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RESEARCH ARTICLE

Do slope orientation and sampling location determine soil biota composition?

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Abstract "Evolution Canyon" is a typical Mediterranean-basin canyon with a summer dry stream at the bottom and large differences in vegetation cover and solar radiation between the north-facing slope (NFS) and the south-facing slope (SFS). It is known to act as an abiotic mediator influencing the community structure of soil fauna. The aim of this study was to determine the spatial dispersion of soil microbial and free-living nematode communities in the open sites (between shrubs) in the upper (0–10 cm) soil layer at four altitudes on both slopes. The combination of relative soil moisture availability and temperature, known to be one of the main triggers for soil biota activity, was explained by slope orientation. The above-mentioned differences were found to significantly affect microbial biomass and CO_2 evolution resulting in temporary stress, corresponding to higher values in metabolic quotient (qCO_2) values. These differences may represent microbial investment in energy in order to overcome stress resulting from the microclimatic differences between the two slopes. Moreover, the degree of substrate limitation (primary production due to the differences in plant cover) of microbial activity was explained by the difference in microbial functional groups. The total abundance of soil free-living nematodes was found to be 2-fold higher on the SFS than on the NFS. Thirty-nine genera, including 12 bacteria-feeders, 5 fungi-feeders, 12 plant-parasites, and 10 omnivore-predators, were found at the study site, with 34 genera on the NFS and 29 on the SFS. The generic diversity of the bacteria-feeding nematodes was higher on the SFS than on the NFS. This study elucidates the importance of slope orientation and its effect on the structural levels of soil microbial and nematode communities.

Keywords community structure, "Evolution Canyon", free-living nematode, sampling location, slope orientation

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1 Introduction

Soil contains a naturally occurring layer composed of mineral organic material and biota components that are capable of supporting plant growth by their intensive interactivity at different depths. Any particular type of soil anywhere on earth is a result of parent material, climate, biota, and topography, on a time scale. "Evolution Canyon" is an impressive Plio-Pleistocene canyon dated to 3–5 million years of age (Nevo, 1995), with a similar geological formation. The uniqueness of this canyon is in its two opposite slopes, which have different orientations (south and north), with the same slope and length (400 m from the bottom to the top), separated at the bottom by 100 m, and which display a dramatic physical and biotic contrast at the microscale level (Nevo, 1994). In spite of the small distance between the two slopes, Auslander et al. (2003) showed the existence of a sharp and significant difference in microclimatic conditions influencing the biology, biodiversity, and ecology of aboveground organisms, leading to an increasing divergence between species located on the south-facing slope (SFS) and the north-facing slope (NFS). Due to its uniqueness, the SFS, often called the Afro-Asian slope, is dominated mainly by paleotrophic, xeric biota, whereas the NFS, often called the Euro-Asian slope, has a higher density of mesic temperate species (Nevo, 1994, 2001). Long-term studies conducted by Nevo (1997) at the "Evolution Canyon" microsite attempted to draw generalizations across life and organizational levels and to highlight controversial and unresolved problems of biological evolution. Hutchinson (1959) emphasized that one of the important questions in ecology is, "Why are there so many different organisms on earth?" In trying to answer this, Rosenzweig (1995) showed that most available data were on macroorganisms, while considerably less knowledge is available on microorganisms, which were rarely incorporated into studies on diversity, composition, trophic composition, etc. (Tiedje,

1995; Ohtonen et al., 1997; Schlapfer and Schmid, 1999; Broughton and Gross, 2000).

Temperature, radiation, moisture availability, evaporation, and other abiotic variables affect plant coverage and soil communities separately, although they are functionally linked. Few studies have examined the co-variation of the topography and the diversity of plant and soil biota communities. Primary production is known to be the main source of C and N (Zak et al., 1990, 1994) and determines the composition and diversity of the soil biota, especially those associated with the plant community (Whitford, 2002).

Soil microbial and free-living nematode communities were chosen for study at this "Canyon Evolution" site in order to elucidate this interplay between biotic and abiotic components. The soil microbial community is an integral part of all existing living ecosystems and plays a significant and often unique role in various biological processes such as nitrogen fixation and the transformation and elaboration of dead organic compounds (Paul and Clark, 1989; Wardle et al., 1999; Coleman et al., 2000).

The soil free-living nematode community is known as one of the most important components of the soil biota (Sohlenius, 1980; Bongers, 1990; Whitford, 2002) and is an important factor in regulating the microbial community. The community distribution and density are correlated with plant distribution and, in addition, strongly correlated with abiotic factors (Yeates, 1982; Steinberger and Loboda, 1991; Liang et al., 2000; Wright and Coleman, 2000; Pen-Mouratov et al., 2004a; Li et al., 2008).

Nevo (1995, 2001) and Finkel et al. (2001) studied "Evolution Canyon" and demonstrated that the plants covering the opposite slopes differ significantly from each other. The opposing slopes share the same geology with limestone from the upper Cenomian period (Ellanskaya et al., 1997). However, due to interslope differences in topology and geographic orientation, the slopes of the canyon differ both physically and biotically. The SFS of the canyon, called the "Afro-Asian," receives up to 600% more solar radiation than the mild NFS, called the "Euro-Asian." The SFS dips 43°C, whereas the NFS inclines at 33°C. The SFS is warmer, drier, and characterized by larger spatial and seasonal changes in temperature and more dryness than the NFS. Due to these differences, the southern "African" slope creates a warmer, drier, and climatically more fluctuating environment than the northern "European" slope (Dvornyk et al., 2002). Such ecological contrasts produce significant biotic and abiotic differences between the two slopes. The SFS harbors African-like xeromorphic vegetation, whereas the cooler and wetter NFS is covered by Mediterranean dense green (Nevo, 1995).

A strong effect on different aboveground and belowground processes is inevitable due to the strong correlation between plant coverage and microclimatic differences between the two slopes. We hypothesized that there would be a close association between slope orientation and sampling location throughout the slope and the soil microbial and nematode communities. The aim of the present study was to determine the importance of slope orientation on the soil microbial community and its effect on the trophic levels, community structure, and generic diversity of soil free-living nematodes.

2 Materials and methods

2.1 Study site

The study site chosen was at "Evolution Canyon," lower Nahal Oren, Mount Carmel, Israel (32°43′ N; 34°58′ E). It consists of opposite south-facing and north-facing slopes where other studies, as reported above, had been carried out (Nevo, 1994, 1995). These two slopes dip 35° and 25° and are 120 and 180 m long, respectively (Nevo, 1994, 1995). The canyon was eroded from tectonically uplifted upper Cenomanian limestone (Karcz, 1959). It is geologically identical on both slopes, and is characterized by a regional Mediterranean climate (Atlas of Israel, 1970). Solar radiation on the SFS is significantly higher (up to 300% more) than on the NFS (Nevo, 1997).

"Evolution Canyon" is a typical Mediterranean-basin canyon with a summer dry stream at the bottom and sharply contrasting microclimates between the SFS and the NFS, clearly demonstrated by sharp biotic contrasts (Nevo, 2001). The SFS represents a broader niche (van Valen, 1965) with tropical, dry, savanna-like biota. It contains more microhabitat patches than the NFS, exhibiting a mosaic of habitats consisting of open park-forest of *Ceratonia siliqua*, *Pistacia lentiscus* plant association, a savanna plant formation, and bushy islands. In contrast, the milder and more homogeneous NFS consists of lush and dense live-oak Maqui forests with a few island openings between the plant cover.

Four sampling stations (STs) on each slope (a total of eight) were established in the summer of 2004. The stations on the slopes were located from the foot of the canyon to the top with 45-m intervals on the NFS and 30-m intervals on the SFS (Fig. 1). Four replicates were collected from the upper (0–10 cm) soil layer of each of the eight stations.

2.2 Laboratory analysis

Soil water content was determined gravimetrically (105°C, 48 h). Soil organic carbon was determined by oxidization with dichromate in the presence of H_2SO_4, without application of external heat (Rowell, 1994). pH was determined in H_2O (soil:solution ratio 1:2.5) with a potentiometric glass electrode. Soluble cation (Ca^{2+}) was determined by a flame photometer (Rhoades, 1982).

Soil nematodes were extracted from 100-g soil samples

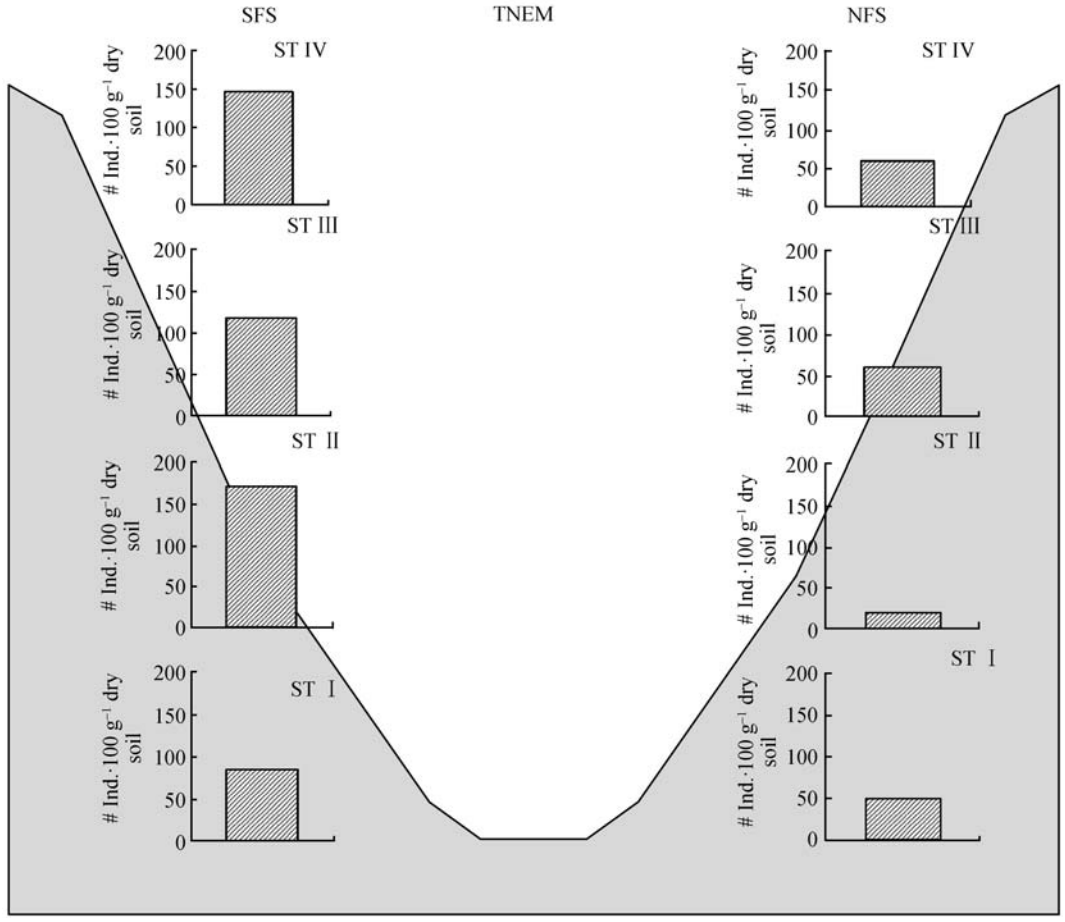

Fig. 1 Mean abundance of soil free-living nematodes at the sampling locations on the south-facing (SFS) and north-facing (NFS) slopes in "Evolution Canyon". TNEM: total number of nematodes(individuals per 100 g dry soil); ST: sampling station.

using the Baermann funnel procedure (Cairns, 1960). The recovered organisms were counted and preserved in formalin (Steinberger and Sarig, 1993), and identified according to order, family, genus level, sex definition (male, female), and juveniles (Yeates, 1972) using a compound microscope. The 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; Steinberger and Loboda, 1991; Pen-Mouratov et al., 2004a, 2004b); (3) Trophic diversity $T = 1/\sum pi^2$, in which pi is the proportion of the *i*-th trophic groups (Heip et al., 1988); (4) Dominant, $\lambda = \sum pi^2$ (Simpson, 1949); (5) Shannon index, $H' = \exp(-\sum pi[\ln pi])$, where p is the proportion of individuals in the *i*-th taxon (Shannon and Weaver, 1949); (6) Maturity indices (MI), a measure based on life-history strategy characteristics of nematode taxa (Bongers, 1990); and (7) Maturity index modification (∑MI), which includes plant-feeding nematodes (Yeates, 1994).

Fungal and bacterial visible count (CFU) were measured. Microbial populations were quantified using the soil dilution plate count method. Duplicate soil dilutions were plated on tryptic soy agar (Martin, 1975) and Martin's Rose-Bengal agar (Martin, 1950) for enumeration of bacteria and fungal populations, respectively. Soil microbial biomass and CO_2 production were evaluated using an infrared gas analyzer (IRGA), which measures the CO_2 levels produced by soil (Heinemayer et al., 1989; Kaiser et al., 1992). Atmospheric CO_2 levels were used as a baseline. In order to measure soil respiration, 100-g subsamples were used after increasing the soil moisture up to 40% of the soil water-holding capacity. The subsamples remained under stable air flow, in the dark, with incubation at 22°C under the control of the IRGA system for 24 h. The IRGA unit is a 24-channel computerized system that records CO_2 levels. It can continuously determine both microbial activity and microbial biomass. These two results enable calculation of the competition efficiency of the soil microbial population under environmental conditions, which is

termed the metabolic quotient (qCO_2 index) and calculated as follows:

$$qCO_2 = \frac{CO_2 \text{production}}{\text{biomass}}.$$

The qCO_2 is a specific parameter for evaluating the effects of environmental conditions on the soil microbial biomass (Anderson and Domsch, 1978, 1993). Subsamples of 25 g each were used for measuring the soil microbial biomass with the substrate-induced respiration method. These subsamples were wetted and incubated as described above. A mixture of glucose and talcum (1:3) was added to each subsample, which was kept under the same conditions under IRGA control for 8 h. The microbial coefficient, known as the ratio between microbial biomass carbon to total organic carbon (C_{mic}/C_{org}), was determined in order to evaluate substrate availability (Insam et al., 1989, 1996).

All data were subjected to statistical analysis of variance using the SAS model (GLM, 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. In addition, the data were tested by computing redundancy discriminate analysis (RDA) in order to provide more information by taking into account the slope orientation. The sampling sites along the slopes were related to the different soil biotic components and the soil physical parameters in order to obtain the proportional variations that contribute to the understanding of each component (Braak–Canoco; ter Braak, 1986). The Monte Carlo permutation test was used to calculate the significance of a given factor and, thus, its relevance to measurable parameters (ter Braak and Prentice, 1996).

3 Results

3.1 Soil properties

Soil water content (SWC) was found to range between 5.1% and 6.0%, with no significant differences between the slopes or between the different sampling locations along the slopes (Tables 1 and 2). A similar trend was observed for total soil organic carbon (C_{org}), where the values ranged between 3.0% and 5.3% (Tables 1 and 2).

Soil pH was found to vary compared with the SWC and C_{org}. The pH values exhibited differences between the two slopes ($P < 0.0001$) as well as along the sampling stations on the slope, reaching the highest values on the SFS (pH 8.3), and lower values on the NFS (pH 7.8; Tables 1 and 2).

The calcium content was found to decrease with altitude on the NFS from the bottom station to the upper part, from 378.3 to 99.0 $mg \cdot kg^{-1}$, a decrease of more than 4-fold. On the opposite (SFS) slope, the values ranged from 99.0 to 153.8 $mg \cdot kg^{-1}$, without any observed trend, leading to negligible differences along the slope (Table 1). The lowest Ca^{2+} concentrations ($P < 0.0003$) were found on the top of each slope (90 and 99 $mg \cdot kg^{-1}$ on SFS and NFS, respectively), also leading to significant differences between the slopes (Table 2).

3.2 Nematode abundance and community structure

The mean density of soil nematodes of each slope was found to be significantly higher on the SFS (131 individuals $\cdot 100\ g^{-1}$ dry soil) than on the NFS (64 individuals $\cdot 100\ g^{-1}$ dry soil; Fig. 1 and Table 1). The total number of nematodes was greatest (171.3 individuals $\cdot 100\ g^{-1}$dry soil) at the second sampling site (station II) on the SFS and lowest (20.6 individuals $\cdot 100\ g^{-1}$

Table 1 Statistical data of soil properties and total number of soil free-living nematodes (TNEM) from different altitudes on different slopes of "Evolution Canyon"

slope/location	SWC/%	C_{org}/%	pH	Ca^{2+}/ $mg \cdot kg^{-1}$	TNEM
NFS					
ST I	5.98±1.16^{a}	5.33±0.98^{a}	7.03±0.10^{d}	378.25±144.4^{a}	70.5±51.4^{ab}
ST II	5.63±0.87^{a}	3.48±2.03^{a}	8.25±0.06^{a}	188.25±72.38^{cb}	23.5±23.2^{b}
ST III	5.88±1.20^{a}	4.28±1.18^{a}	7.68±0.10^{c}	125.25±30.02^{cb}	78.5±45.8^{ab}
ST IV	5.43±0.42^{a}	4.05±0.48^{a}	8.33±0.05^{a}	90.00±16.99^{c}	84.3±32.9^{ab}
SFS					
ST I	5.28±0.37^{a}	4.13±0.25^{a}	8.18±0.10b^{a}	132.25±28.84^{cb}	85.5±64.7^{ab}
ST II	5.45±0.47^{a}	4.37±0.40^{a}	8.30±0.02^{a}	104.75±40.72^{c}	171.3±45.5^{a}
ST III	5.08±0.33^{a}	3.93±0.21^{a}	8.08±0.05^{b}	153.75±45.89^{cb}	117.8±76.7^{ab}
ST IV	5.08±1.46^{a}	3.08±1.40^{a}	8.20±0.01b^{a}	99.00±47.62^{c}	148.5±34.3^{ab}

NFS: north-facing slope; SFS: south-facing slope; ST: sampling station; SWC: soil moisture; C_{org}: organic matter; Ca^{2+}: calcium; TNEM: total number of nematodes (individuals per 100 g dry soil). Significant differences ($P < 0.05$), according to Duncan's Multiple Range Test between sampling sites are indicated by different uppercase letters.

Table 2 Univariate analysis of variance (GLM) for soil properties, bacteria, fungi, nematodes and ecological indices on the different slopes and different altitudes of "Evolution Canyon"

indicator	between slopes		between altitudes	
	F-test	*P* value	*F*-test	*P* value
SWC	0.53	NS	0.48	NS
C_{org}	0.06	NS	1.48	NS
pH	119.5	0.0001	90.48	0.0001
Ca^{2+}	37.57	0.0001	9.03	0.0003
TNEM	12.34	0.002	2.05	0.049
BF	21.98	0.0001	1.46	NS
FF	1.72	NS	1.61	NS
PP	20.89	0.0001	2.28	NS
OP	3.13	0.05	2.7	0.04
J	8.27	0.009	0.49	NS
F	0.02	NS	4.81	0.008
M	3.81	NS	0.3	NS
T	4.2	0.048	1.26	NS
λ	0.96	NS	2.05	0.049
H′	10.9	0.002	1.75	NS
MI	0.33	NS	2.31	0.03
ΣMI	0.04	NS	1.4	NS
bacteria (CFU)	0.65	NS	0.89	NS
fungi (CFU)	0.47	NS	2.49	0.05

Note: Trophic structure: BF, Bacterivores; FF, fungivores; PP, plant-parasites; OP, omnivores-predators. J, juveniles; F, female; M, male. Ecological indices: T, trophic diversity; λ, dominance; *H′*, Shannon Index; MI, maturity index; ΣMI, modified maturity index; NS, non-significant; SWC, soil moisture; TNEM, total number of nematodes (individuals per 100 g dry soil).

dry soil) at station II on the NFS (Fig. 1 and Table 1). The total number of soil nematodes was found to be statistically different between slopes ($P < 0.002$) and between altitude stations ($P < 0.05$; Tables 1 and 2 and Fig. 1), although no significant differences were obtained between the same sampling locations of the two slopes except for station II. This might be the case affecting all the data analyses (Table 1).

The percentages of the four trophic groups, BF, FF, PP, and OP, were found to be 34.4, 14.2, 29.1, and 22.3, respectively, on the SFS, and 30.7, 26.1, 32.2, and 19.9, respectively, on the NFS (Table 3). From the total of four trophic groups, only the BF, PP, and OP were found to show significant differences between the two slopes (Fig. 2A and Table 2).

The total number of juveniles in the soil samples collected at the different locations exhibited a significantly higher density on the SFS (86 individuals$\cdot 100\,g^{-1}$ dry soil) than on the NFS (31 individuals$\cdot 100\,g^{-1}$ dry soil; $P < 0.009$; Fig. 2B and Table 2). However, no differences were observed in sex density between males and females of soil free-living nematodes between the slopes (Fig. 2B and Table 2). However, the density of the females was found to increase significantly along the altitude on the SFS ($P < 0.008$), increasing from 0 to 37.7 individuals$\cdot 100\,g^{-1}$ dry soil, whereas the total number of both males and juveniles was found to be distributed homogenously along the canyon slopes.

3.3 Generic diversity

A total of 39 genera, including 12 bacteria-feeders, 6 fungi-feeders, 12 plant-parasites and 9 omnivore-predators, were found in the soil samples collected during the study period on the NFS and the SFS, and amounted to 34 and 29 genera, respectively, at the above-mentioned sampling sites (Table 3). The total number of bacteria-feeding genera was 1.5-fold higher on the SFS than on the NFS, whereas the total number of fungi-feeding, plant-parasite, and omnivore-predator genera was 1.3-, 1.4-, and 2-fold lower, respectively, on the SFS than on the NFS.

3.4 Ecological indices

A total of five ecological indices—trophic diversity (T), genus dominance (λ), Shannon index (*H′*), maturity index (MI), and maturity index modification (ΣMI)—were used to assess soil environmental differences between and along the slopes (Fig. 3A and B and Table 2). Our results demonstrated that the trophic diversity (T) and Shannon

Table 3 Changes in abundance of soil nematodes on SFS and NFS of "Evolution Canyon"

trophic groups/genus[a]	c-p value[b]	SFS	NFS
bacterivores			
Acrobeles	2	4 (0–32)	0
Acrobeloides	2	9 (0–11)	3 (0–17)
Cephalobus	2	10 (0–42)	3 (0–16)
Cervidellus	2	6 (0–19)	8 (0–45)
Chiloplacus	2	9 (0–28)	6 (0–36)
Eucephalobus	2	0.7 (0–8)	0.2 (0–2)
Monhystera	2	7 (0–36)	4 (0–22)
Panagrellus	1	0.5 (0–8)	0
Panagrolaimus	1	5 (0–21)	3 (0–17)
Plectus	2	0.7 (0–11)	0
Rhabditis	1	0.6 (0–10)	0.3 (0–3)
Wilsonema	2	3 (0–20)	0
ITG[c]		34.4	30.7
fungivores			
Aphelenchoides	2	9 (0–38)	12 (0–81)
Aphelenchus	2	9 (0–54)	7 (0–22)
Ditylenchus	2	1 (0–10)	0.4 (0–4)
Nothotylenchus	2	0	2 (0–8)
Paraphelenchus	2	4 (0–23)	2 (0–17)
Tylencholaimus	4	0	2 (0–9)
ITG		14.2	26.1
plant-parasites			
Filenchus	2	4 (0–19)	3 (0–9)
Hoplotylus	3	1 (0–16)	1 (0–17)
Longidorus	5	0	0.3 (0–4)
Paratylenchus	2	6 (0–32)	3 (0–9)
Pratylenchus	3	7 (0–32)	2 (0–27)
Telotylenchus	3	13 (0–58)	0.9 (0–7)
Tetylenchus	2	0	2 (0–22)
Tylenchorhynchus	3	13 (0–58)	2 (0–9)
Tylenchus	2	2 (0–13)	6 (0–36)
Trophonema	2	1 (0–16)	0
Trophurus	3	0	0.5 (0–4)
Xiphinema	5	0	0.6 (0–9)
ITG		29.1	23.2
omnivores-predators			
Discolaimus	5	0	0.9 (0–11)
Dorylaimus	4	10 (0–42)	3 (0–9)
Eudorylaimus	4	11 (0–42)	6 (0–18)
Mesodorylaimus	5	3 (0–21)	1 (0–8)
Mononchus	4	0	0.2 (0–3)
Nygolaimus	5	7 (0–43)	2 (0–9)
Paractinolaimus	4	0	0.7 (0–9)
Prionchulus	4	0	2 (0–9)
Tobrilus	3	5 (0–23)	2 (0–11)
ITG		22.3	19.9

[a]: by classification of Yeates and King (1997); [b]: values taken from Bongers (1990); [c]: relative input (%) of each trophic group in a nematode trophic assemblage. ITG: initiation time of germination.

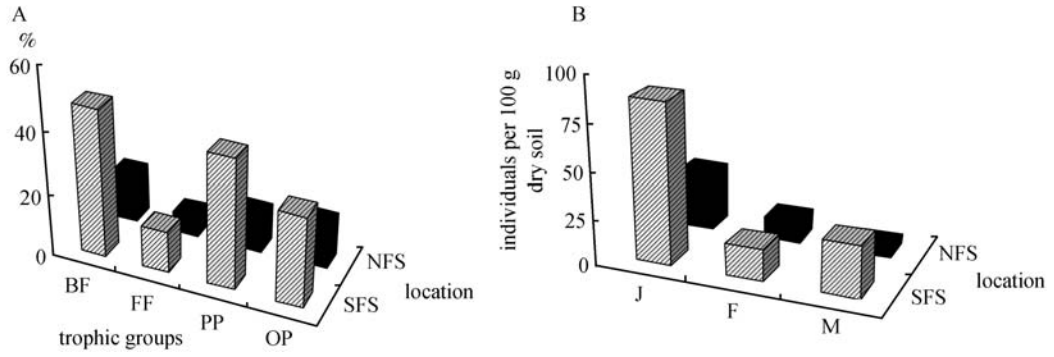

Fig. 2 Distribution of nematode trophic groups (A) and sexual differences (J: juveniles; M: male; F: female) (B) in the nematode population on opposite (SFS, NFS) slopes of "Evolution Canyon"

index (H') exhibited significant (below $P < 0.05$) differences between slopes (Table 2 and Fig. 3A). The genus dominance (λ) along with the maturity index (MI) was found to be useful tools for differentiation between the different sampling sites along the altitude ($P < 0.05$; Table 2 and Fig. 3A and B).

3.5 Bacteria and fungi (CFU)

The bacterial population in the soil samples was found to range between 270×10^9 and 504×10^9 CFU·g^{-1} dry soil. Although no significant differences were observed between the two slopes, the results (Fig. 4) show two different trends for the two slopes. On the NFS, the bacterial population increased with elevation, with a decrease at the last sampling location. An opposite trend was observed on the SFS, with an increase from the top sampling site toward the bottom of the slope, although a decrease was obtained at station I. The lowest number of bacterial-colony-forming units (270×10^9 CFU·g^{-1} dry soil) was found in the soil collected at the control site, in the valley between the northern and southern slopes.

A data set almost paired to the bacterial counts was obtained for the fungi population (Fig. 4), which exhibited a relatively high count at station I on the NFS as well as at station II on the SFS.

3.6 CO_2 evolution and microbial biomass

CO_2 evolution ranged between 0.5 and 2.4 μg CO_2-C (g soil·h)$^{-1}$, with no significant differences between the two slopes (Fig. 5A). On the SFS, the highest as well as the most significantly different value was obtained at station III (2.4 μg CO_2-C (g soil·h)$^{-1}$). This value decreased gradually to the control sampling site, where the lowest value was obtained at the top location (station IV). On the NFS, an opposite trend was observed, starting at station IV (1.0 μg CO_2-C (g soil·h)$^{-1}$) at the top, increasing toward station II (2.2 μg CO_2-C (g soil·h)$^{-1}$), followed by a significant decrease at station I [0.5 μgCO_2-C (g soil·h)$^{-1}$; Fig. 5A].

Soil microbial biomass exhibited a relatively wide range of values, from 18 μg C·g^{-1} soil on the SFS (station IV) to 122 μg C·g^{-1} soil on the NFS (station I; Fig. 5B). The soil microbial biomass in samples collected from the SFS had a mean value of 28.3 μg C·g^{-1} soil, which was significantly ($P < 0.03$) lower than that of the NFS, with a mean of 73.5 μg C·g^{-1} soil. No significant differences between the sampling sites along the slope were obtained for the SFS, while on the NFS, station I was found to be significantly ($P < 0.03$) lower than the other northern sampling sites.

Metabolic quotient (qCO_2) coefficient values were found to be significantly higher ($P < 0.02$) on the SFS than on the NFS, elucidating the significant xeric pressure on the former compared with the latter (Fig. 5C).

Figure 6 displays the main variations in the abiotic and biotic variables measured in relation to sampling location. The NFS and the SFS exhibit clear discrimination, with a significant difference between the slopes (elucidated by the length and direction of the arrow), followed by similar discrimination between the two sampling-site locations 2 and 3 along the slopes. In a redundancy analysis (RDA; Fig. 6), all the abiotic variables and the bacterial community (with a significantly shorter arrow–indicating a weak correlation) indicated by arrows point in the same direction, signifying a positive correlation in the NFS. In contrary to the above trend, the fungi and total soil free-living nematode community tend to be positively correlated with the SFS (Afro-Asian slope).

Figure 7 displays the variation in the nematode community trophic composition, with a strong relation between the bacteria feeders (BF), omnivore-predators (OP), and plant parasites (PP) and the SFS. The NFS was found to be only weakly correlated with fungi feeders (FF).

4 Discussion

The uniqueness of this canyon is in its two opposite slopes of different orientations (south and north), displaying a dramatic physical and biotic contrast at the

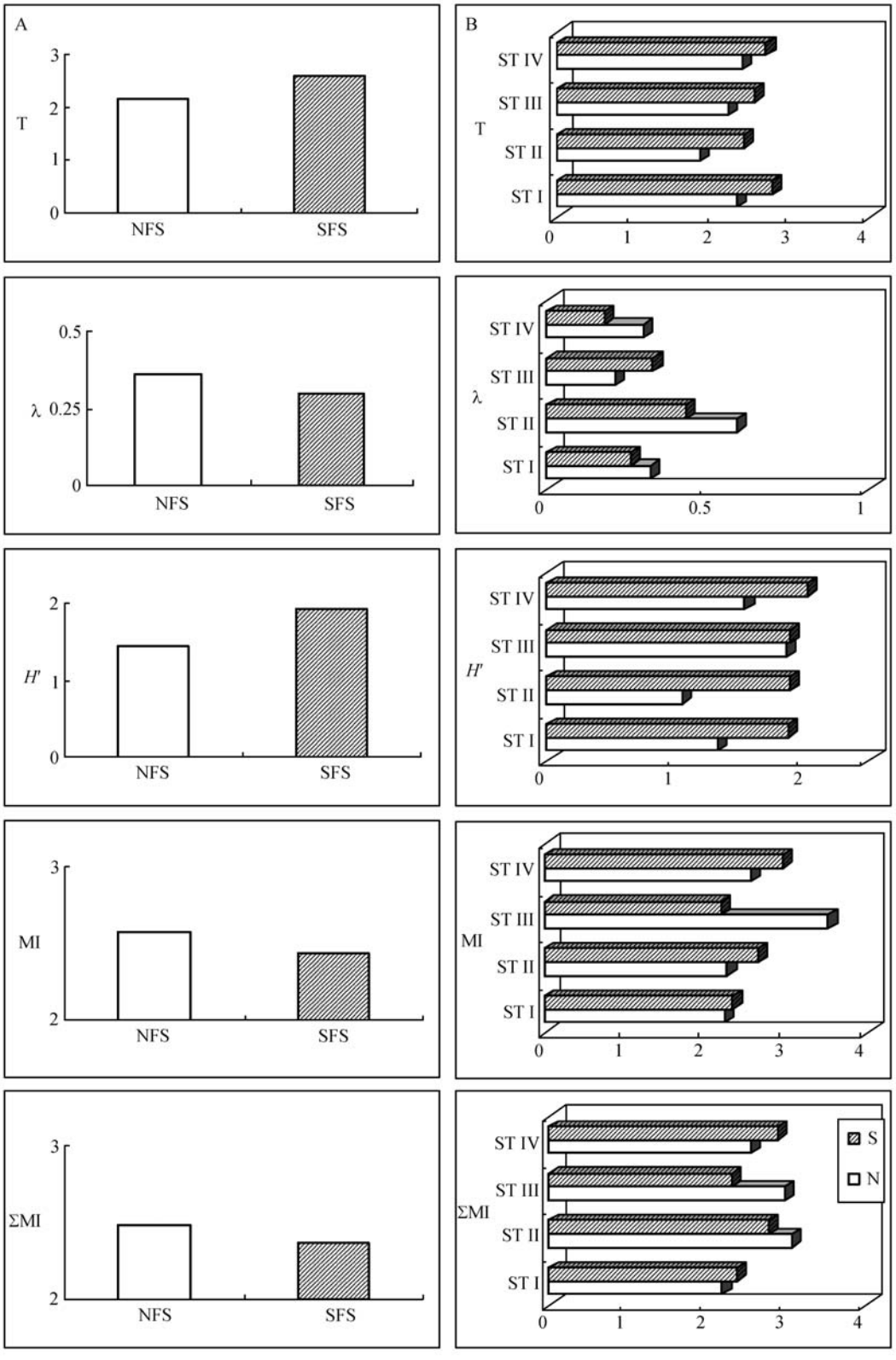

Fig. 3 Ecological index values of soil free-living nematodes at the different (SFS, NFS) slopes (A) and at the different sampling locations along the slopes (B) (T: trophic diversity; λ: dominance; *H'*: Shannon index; MI: maturity index; ΣMI: modified maturity index)

microscale level (Nevo, 1994). Auslander et al. (2003) had demonstrated the existence of a sharp and significant difference in microclimatic conditions. As a result, the SFS, often called the Afro-Asian slope, is dominated

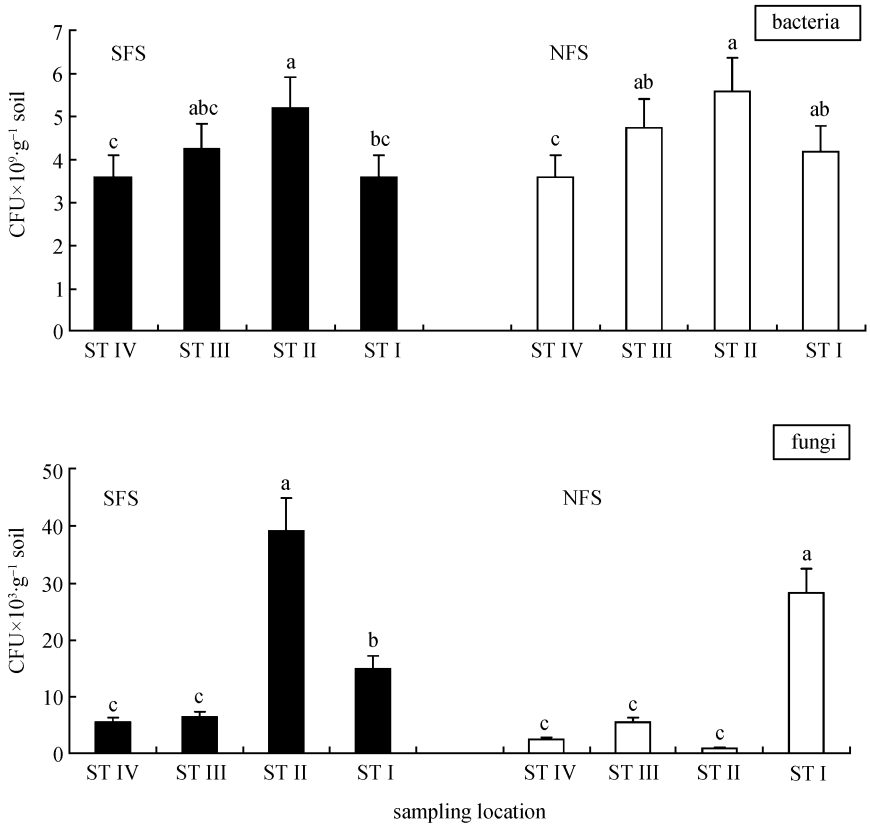

Fig. 4 Mean values of bacteria and fungi colony-forming units (CFUs) at the different sampling locations on the south facing slope (SFS) and the north facing slope (NFS) at the study site

mainly by paleotrophic, xeric biota, whereas the NFS, often called the Euro-Asian slope, has a higher density of mesic temperate species (Nevo, 1994, 2001).

In his studies at the "Evolution Canyon" site, Nevo (1995, 1997, 2001) found that the species richness of the so-called terrestrial taxa, which included a wide range of biota, e.g., cyanobacteria, land snails, scorpions, beetles, moths, grasshoppers, butterflies, reptiles, birds, and rodents, was found at a higher density on the SFS than on the NFS. However, other components of biota, e.g., euglenophyta, bacillariophyta, lichens, micromycetes, agaricales, and mosses, exhibited an opposite trend, with SFS > NFS.

The present study demonstrates a more complex distribution of the free-living nematode community than for previously studied organisms. On the one hand, the genus diversity of nematodes was higher on the NFS, so they could be attributed to the aquatic-dependent taxa, according to the above gradation. On the other hand, the greater abundance of nematodes on the SFS raises more questions. A more detailed analysis showed that certain groups of nematodes prefer the southern to the northern slope. Using names for our nematode community similar to those used by Nevo (1997, 2001), such as terrestrial and aquatic-dependent, enabled us to divide the species into terrestrial (i.e., *Acrobeles*, *Panagrellus*, *Plectus*, *Wilsonema*, and *Trophonema*, which were found only on the SFS) and aquatic-dependent (i.e., *Nothotylenchus*, *Longidorus*, *Tetylenchus*, *Trophurus*, *Xiphinema, Discolaimus*, *Mononchus*, *Paractinolaimus*, *Prionchulus*, and *Tylencholaimus* species, which were found only on the NFS). Moreover, of the total 39 observed nematode genera, 24 were found to be present on both the Afro-Asian and the Euro-Asian slopes.

According to Pavliček et al. (2002), evolutionary forces control the heterogeneity of biodiversity at the microgeographic level and increase biodiversity differences under conditions of contrasting microclimates. According to our study, slope orientation affects structural levels of the soil nematode population, including the trophic level. Therefore, the diversity of BF nematodes was found to be higher on the SFS than on the NFS, while the diversity of the FF, PP, and OP nematodes was higher on the NFS. Considering the contribution of separate trophic groups within the trophic nematode assemblage on the two slopes, we can conclude that the input of FF nematodes in the trophic assemblage of nematodes on the NFS is greater than on the SFS. According to Yeates (1982), de Goede and van Dijk (1998), and Pen-Mouratov et al. (2004b), one of the reasons for the difference in nematode abundance and species diversity observed on the two slopes may be differences in the type and physical characteristics of the

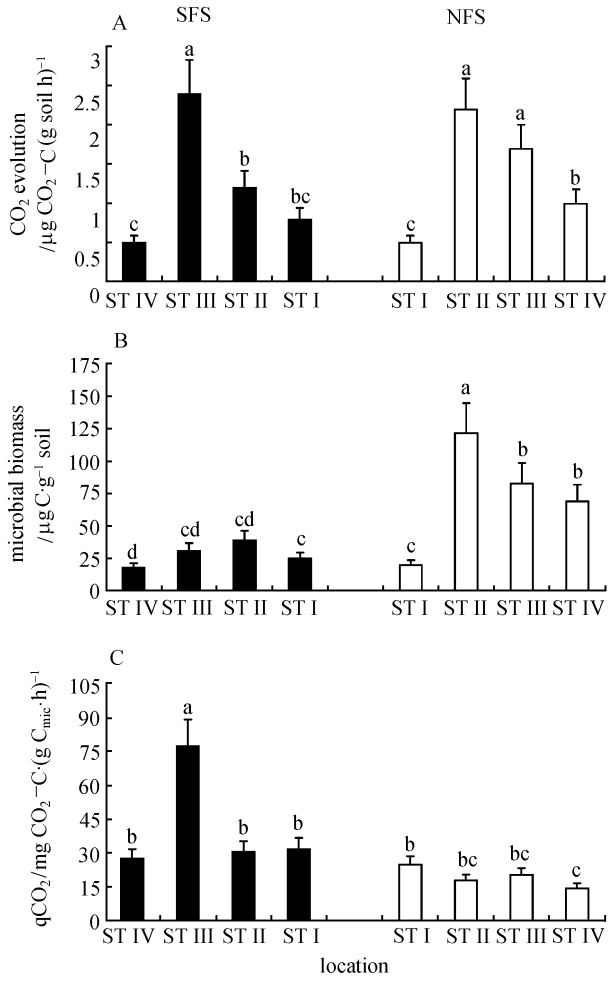

Fig. 5 Mean values of microbial activity expressed as CO_2 evolution (A), microbial biomass (B), and qCO_2 (C) at the different sampling locations along the SFS and the NFS at the study site in "Evolution Canyon"

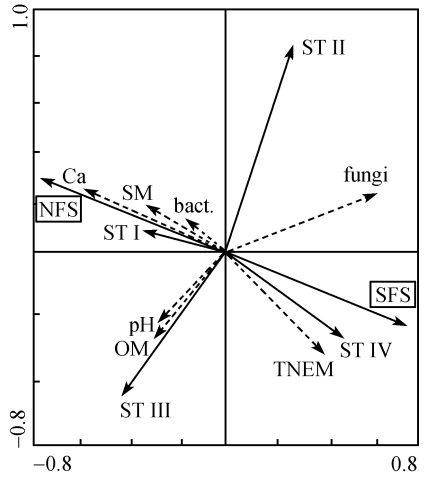

Fig. 6 Ordination diagram showing the spatial distribution in the different abiotic variables (SM: soil moisture; OM: organic matter; pH; Ca: calcium) and the biotic components (TNEM: total soil free-living nematodes; Fungi, and Bac: bacteria) at the different sampling locations along the NSF and the SFS at the study site at "Evolution Canyon"

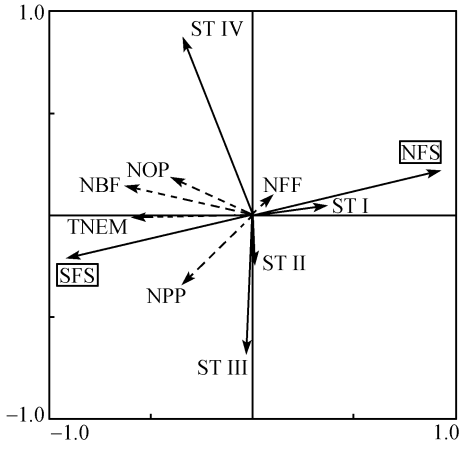

Fig. 7 Ordination diagram showing the spatial distribution of the different trophic group components of the soil free-living nematodes (NBF: bacterivores; NFF: fungivores; NPP: plant-parasites; NOP: omnivores-predators) and total nematode population (TNEM) at the different sampling locations along the slopes: station I (ST I), station II (ST II), station III (ST III), and station IV (ST IV) on both the NFS and the SFS at the study site in "Evolution Canyon"

soil, i.e., the southern slope is more alkaline than the northern slope. Another explanation for the higher total number of species on the NFS may indicate that the NFS is an older, more stable, climatic ecosystem with higher biodiversity than the SFS ecosystem (Odum, 1971).

Differences in the total number of juveniles between the two slopes demonstrated that the microenvironment also has a significant effect on the age-structure of the nematode population (Flegg, 1968; Yeates, 1979; van Straalen and van Gestel, 1993). Moreover, the microenvironment on the SFS created conditions for increasing the total number of juveniles, while the adult nematodes remained more resistant to the ecological differences of the studied microenvironments and were not different on the opposite slopes.

Ecological indices such as trophic diversity (Yeates and Bird, 1994; Steinberger et al., 2001; Neher and Darby, 2005) and Shannon index (Freckman and Ettema, 1993) were useful for defining the differences between the slopes, whereas the genus dominance (McSorley and Frederick, 1996) and maturity index (Bongers, 1990; Wasilewska, 1994) changed with altitude.

According to Comanor and Staffeldt (1978), the summer season is the time of maximum litter disappearance. Most of the annual primary production biomass will become a source for the decomposers, after the dry plant reaches the soil surface. The combination of relative soil moisture availability and temperature is known to be one of the main

triggers, providing the greatest potential for carbon loss (as CO_2) from the system. In such an optimal environment, the microbial community plays a key role in the decomposition and mineralization of dead organic matter, and thus in the cycling of carbon and nutrients.

Vance and Chapin (2001) suggested that differences in qCO_2 between forest ecosystems may reflect several kinds of disparities, such as differences in the proportion of inactive microbial biomass, in the degree of substrate limitation of microbial activity, or in the metabolic rates, turnover, and growth efficiency of different microbial functional groups. Moreover, lower values in microbial biomass, which may reflect temporary stress, correspond to higher values in qCO_2, which may represent microbial investment in energy in order to overcome this stress.

Anderson and Domsch (1993) found that as the level of environmental stress increased, the qCO_2 index values also increased. The results obtained in the present study are compatible with the above findings, where a relatively higher value of qCO_2 was found in the south-facing ("African") slope compared with the north-facing ("European") slope.

The multivariate approach stimulated us to look at the spatial variation and the contribution of the sampling location not only between the two slopes but also along the slope. The model has elucidated the importance of slope orientation and sampling location on biotic components (e.g., trophic composition and biological activity) as well as on abiotic variables that may lead to an increasing divergence of soil biota as reported in this study. Furthermore, this study elucidates the need for a more extended study with a strong emphasis on temporal as well as spatial dimensions.

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