	0.71	0.52
SS:Gyp	0.59	**0.51**	**0.29**	**0.07**
Gr:Gyp	**0.33**	0.68	0.47	**0.04**

SP, soil properties; BR, basal respiration; MB, microbial biomass; NC, nematode community. Bold indicates the lowest similarity values.

properties of the study area's micro-environment. Species of the genus *Wilsonema*, belonging to bacterivores, were the most numerous (31–100%) nematode species in all soil formations, except for gypsum, where the genus *Ditylenchus* was dominant (69%). In general, nematodes belonging to the *r*-life-strategy group (colonizers, tolerant to environmental disturbance) were the most numerous in all soil formations (81–100%) compared with nematodes (0–19%), which have a *K*-life-strategy (persisters, sensitive to disturbance).

The values of ecological indices such as qCO_2, λ, MI, $\sum$MI, SR and ISC were found to be useful tools for studying soil quality in the crater. The qCO_2, which is known to increase according to the level of environmental stress [2], reached maximal values in the sandstone soil formation. The mean qCO_2 values were lower than those observed by Sarig et al. [30] under *Artemisia monosperma* and *Retama raetam* for coastal sand dunes during a wet period, but were comparable to inter-shrub areas during a dry period. The genus dominance (λ) was higher than the value (0.22) obtained by Yeates and King [44] for the New England Tablelands. The MI and $\sum$MI indices were similar to each other and were comparable to values obtained by Wasilewska [40] for meadows in Poland. The mean of the SR index reaching maximum values in the sandstone soil formation and minimal values in the basalt soil formation. The SR index in the present study was lower than values obtained by Yeates and Bird [43] but was similar to those observed by Pen-Mouratov and Steinberger [24] in pesticide-treated desert soil. The ISC similarity index indicated significant similarity/dissimilarity between soil properties as well as between soil biota in observed soil formations.

5. Conclusions

The results of the present investigation demonstrate that the severe erosion initiated by climatic changes during the Late Pleistocene–Early Holocene period had significant consequences on abundance and composition of soil communities. The correlation between soil properties and living organisms indicates that in the process of soil formation, the development of living organisms is more directly dependent on physical–chemical properties of soil-forming rocks than in well-developed and well-formed soils. Moreover, the limestone formation is apparently more preferable for the existence of the observed soil organisms than other soil formations. The sensitivity of the free-living nematode population is very different among the trophic levels, with BF and FF being the most dependent on the physical–chemical properties of the environment. The species belonging to the genus *Wilsonema* were the most numerous nematode species in all soil formations, except for gypsum, where the *Ditylenchus* genus was dominant.

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