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Distribution of Soil Microbial Biomass and Free-living Nematode Population in Terrace Chronosequences of Makhtesh-Ramon Crater

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In this study, we examined the effects of the age of erosional fluvial terraces of Makhtesh Ramon (Ramon crater) in the central Negev Desert on soil chemical and biological properties. There were significant effects of erosion age of these terraces on soil moisture, organic carbon, soil salinity, and electrical conductivity. It is known that soil biological activity in arid ecosystems is determined by well-known limiting factors such as soil moisture and organic matter. Significant ($P < 0.002$) *differences in total nematode population and microbial biomass [(22.0–3.4* C_{mic} *(*μg *C* g^{-1} *soil)] were observed between terraces. Biological activity of soils in lower and younger terraces was greater than in older and higher terraces. The ecophysiological status (*qCO_2*) of the soil microbial community was found to decrease from a maximal value of 1.3 to 0.32 mg* $CO_2{-}C$ $(gC_{mic}h)^{-1}$ *along the terraces (from younger to older ones). This study illustrates the integrated effect of age, altitude, and the morphostratigraphic position of terraces on the biological activity of soils.*

Keywords Makhtesh Ramon, microbial biomass, nematodes, soil, terraces

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Makhtesh Ramon is the largest of the three erosional valleys formed along anticlinal axes in the Negev Desert, Israel. This erosional feature is an oval, elongated, few-to-several kilometers long, bowl-shaped depression formed by erosion with one drainage system and one outlet. The Ramon erosional cirque is a major geomorphic feature in this region, forming a deep feather- or arrowhead-shaped valley, 40 km long and up to 12 km wide, incised along the crest of the Ramon anticline, surrounded by steep cliffs up to 400 m high (Figure 1).

Geochronological evolution, morphology, structures, morphostratigraphy of fluvial terraces and pediments, and climatic conditions during the last stages of development of Makhtesh Ramon terraces have been well described by Plakht et al. (2000), who undertook quaternary mapping projects and other geomorphological investigations in these craters between 1994 and 2001 (Plakht, 1995, 1996, 1998, 2000; Plakht et al., 2000). In their study they showed that the evolution of the present exposure of Makhtesh Ramon is the result of post-Eocene erosion followed by structural modification. Soil formation, its chemical and physical characteristics along this crater, was found to be influenced by its geological structure, and age of exposure to abiotic conditions. The abundance and species of soil organisms are related and affected by the physical and chemical characteristics of soil (Yeates, 1982; Pen-Mouratov et al., 2004). Parameters describing the amount, activities, and diversity of soil microbial populations and soil free-living nematode communities in general and their structural changes in particular, are known to be among the best biological tools for assessing soil condition, integrating the chemical and physical properties of the ecosystem (Yeates & King, 1997; Wright & Coleman, 2000).

Arid-land soils show several distinctive differences from soils of humid regions, some of which are due to geochemical transformations and organic matter availability. Schlesinger et al. (1990, 1996) and Lajtha and Schlesinger (1988) examined the weathering, chemical transformations, availability, and movement of soil nutrients in an arid

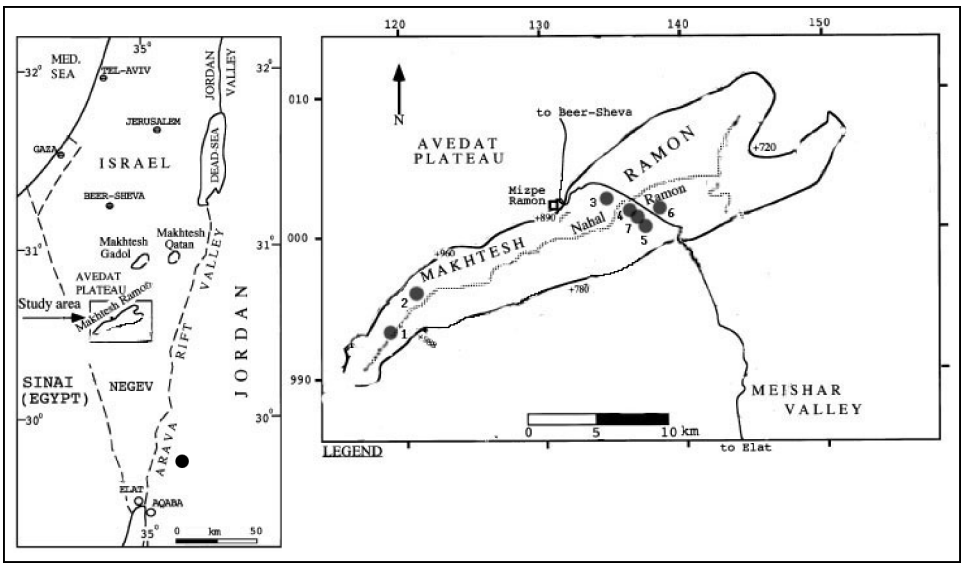

Figure 1. Makhtesh Ramon crater and sampling site. 1 – Terrace I; 2 – Terrace II; 3 – Terrace III; 4 – Terrace IV; 5 – Terrace V; 6 – Terrace VI; 7 – Terrace VII.

ecosystem in southwestern USA. They reported that soil nutrients, namely phosphorus, in soil decreased with increasing soil age. Similar studies have been reported by Ward et al. (2001) for the central Negev Desert ecosystem.

Danin et al. (1998), studying desert crust morphology and its relation to microbiotic succession along a time sequence of terrace formation in the Judean Desert, found an increase in biological activity on a time scale, whereas Evenari et al. (1982) elucidated the importance of organic matter accumulation in terraces in order to increase the activity of decomposers to enhance immobilization and mineralization processes and increase the availability of nutrients to primary producers.

The uniqueness of the terrace chronosequence formation in the Makhtesh Ramon crater is in the similarity of exposure to environmental pressure along with a bio-eco-evolutionary process. Therefore, we hypothesize that soil biological activity will be correlated with the chronosequence—aging of terraces with increasing soil organic matter. The aim of this study was to determine the relation between the soil biological activities in terrace sediments formed along a chronosequence scale.

Description of the Study Area and Terraces

Makhtesh Ramon is a deep erosional "cirque" 40 km long and 12 km wide entrenched along an anticline axis and surrounded by steep walls. It is centered at 30°35′N, 34°50′E, the long axis running ENE to WSW (Figure 1). It has an area of 241 km^2. Altitudes range from 1.020 m on the western rim to 420 m a.s.l. near the outlet of the main wadi, Nahal Ramon. This ephemeral stream is 39 km long within the makhtesh, and drains most of it. Nahal Neqarot, which flows east of the Ramon anticline towards the Dead Sea, serves as the local erosional base level of the Ramon Valley (Plakht et al., 2000).

The climate of the area is arid to extremely arid. The mean multiannual rainfall is 85 mm at the northern rim and 56 mm at the "cirque" bed in the central part. A mean maximal daily temperature of 34°C is measured in July, whereas a mean minimal temperature of 12.5°C is measured in January. The Quaternary development of Makhtesh Ramon can be generalized as an alternation of periods of erosion and stability, caused by periodic lowering of base level. The first stage of base-level lowering began with erosional activity, associated with the deformation along the Dead Sea-Arava Rift Valley (Zilberman, 1991). Erosion destroyed the regional Oligocene erosion surface and exposed the Ramon anticline structure. The lower landforms are younger because of the higher topographic position of Makhtesh Ramon in relation to its base level in the Dead Sea basin. An interrupted incision of the Makhtesh Ramon drainage system occurred since the Pliocene (Zilberman, 1991; Ben-David, 1993; Ben-David et al., 2002). During the Pleistocene, Makhtesh Ramon was situated high relative to its drainage base level (Ben-David et al., 1992). This resulted in the preservation of stepped fluvial terraces, the lowest of which is the youngest (Plakht, 1996).

Seven terraces, dated by the RTL (radio-thermo-luminescent) method, ages from 10 Ka to 500 Ka, were found in the Makhtesh Ramon crater and described by Plakht (2000). These terraces are as follows. The alluvium of terrace I (aged as 10 Ka), is relatively homogeneous and consists mainly of pebbles interbedded with thin bands of sand. The alluvium of terrace II (27–36 Ka of age) in Makhtesh Ramon contains a large amount of fine material with alternating calcic horizons, mostly of aeolian origin. The alluvium of terrace III (48–60 Ka of age) is composed mainly of pebbles in the sandy matrix of Makhtesh Ramon. It sometimes contains buried

gypsic paleosol. The alluvium of terrace IV (101–150 Ka of age) in Makhtesh Ramon is composed mainly of interbedded pebbles and sandy-loamy layers, alternating with horizons of buried calcic paleosol containing carbonate nodules. Coarse gravel dominates the composition of the alluvium of terrace V (205–240 Ka of age) in Makhtesh Ramon. Terrace VI (220–278 Ka of age) is capped by interbedded layers of pebbles and sands, and contains 2–3 horizons of brownish buried soil 0.5 m thick. Terrace VII (375–443 Ka of age) is the highest in Makhtesh Ramon, consisting mainly of a well-rounded conglomerate interbedded with layers of well-cemented carbonate sand (Table 1).

Materials and Methods

Five random soil samples were collected from the upper 0–10 soil layer of each of the seven erosion terraces (Table 1) in the early hours at the end of the rainy season of 2003–2004. The soil samples were collected and placed in individual plastic bags, and stored in an isolated container during transportation to the laboratory. After arrival at the laboratory, the soil samples were sieved through a 2-mm mesh sieve in order to remove organic debris before biological and chemical analyses. During analysis, the soil samples were kept at 4°C.

The following analyses were undertaken on each one of the samples collected at the study site:

1. **Soil water content** (SWC) was determined gravimetrically as percentage of dry mass by drying the samples to a constant weight at 105°C.
2. **Total organic carbon** (C_{org}) was determined using a modified method of Rowell (1994).
3. **Total soluble nitrogen** (TSN) in soil was determined by using the method of Houba et al. (1987). The amounts of TSN in the soil extracts were determined using a Skalar Autoanalyzer unit (S.F.A.S., 1995).
4. **pH** was determined in H_2O (soil:solution ratio 1:2.5) with a potentiometric glass electrode.
5. **Soil salinity** was determined in soil extracts and expressed as electrolytic conductivity (EC) S m^{-1}.
6. **Soluble cations** (Ca^{2+}, K^+, Na^+) were determined by flame photometer (Rhoades, 1982).
7. **Soil microbial biomass** (C_{mic}) was determined using a chloroform fumigation incubation (CFI) assay, according to Jenkinson & Powlson (1976). 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 nonfumigated (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 & Domsch (1990).
8. **Soil basal respiration** (BR)—as the CO_2 evolution was determined by GC (Sparling & West, 1990).
9. **Metabolic coefficient** (qCO_2) was calculated as the ratio between CO_2 production and microbial biomass (Anderson & Domsch, 1990). The qCO_2 is a specific parameter for evaluating the effects of environmental conditions on the soil microbial biomass.

Table 1. Main ecophysiological characteristics of soil samples from different Terraces of Makhtesh Ramon Crater (mean + standard deviation, n = 35)

Terraces	Age Ka	SWC $g \cdot kg^{-1}$	C_{org} $g \cdot kg^{-1}$	TSN $g \cdot kg^{-1}$	EC $dS \cdot m^{-1}$	Ca^{+2} $mg \cdot kg^{-1}$	Na^{+} $mg \cdot kg^{-1}$	K^{+} $mg \cdot kg^{-1}$
I	up to 10	$69.2 \pm 5.1^{a,b}$	2.2 ± 0.4^{a}	$0.57 \pm 0.43^{c,d}$	0.04 ± 0.011^{c}	265 ± 213^{c}	$541 \pm 93^{c,d}$	17.0 ± 5.1^{a}
II	27–36	73.3 ± 9.3^{a}	$1.4 \pm 0.5^{b,c}$	0.26 ± 0.18^{d}	0.034 ± 0.009^{c}	219 ± 101^{c}	450 ± 97^{d}	6.8 ± 7.8^{b}
III	48–60	73.4 ± 10.1^{a}	$1.2 \pm 0.4^{b,c}$	1.09 ± 0.5^{b}	$0.05 \pm 0.010^{b,c}$	706 ± 104^{c}	$588 \pm 69^{b,c}$	$12.6 \pm 6.3^{a,b}$
IV	101–150	$65.0 \pm 6.3^{a,b,c}$	1.0 ± 0.0^{c}	$1.19 \pm 0.14^{a,b}$	0.074 ± 0.015^{a}	1209 ± 385^{b}	$635 \pm 76^{a,b,c}$	$12.6 \pm 6.3^{a,b}$
V	205–240	$62.1 \pm 12.1^{a,b,c}$	1.0 ± 0.0^{c}	1.53 ± 0.01^{a}	0.086 ± 0.011^{a}	1794 ± 829^{a}	$692 \pm 88^{a,b}$	$10.2 \pm 4.9^{a,b}$
VI	220–278	$56.4 \pm 18.2^{b,c}$	1.6 ± 0.5^{b}	$0.91 \pm 0.24^{b,c}$	0.094 ± 0.031^{a}	410 ± 103^{c}	743 ± 125^{a}	4.4 ± 3.3^{b}
VII	375–443	53.3 ± 9.0^{c}	1.0 ± 0.0^{c}	0.51 ± 0.23^{d}	0.036 ± 0.013^{c}	650 ± 243^{c}	266 ± 104^{e}	7.4 ± 4.9^{b}

SWC, soil water content; Corg, total organic carbon; TSN, total soluble nitrogen; EC, soil salinity.
Significant differences ($P < 0.05$) between sampling terraces are indicated by different letters (a, b, c).

10. **Microbial coefficient**, known as substrate availability, was determined as the C_{mic}/C_{org} ratio.
11. **Nematode population** was determined by extraction from 100 g soil samples using the Baermann funnel procedure (Cairns, 1960). The recovered organisms were counted using a compound microscope and preserved in formalin (Steinberger & Sarig, 1993). The nematodes from each sample were collected and identified according to order, family, and genus, using a compound microscope. Nematodes were classified into the following trophic groups: (1) bacterivores; (2) fungivores; (3) plant parasites; and (4) omnivores-predators, according to known feeding habitats or stoma and esophageal morphology (Steinberger & Sarig, 1993; Yeates et al., 1993). The nematode community was analyzed using the following approaches: (1) absolute abundance of individuals $100\,g^{-1}$ dry soil; (2) absolute number of trophic structure; and (3) ecological indices: (a) trophic diversity (TD), where $TD = 1/\Sigma Pi^2$ (Heip et al., 1988) (b) Shannon Index (H′), where $H' = -\Sigma Pi(lnPi)$ (Shannon & Weaver, 1949); (c) modified maturity index (ΣMI), nematode maturity index (MI) of Bongers (1990) is modified to include plant feeding nematodes and thus better reflects ecosystem development (Yeates, 1994). ΣMI incorporates ecological characteristics of families based on a colonizer-to-persister scale 1–5, lower ΣMI values indicating more disturbed environments; (d) richness index (SR), $SR = (S-1)/In(N)$, where S is the number of taxa and N is the number of individuals identified (Yeates & King, 1997); (e) evenness index (J′), where $J' = H'/lh\,(S)$, H′ is the Shannon Index, ln is the log base (e) and S is equal to number of taxa (Pielou, 1975).

The data presented in our study are reported as oven-dried weights. All data were subjected to statistical analysis of variance (ANOVA). When significance at a level of $p < 0.05$ was observed, Tukey's values were calculated for separation of the means.

Results

Soil water content ranged between 53.3 and 73.4 g kg^{-1} in soil samples collected along the seven terraces (Figure 2). In the youngest terraces (I, II, III), the mean values of soil water content was relatively higher (69.2–73.4 g kg^{-1}) than in the other four older terraces (IV, V, VI, and VII), where the mean values ranged between 53.3–65.0 g kg^{-1} (Table 1). The differences in soil water content between the terraces yielded significant ($p < 0.05$) differences between the different terraces (Table 1).

Soil total organic carbon (C_{org}) was found to decrease gradually from a mean level of 2.2 g kg^{-1} in the youngest terrace (aged 10 Ka) to a minimal value of 1.0 g kg^{-1} for terraces IV, V, and VII (Table 1), while in terrace VI the soil organic carbon reached a relatively higher mean value of 1.6 g kg^{-1}. Although little differences were found in soil organic carbon levels between the terraces, the increasing age of the terraces (except terrace VI) yielded a significant decrease in C_{org} (Figure 2; Table 1).

Total soluble nitrogen in soil samples taken from the difference terraces (Figure 1) exhibited a relatively low mean value of 0.57 and 0.26 g kg^{-1} for terraces I and II. In terraces III, IV, V, and VI, the values increased two to three times, to maximum mean levels of 1.53 g kg^{-1} (terrace V). The pattern obtained exhibited significant accumulation of TSN in terrace aged between 48 to 240 Ka, after that a gradual decrease in TSN was obtained (Figure 2; Table 1).

The soil sample taken from the seven terraces was weakly alkaline, with the pH ranging from 7.3 to 7.9, without any significant differences between the samples.

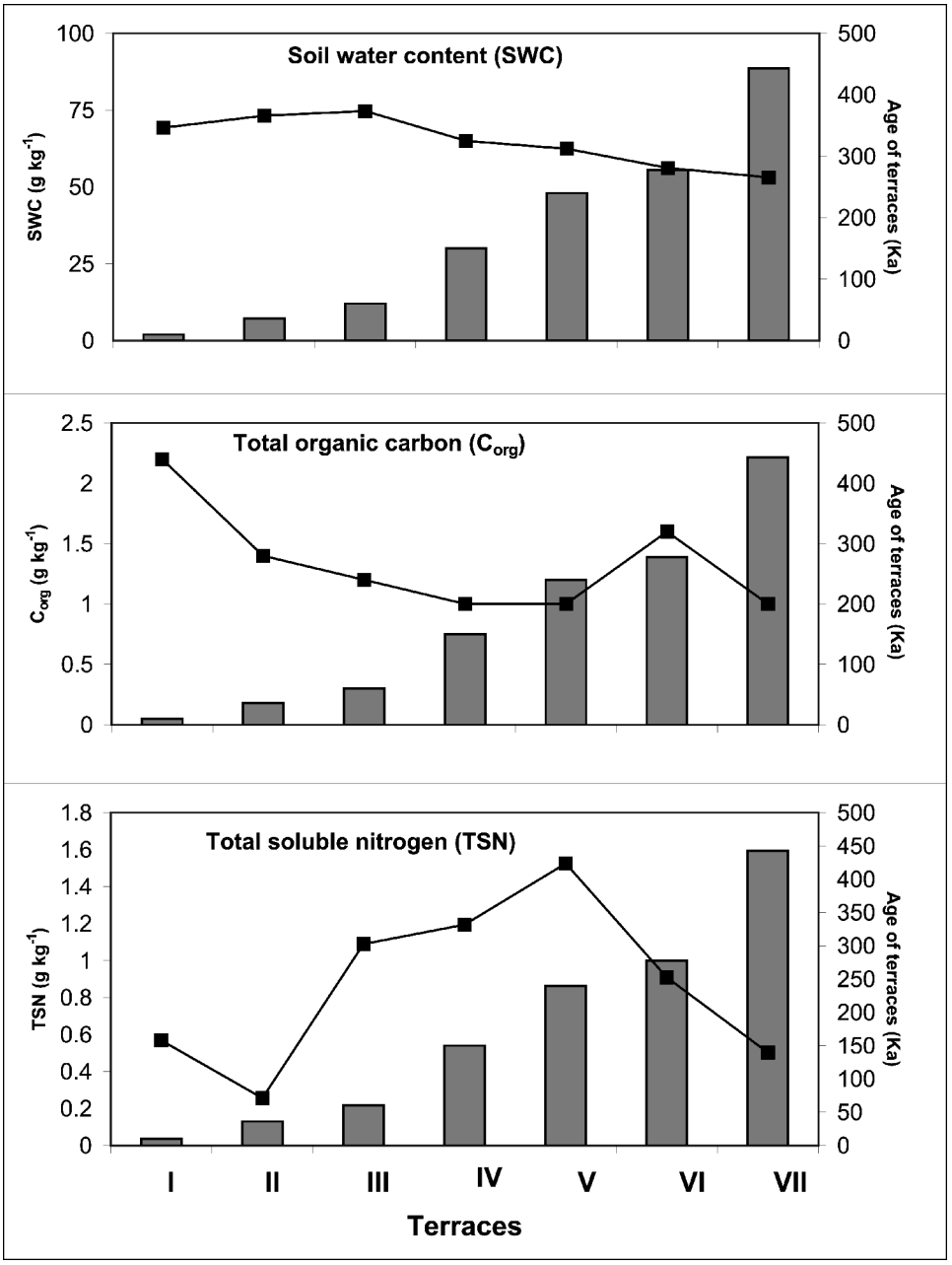

Figure 2. Soil moisture and organic matter contents in soil samples taken from the different terraces of the Makhtesh Ramon erosion cirque. 1 – Terrace I; 2 – Terrace II; 3 – Terrace III; 4 – Terrace IV; 5 – Terrace V; 6 – Terrace VI; 7 – Terrace VII.

Electrolytic conductivity values were found to follow a pattern similar to that reported for TSN, with relatively low values for terraces I and II (0.04 and 0.034 dS m^{-1}, respectively) followed by a gradual increase to a mean maximal level of 0.094 dS m^{-1} in terrace VI, followed by a significant ($p < 0.05$) decrease

compared to terrace IV, V, and VI with mean values of 0.074, 0.086, and 0.094 dS m^{-1}, respectively (Figure 3, Table 1).

A spatial comparison of the cation content of soil samples from different erosional terraces revealed that the concentration of Ca^{2+} and Na^{+} in the soils (Figure 3) followed a pattern similar to EC and TSN, with lower values in the young terraces and an increase in the older ones, leading to partially significant differences between them ($p < 0.05$; Table 1). The K^{+} content in the soil samples followed patterns similar to the Ca^{2+} and Na^{+} ions (Table 1).

Soil microbial biomass (Figure 4) was found to reach significantly higher values, such as 18.97 and 22.02 C_{mic} ($\mu g\, C\, g^{-1}$ soil), in soil samples taken from terraces I and II, respectively. A 2–7-fold decrease in microbial biomass was obtained with increase in terrace age from 60–443 Ka. These significant differences led to significant differences between sampling locations ($p < 0.0001$; Table 2).

Soil Basal Respiration (BR) showed a relatively similar pattern to those obtained by microbial biomass, with the values obtained in the youngest terraces I and II, the BR being 46.6–53.2 $\mu g\ CO_2{-}C(g\ soil\ h)^{-1}$, respectively. In the older terraces IV, V, VI, and VII, CO_2 evolution decreased 1.5- to 2-fold lower than in terraces I and II, to values ranging between 27.4 and 40.7 $\mu g\, CO_2{-}C(g\, soil\, h)^{-1}$ (Figure 4), yielding a significant difference ($P < 0.005$) between them (Table 2).

As a result of the significant changes in microbial biomass and CO_2 evolution, the ***Ecophysiological Status (qCO_2)*** of the soil microbial community was found to decrease from a maximal value of 1.3 to 0.32 $mgCO_2{-}C(gC_{mic}h)^{-1}$ along the terraces (from younger to older) (Figure 4, Table 1). These "mirror images" of qCO_2 behavior, which decreased significantly with the increase in terrace age, showed the difference in utilization of substrates for the microbial biomass.

The pattern obtained for the microbial coefficients (C_{mic}/C_{org}) which can be interpreted as substrate availability, was found to follow the ecophysiological index, with values ranging from 2.38–3.74% in terraces aging up to 150 Ka (Figure 4), whereas the values obtained for terraces V, VI, and VII decreased significantly (over 1,5 times to 0.46–188%) (Table 2).

Nematode Population, the total number of soil free-living nematodes among the terraces, ranged from a mean of 1 to 25 individuals 100 g^{-1} dry soil (Figure 4). The maximal population was found in terrace I, with 25 individuals 100 g^{-1} dry soil which decreased gradually to a mean value of 1 individual 100 g^{-1} dry soil at terrace 5, with a similar value for the remaining locations, leading to significant differences ($P < 0.002$) (Table 2) between them.

A significant positive correlation was found between the total density of the soil free-living nematode population and soil moisture ($P < 0.005$, $n = 35$), soil organic matter ($P < 0.04$, $n = 35$), soil microbial biomass ($P < 0.001$, $n = 35$), and the microbial coefficient C_{mic}/C_{org} ($P < 0.01$, $n = 35$). Total nematode density was found to be negatively affected at a level of $P < 0.05$ by Ca^{2+}, TSN concentration, and soil electrical conductivity.

For Nematode taxa and trophic group, A total of 11 genera were found, including four bacterivores, four fungivores, and three plant-parasites (omnivore-predators were not found) (Table 3). The bacterivore trophic group was the dominant group, represented by over 50% of the total taxa, followed by the fungivores and the plant-parasites. Of all the taxa, the *Wilsonema*, belonging to the bacterivore trophic group, was the most dominant taxon in the young as well as old terraces (Table 4). Most of the taxa were found in the youngest terraces (I, II, III, IV), whereas in terraces V, VI,

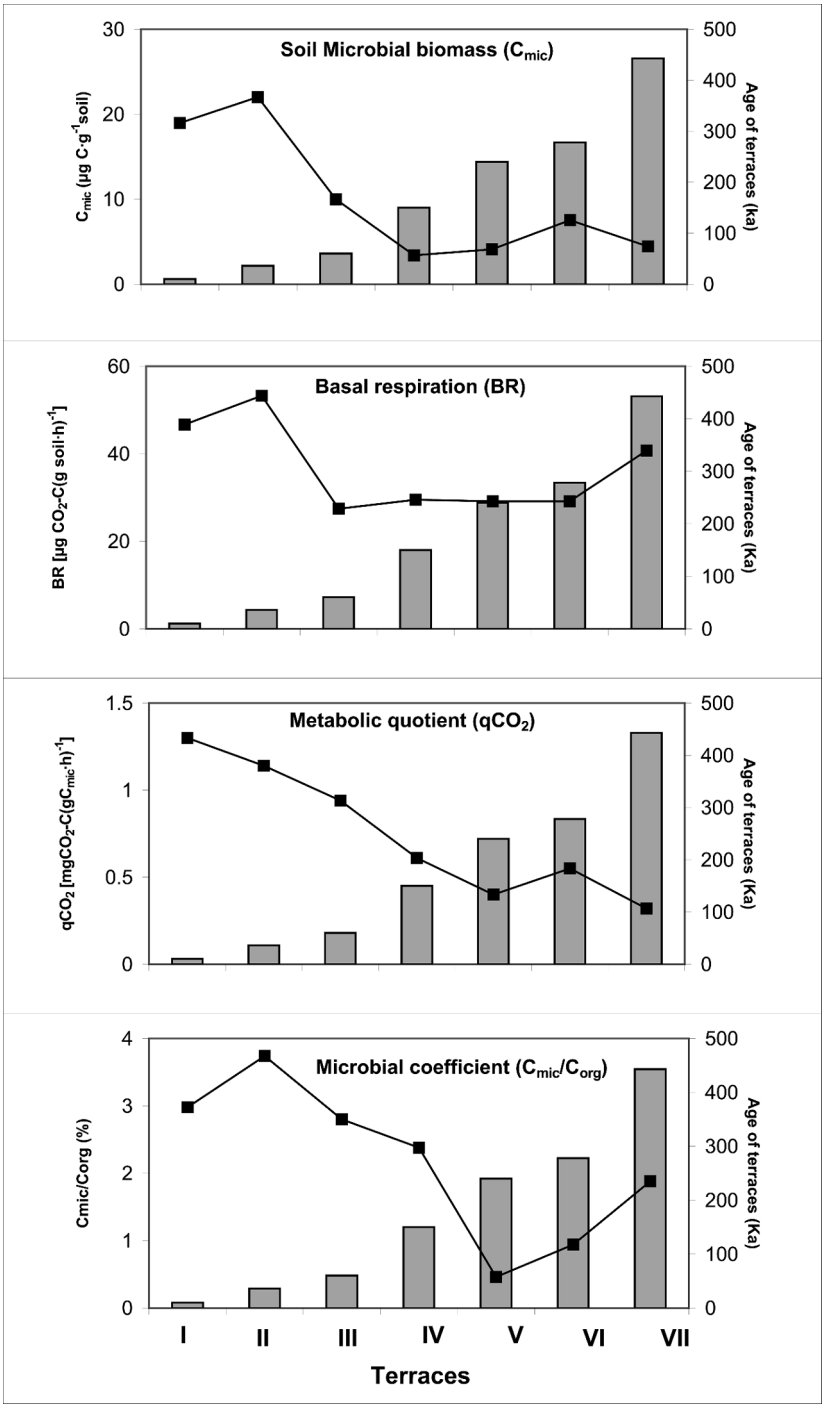

Figure 3. Soil microbial biomass (C_{mic}) and soil respiration (BR) in soil samples taken from the different terraces of the Makhtesh Ramon erosion cirque. 1 – Terrace I; 2 – Terrace II; 3 – Terrace III; 4 – Terrace IV; 5 – Terrace V; 6 – Terrace VI; 7 – Terrace VII.

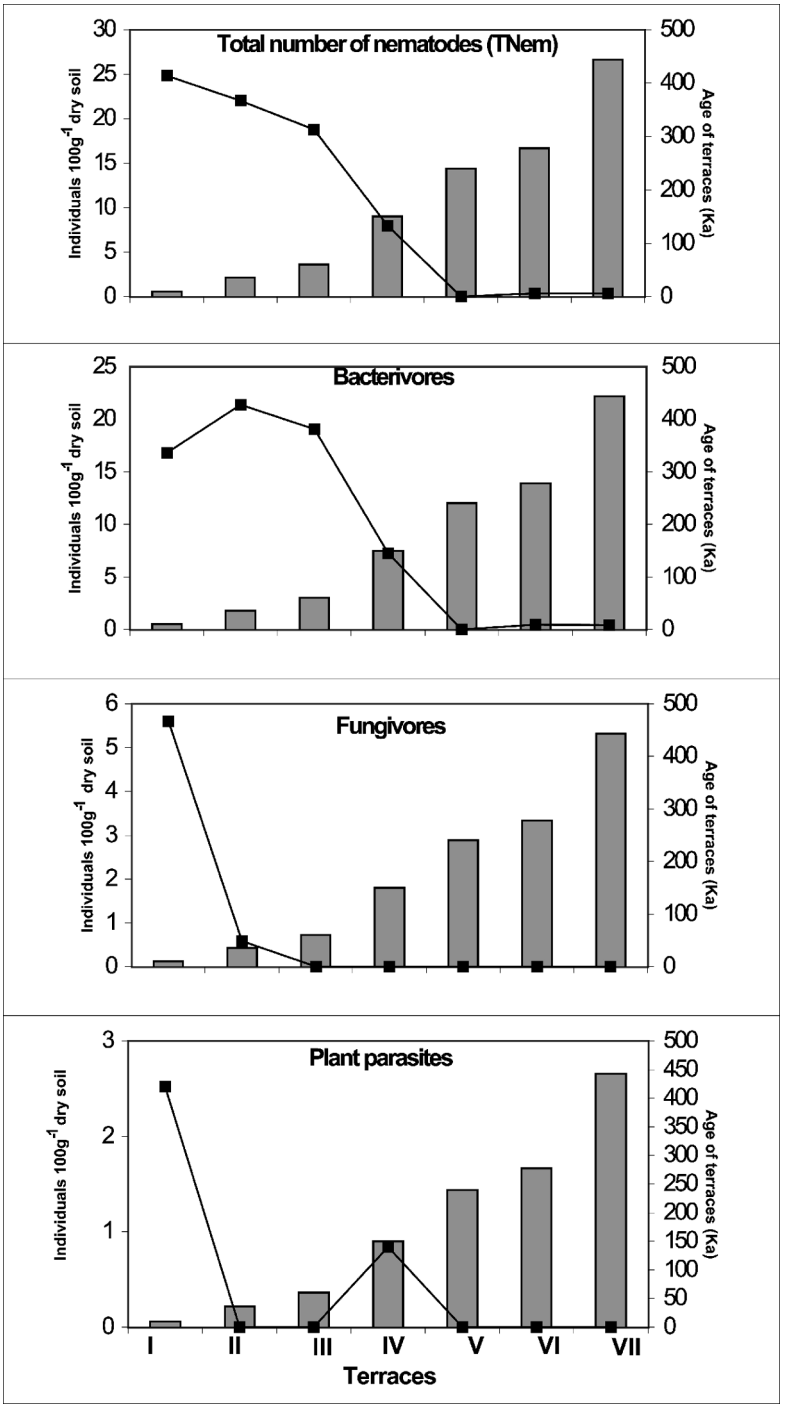

Figure 4. Distribution of total number of nematodes and trophic groups in the different terraces of the Makhtesh Ramon erosion cirque. 1 – Terrace I; 2 – Terrace II; 3 – Terrace III; 4 – Terrace IV; 5 – Terrace V; 6 – Terrace VI; 7 – Terrace VII.

Table 2. Univariate analysis of variance (ANOVA) for soil microbial activity and nematode indices in different terraces of Makhtesh Ramon crater

	Locations	
	F-test	P value
Soil microbial activity		
Microbial biomass (C_{mic})	13.87	<0.0001
Basal respiration (BR)	3.92	0.005
Metabolic coefficient (qCO_2)	4.68	0.002
Microbial coefficient (C_{mic}/C_{org})	3.96	0.005
Nematodes trophic structure		
Total nematode abundance (TNem)	4.45	0.002
Bacterivores (BF)	3.5	0.01
Fungivores (FF)	4.78	0.001
Plant-parasites (PP)	4.83	0.001
Omnivores-predators (OP)	0	0
Nematode indices		
Trophic diversity (TD)	10.78	<0.0001
Shannon index (H′)	3.6	0.01
Richness (SR)	2.9	0.02
Modified maturity index (ΣMI)	12.11	<0.0001
Evenness (J′)	5	0.001

and VII, only *Wilsonema* was present while the other two trophic groups disappeared with the increase in terrace age (Table 3; Figure 5).

According to Bongers (1990), c-p indices, with values ranging between 1 and 5, describe nematode life strategies from a population that is tolerant to a population known as colonizers, that is sensitive to environmental distribution. He divided this range into three distinct parts, where values 1 and 2 are known to be tolerant, and consist mainly of bacterivores and fungivores. The second groups consist of c-p values of 4 and 5, are sensitive to abiotic fluctuations, and are known as persisters. The third c-p group, with a value of 3, is known as an intermediate group that includes some colonizers and some persisters. In our study, 91% of the population was found to be represented by c-p values of 2, and only 9% (one representative—*Pratylechus*) with a c-p value of 3 was found in the soil samples taken from the youngest terrace (terrace I) (Table 3).

Five Ecological Indices, which can be divided into two main groups, were determined in this study (Figure 5). The first one includes the trophic diversity (TD) and the modified maturity index (**ΣMI**) and the second group includes the Shannon Index (**H′**), richness (**SR**) and the evenness index (**J′**). The first group exhibited values that are 5–8 fold higher in the first four terraces than in the remaining three (V, VI, VII). In the second group, the values of the first and third terraces were significantly higher than in terraces two and four, whereas no values were obtained for the other terraces (V, VI, and VII). These two main patterns demonstrated a significant sampling location effect (Table 2).

Table 3. Correlation coefficients between soil biological activity and soil conditions in different terraces of Makhtesh Ramon Crater

	Age of terraces	SWC	EC	Ca^{2+}	K^{+}	Na^{+}	C_{org}	TSN
Age of terraces		**–0.55****	0.327	0.300	**–0.398***	–0.056	**–0.456****	0.228
Soil microbial activity								
Basal respiration (BR)	–0.317	–0.005	**–0.393***	**–0.363***	0.212	**–0.405***	0.067	**–0.531****
Microbial biomass (C_{mic})	**–0.748****	0.343	**–0.467****	**–0.518****	0.024	–0.266	**0.502***	**–0.552****
Metabolic coefficient (qCO_2)	**–0.673****	**0.363***	**–0.327***	**–0.377***	–0.092	–0.100	**0.502***	**–0.346***
Microbial biomass (C_{mic}/C_{org})	**–0.506****	0.275	**–0.542****	**–0.399***	–0.028	**–0.386***	0.006	**–0.459****
Nematodes trophic structure								
Absolute total abundance (TNem)	**–0.662****	**0.457****	**–0.411***	**–0.342***	0.240	–0.176	**0.344***	**–0.490***
Bacterivores (BF)	**–0.583****	**0.463****	**–0.384***	–0.302	0.175	–0.180	0.161	**–0.447****
Fungivores (FF)	**–0.348***	0.085	–0.221	–0.211	0.227	–0.060	**0.614****	–0.271
Plant-parasites (PP)	**–0.436****	0.085	0.002	–0.108	0.256	0.063	**0.453****	–0.090
Nematode indices								
Trophic diversity (TD)	**–0.754****	**0.483****	**–0.456***	**–0.415***	0.302	–0.146	**0.399***	–0.331
Shannon index (H′)	**–0.556****	0.308	–0.179	–0.231	0.229	–0.017	**0.421***	–0.221
Modified maturity index (ΣMI)	**–0.717****	**0.64****	**–0.528****	**–0.424***	0.270	–0.168	0.178	–0.267
Evennes (J′)	**–0.517****	**0.371***	–0.184	–0.196	0.245	0.012	0.239	–0.114
Richness (SR)	**–0.505****	0.271	–0.147	–0.209	0.253	0.021	0.317	–0.091

SWC, soil water content; Corg, total organic carbon; TSN, total soluble nitrogen; EC, soil salinity.
*, **—Correlation coefficients significant at $p < 0.05$ and 0.01, respectively (n = 35).

Table 4. Mean relative abundance (%) of soil nematodes in different terraces of Makhtesh Ramon crater

Locations Trophic groups/ genus/family*	c-p	I	II	III	IV	V	VI	VII	Mean
Bacterivores		**67.3**	**97.3**	**100.0**	**89.6**	**00.0**	**100.0**	**100.0**	**92.4**
Acrobeles	2	06.7	00.0	03.4	03.5	00.0	00.0	00.0	02.3
Acrobeloides	2	00.0	00.0	00.0	03.5	00.0	00.0	00.0	00.6
Chiloplacus	2	02.9	02.7	23.2	03.5	00.0	00.0	00.0	05.4
Wilsonema	2	57.7	94.7	73.4	79.2	00.0	100.0	100.0	84.2
Fungivores		**22.5**	**02.7**	**00.0**	**00.0**	**00.0**	**00.0**	**00.0**	04.2
Anguina	2	00.0	01.3	00.0	00.0	00.0	00.0	00.0	00.2
Aphelenchoides	2	20.1	00.0	00.0	00.0	00.0	00.0	00.0	03.4
Ditylenchus	2	01.2	00.0	00.0	00.0	00.0	00.0	00.0	**00.2**
Nothotylenchus	2	01.2	01.3	00.0	00.0	00.0	00.0	00.0	00.4
Plant-parasites		**10.2**	**00.0**	**00.0**	**10.4**	**00.0**	**00.0**	**00.0**	03.4
Pratylenchus	3	02.6	00.0	00.0	00.0	00.0	00.0	00.0	00.4
Psilenchus	2	04.7	00.0	00.0	00.0	00.0	00.0	00.0	00.8
Telotylenchus	2	02.9	00.0	00.0	10.4	00.0	00.0	00.0	02.2

*By classification of Yeates & King (1997) and Liang et al. (2000).

Discussion

Geochronological evolution and climatic conditions in desert ecosystems along a chronosequence scale may lead to an increase in the spatial and temporal heterogeneity of moisture, nitrogen, and other soil resources promoting soil biota community and plant settlement. The huge diversity of soils is a function of five main factors: parental material, climate, biota, topography, and time, which are all closely interrelated (Gray, 2004), and lead to a range of geological, geomorphological and soil assemblages that underpin soil biota activity.

Makhtesh Ramon is known to be one of the deepest erosional cirques exposing numerous geological features from the Triassic ($\sim$220 million years ago) up to the upper Cretaceous ($\sim$70 million years ago), as well as a multitude of well-preserved Lower Cretaceous basanite volcanoes and syenite intrusions basanite (Mazor, 1993). Soil formation at this site, which has undergone similar climatic conditions along a chronosequence period, has been found to affect the soil biota community. Soil sampling in open spaces allowed us to increase site similarity, whereas according to Schlesinger et al. (1990), soil nutrient losses are mainly due to erosion and gaseous emission. Therefore, the similarity and divergence between the terraces in local distribution of soil resources along the chronosequence, geo-chronological evolution, will be differentiated by the presence of soil biota.

The results demonstrate a significant decrease in organic carbon, whereas total soluble nitrogen increased with the increase in terrace age. These results are in agreement with others that changes in soil nutrient content are not always congruent, due to the relatively high nitrogen input via desert dust (Offer & Steinberger, 1994; Ward et al., 2001) and the uptake of soil biota (Whitford, 2002).

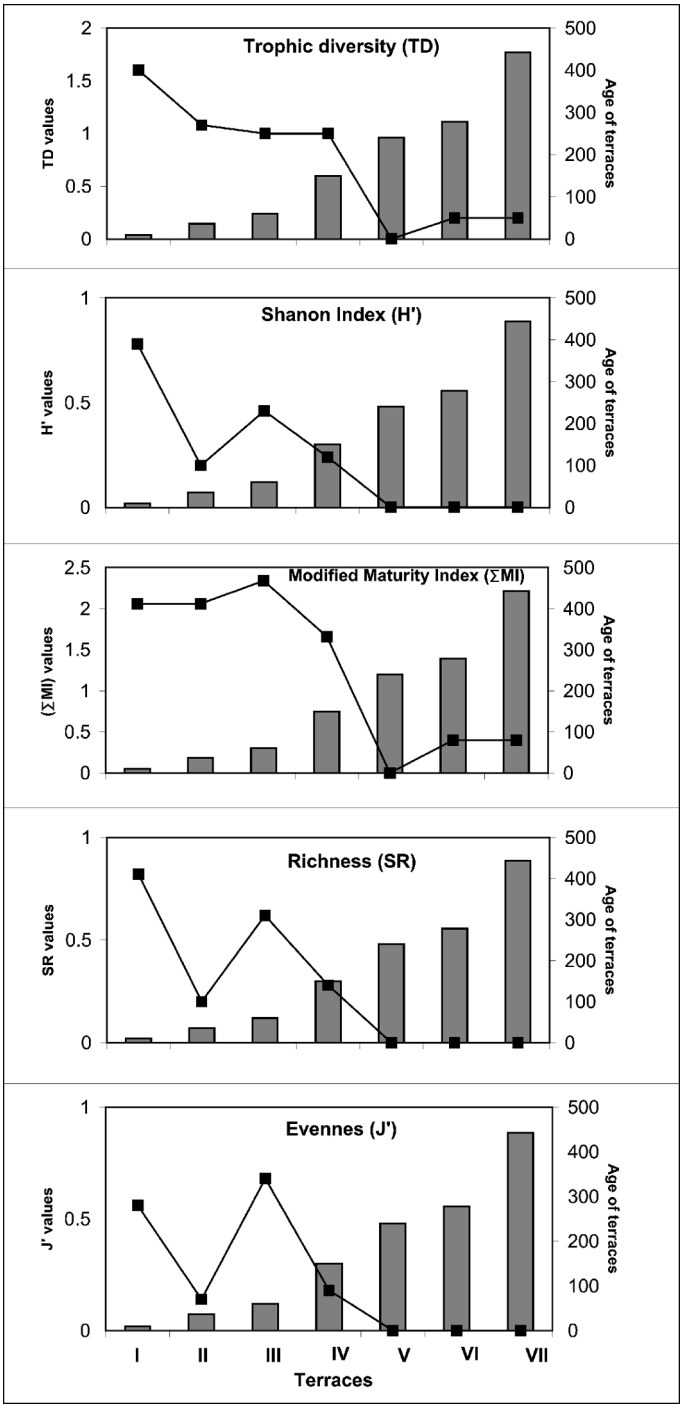

Figure 5. Ecological indexes values for the soil free-living nematodes in soil samples taken from the different terraces at the Makhtesh Ramon erosion cirque. 1 – Terrace I; 2 – Terrace II; 3 – Terrace III; 4 – Terrace IV; 5 – Terrace V; 6 – Terrace VI; 7 – Terrace VII.

In their studies, Plakht et al. (2000) were able to define the age structure and negative impact of erosion without emphasizing the changes in soil quality. The consistent results of abiotic parameters for different terrace ages elucidate the importance of soil quality modification, evolution, and the changes undergone on a chronosequence basis. The soil biota community is an essential component of soil viability, which diminished during the studies on soil quality. They are known to be the primary recyclers of carbon and nitrogen in the soil environment and are important in the production and consumption of soil gas, mobilization of nutrients and metals, and the dissolution of soil minerals.

The consistent results in microbial and nematode population activity were found to be complementary with the increase in terrace age, followed by changes in carbon and total soluble nitrogen in the soil samples. Such changes could be caused at the first step by immobilization activity of soil biota that in the young terraces have a relatively high carbon and nitrogen content. We assume that the increase in nitrogen levels with the increase in terrace age originates in inputs of airborne particles (Offer et al., 1996).

The coherent decrease in the number of soil free-living nematode trophic groups, species richness, and ecological indices with the increase in terrace age, may be consistent with Grime's (1979) "Intermediate Disturbance Hypothesis." According to this hypothesis, stable environments tend to have few species that are able to dominate the others, whereas in highly disturbed sites, only a few species can withstand the extreme conditions and are able to fulfill their biological functions. The geochronological evolution, morphology, and sedimentary structure of alluvial terraces developed under changing climatic conditions create many unique niches where divergence can be compared in many species from prokaryotic bacteria to eukaryotic populations. The study along these terrace's chronosequence pediment terraces, which permit multiple taxon comparison and generalization of organism-environment relationships, can lead to the understanding of evolutionary forces in biodiversity patterns, adaptation, and specialization, as suggested by Nevo (1997) for the "Evolution canyon."

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