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Spatial distribution of a microbial community in sandy soil ecosystems as a tillage mediator

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Abstract
The goal of the present study was to determine the influence of fine-scale landscape patchiness on abiotic components and microbial communities and the interplay of these two systems in sandy soil ecosystems. The fieldwork was carried out in stable sandy soil ecosystems near Caesarea, Israel, with a Mediterranean climate. In order to quantify the distribution of soil microbial communities at multiple spatial scales, a survey was conducted to examine the spatial organization of the community structure at two sandy soil sites, yielding a total of 144 soil samples collected from the 0-10 cm and 10-20 cm soil layers. Soil abiotic analysis was performed by soil standard analytical methods, while the biotic components were measured by using a MicroResp™ system. The results obtained established that microbial-community distribution can be highly structured, within a habitat that appears relatively homogeneous on a plot and field scale. This is due to spatial heterogeneity associated with soil physical, chemical, and biological properties. The study provided evidence that a spatially explicit approach to soil ecology can enable identification of factors that drive the spatial heterogeneity of populations and the activities of soil organisms at scales ranging from meters to hundreds of meters.

Key words: multi-scale variation, heterogeneity, CO_2 evolution, sandy soil ecosystem

Introduction

Sandy soils are often considered as having weak or no physical structure, poor water-retention properties, high permeability, and high sensitivity to compaction with many adverse consequences. Due to its weak structure, sandy soil compaction has a negative vertical as well as horizontal effect on physical and biological components from macroscopic to microscopic scales (3). Determination of a 'scale unit' that help understand ecological processes has become one of the important and most debatable problems in recent years. Recent studies have emphasized the importance and role of environmental factors in the erratic distribution of microbial communities in terrestrial ecosystems (4, 12). Since microorganisms play vital roles in surface and subsurface soil geology, hydrology, and ecology, knowledge concerning the microbial-community structure and its composition became important in improving our conceptual and projective understanding of surface and subsurface soil-ecosystem processes, functions, and management (17, 20). Soils are considered the most microbially diverse environments on earth (18). The abundance, composition, and diversity of microbial communities within soils were found to be strongly depth-dependent, as shown by Fierer et al. (8), LaMontagne et al. (11), Agnelli et al. (1), and Kemnitz et al. (9). In their study (1, 8, 9, 11), they showed that the bacterial biomass concentration (bacterial 16S rRNA genes), number of terminal restriction

fragment-length polymorphism peaks, denaturing gradient gel electrophoresis bands (representative of richness), and the proportion of Gram-negative to Gram-positive bacteria, are lower in subsurface than in surface soils. Multi-scale comparisons, in which patterns are analyzed at several different spatial scales, can be more useful when trying to identify the factors that control community development. The characterization of microbial communities on several different scales can help in explaining contradictions that arise by different investigators, studying similar communities on different scales, which reach different conclusions regarding the factors that structure these communities (13).

The present study was designed to address a general question related to multi-scale patterns of spatial organization of microbial community in two sandy soil ecosystems. The aim of the present study was to reveal the influence of fine-scale landscape-patch moisture and organic-matter heterogeneity on microbial-activity linkage in coastal sandy ecosystems. The three main questions are arising: (1) how do such heterogeneous environments affect microbial distribution, (2) how will microbial functional diversity be altered spatially and (3) how microbial community is important for the tillage processes in the sandy soil ecosystems.

Materials and methods

Study area: In order to undertake the present study, two sites were chosen: west and east, 100 and 4,000 m from the Mediterranean Sea shore, respectively, with similar plant cover and topography in a coastal sandy ecosystem. The western (32°28′N, 34°53′E) and eastern (32°28′N, 34°55′E) study sites were located in the northern Sharon region of Israel, south of Caesarea (6). The climate in the region is sub-humid Mediterranean. The annual amount of rainfall is 580 mm. The study sites are dominated by shrub associations (6, 7, 10).

Sampling: Soil samples were collected from the 0-10 cm and the 10-20 cm layers at each point of the 2 × 2 m grid-intersections in a 10/10 m plots, from each of the sites. A total of 144 soil cores from both study sites were collected, during wet season (December), from two depths using a 7-cm diameter soil auger. Each soil sample was placed in an individual plastic bag and transported in an insulated container to the laboratory, where it was stored at 4°C until biological and chemical analyses were conducted.

Laboratory analyses: All chemical and biological analyses were conducted on each replicates collected in the field from each treatment.

Abiotic parameters: Soil moisture (SM) was determined gravimetrically by drying the soil samples at 105°C for 24 h. The total organic carbon (TOC) content in soil samples was determined by muffling soil at 400°C.

Biotic parameters: Basal respiration (CO_2 evolution without the addition of any external substrate), of the microbial community, microbial biomass (MB) (2), the biomass-specific respiration rate or metabolic quotient (qCO_2), microbial functional diversity and community-level physiological profile (CLPP) in soils were measured with a MicroResp™ system (5).

Statistical analysis: Statistical analysis was conducted using JMP software (JMP version 10; SAS Institute, Inc., Cary, NC). Multivariate analysis (pairwise correlation) was used to determine differences between variables within and between layers and between two patches: east and west. The figures were created using MATLAB software (version 7).

Results

***Abiotic parameters*:** Results of abiotic data are presented in Table 1. The soil moisture mosaic patchiness - roughness shows the dissimilarity between layers with a mean moisture level of 2.14% and 2.22% in the 0-10 cm layer and with a mean moisture level of 2.96% and 2.73% in the 10-20 cm layer for the east and west patches, respectively. Multivariate analysis of the east and west patches showed no significant (NS) ($p>0.05$) differences in the spatial distribution of SM between the two layers of the two sampling sites (east and west).

Table 1. Abiotic parameters (soil moisture and organic matter) in the eastern and western patches

Soil ID	Soil Moisture (%)				Organic Matter (%)			
	Eastern patch		Western patch		Eastern patch		Western patch	
	0-10 cm	10-20 cm	0-10 cm	10-20 cm	0-10 cm	10-20 cm	0-10 cm	10-20 cm
1A	2.12	2.62	2.50	2.63	0.39	0.40	0.18	0.40
1B	2.32	2.83	2.12	2.62	0.18 *	0.20 ***	0.19	0.37
1C	1.17	1.98	2.62	2.70	0.78	0.20	0.20	0.18
1D	2.09	3.01	2.11	2.70	0.19	0.20 ***	0.19	0.39
1E	2.04	3.07	2.26	2.51	0.19	0.18	0.19	0.36
1F	2.05	3.25	2.37	3.03	0.19 *	0.20	0.20	0.00
2A	2.00	3.27	2.23	2.47	0.40	0.41	0.19	0.00
2B	2.00	3.82	2.42	2.74	0.40 *	0.38 ***	0.00	0.17
2C	2.19	2.39	2.03	2.55	0.18	0.20	0.18	0.00
2D	3.07	3.04	1.79	2.12	0.19	0.41 ***	0.00	0.19
2E	2.03	2.84	2.08	2.97	0.37	0.61	0.17	0.19
2F	2.29	2.89	2.65	2.83	0.38 *	0.54	0.00	0.35
3A	2.27	3.27	1.87	2.75	0.38	0.20	0.19	0.18
3B	2.07	3.08	1.91	2.72	0.38 *	0.17 ***	0.17	0.00
3C	2.24	3.10	2.58	2.18	0.20	0.17	0.37	0.40
3D	1.95	3.82	2.88	2.94	0.78	0.19 ***	0.00	0.33
3E	2.92	3.12	2.37	2.40	0.36	0.35	0.00	0.18
3F	1.80	2.78	1.91	2.95	0.49 *	0.60	0.17	0.18
4A	1.83	1.81	2.56	2.79	0.41	0.73	0.32	0.00
4B	2.58	2.91	1.73	2.78	0.34 *	0.58 ***	0.19	0.56
4C	2.28	2.06	2.55	2.24	0.19	0.38	0.36	0.19
4D	2.40	3.41	2.39	2.90	0.20	0.54 ***	0.18	0.19
4E	2.06	2.25	1.79	2.80	0.17	0.56	0.18	0.19
4F	2.00	3.23	1.89	1.73	0.40 *	0.38	0.24	0.35
5A	2.57	1.38	2.05	2.88	0.34	0.35	0.32	0.32
5B	2.43	2.81	2.29	2.79	0.20 *	0.20 ***	0.00	0.00
5C	2.37	3.04	2.57	2.62	0.36	0.38	0.00	0.17
5D	2.04	3.49	1.73	2.90	0.20	0.19 ***	0.35	0.18
5E	1.98	4.05	2.36	2.64	0.40	0.40	0.00	0.00
5F	2.38	3.23	1.89	2.65	0.20 *	0.38	0.19	0.00
6A	1.88	3.36	2.14	4.03	0.38	0.37	0.18	0.40
6B	1.24	3.07	2.04	3.18	0.41 *	0.61 ***	0.19	0.19
6C	1.64	2.85	2.06	2.65	0.55	0.20	0.37	0.20
6D	1.76	2.88	1.94	3.23	0.39	0.58 ***	0.35	0.38
6E	2.17	3.27	2.75	2.61	0.59	0.34	0.00	0.19
6F	2.80	3.33	2.41	3.13	0.37 *	0.21	0.19	0.20

** $p<0.01$; *** $p<0.001$

The mean values of soil organic-matter were found to be lower in the deeper soil layer in comparison to the upper soil layer (0.21% and 0.17% for the 0-10 cm layer and 0.36% and 0.35% for the 10-20 cm layer for the eastern and western sites, respectively). The spatial distribution of OM for the east patch study site showed significant differences ($p<0.02$) only for the B and F columns in the 0-10 cm soil layer and for the D and B columns ($p<0.0001$) in the 10-20 cm soil layer. The results show a relatively homogeneous distribution of OM across the sites.

Biotic parameters: *CO_2 evolution*: multivariate analysis of CO_2 evolution in the soil samples collected from the upper 0-10 cm soil layer at the eastern site showed a significant ($p<0.03$) difference between the C and F columns (Fig. 1A), while no significant difference were obtained between the 32 samples in the 10-20 cm soil layer at this site (Fig. 1B). The spatial distribution of CO_2 evolution in soils collected from the western site showed a similar trend to that reported for the eastern site, with significant differences in the 0-10 cm soil layer for the A and D columns ($p<0.02$) and for the F and B columns ($p<0.007$) (Fig. 1A). Moreover, significant differences were observed for the deeper soil layer (10-20 cm) at the D and B columns ($p<0.02$) and E and B columns ($p<0.007$) (Fig. 1B). The mean CO_2 evolution was 0.94 µg CO_2-C g dry soil-1 h^{-1}, 0.74 µg CO_2-C g dry soil-1 h^{-1} in the upper layer and 0.30 µg CO_2-C g dry soil-1 $h^{-1,}$ 0.42 µg CO_2-C g dry soil-1 h^{-1} in the deeper soil layer for east and west sites, respectively.

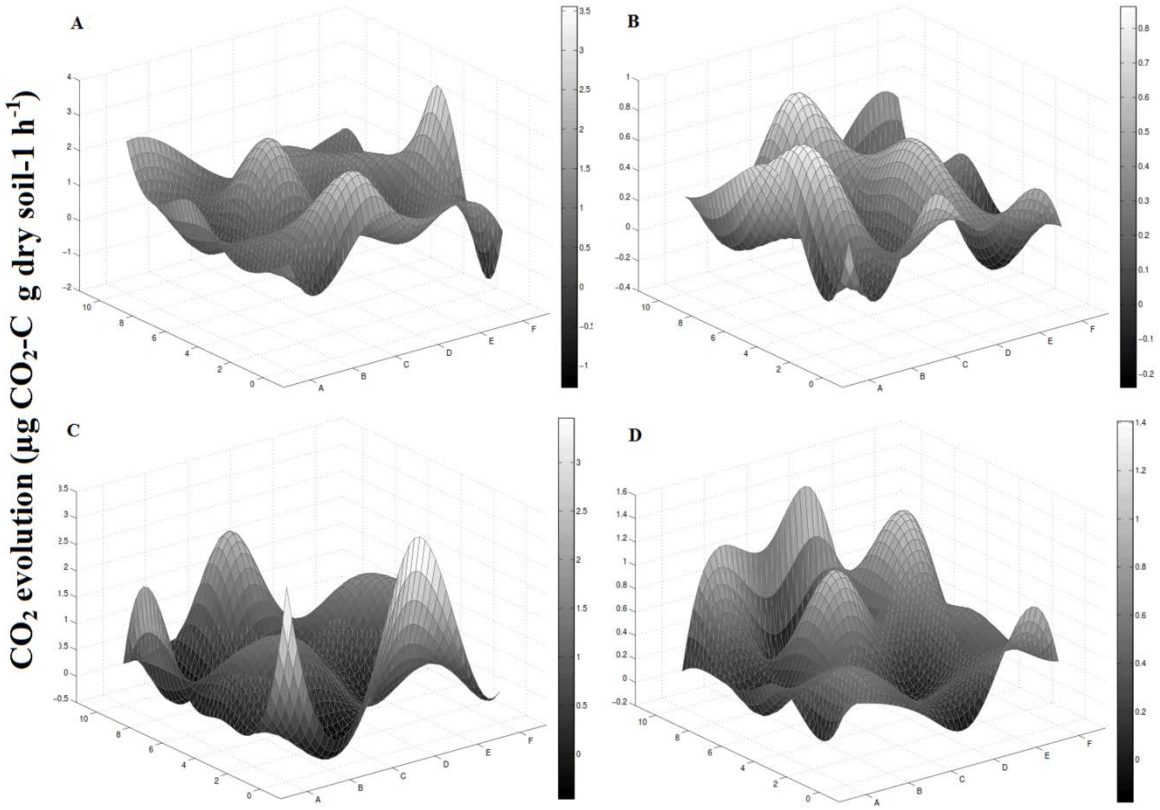

Figure 1. Spatial distribution of CO_2 evolution (µg CO_2-C g dry soil-1 h^{-1}) in the 10 × 10 m grid: **A**- 0-10 cm soil layer in the eastern site; **B**- 10-20 cm soil layer in the eastern site; **C**- 0-10 cm soil layer in the western site; and **D**- 10-20 cm soil layer in the western site.

Microbial biomass (MB): The mean microbial biomass distributed in the 2 layers showed a configuration similar to that of CO_2 evolution: high biomass in the upper soil layer (0-10 cm) and low biomass in the deeper soil layer (10-20 cm) at both sites (Table 2). The results indicate that the non-significance can reflect a homogeneous spatial distribution of MB in the two soil layers at the sites.

The spatial distribution of the metabolic quotient (qCO_2) at the eastern and western sites was represented in Table 2. The spatial distribution of the qCO_2 between the two layers showed a tendency toward homogeneity.

Changes in the community-level physiological profile (CLPP): in the east study sites, the spatial distribution of CLPP was relatively homogeneous between and within soil layers

(Table 2). The mean CLPP for the upper soil layer (0-10 cm) and the deeper soil layer (10-20 cm) were 20.97 µg CO_2-C g dry soil^{-1} h^{-1} and 18.27 µg CO_2-C g dry soil^{-1} h^{-1}, respectively. A homogeneous spatial distribution of CLPP was observed between the patches.

Table 2. Biotic parameters (microbial biomass, CLPP and qCO_2) for the eastern and western patches.

Soil ID	Microbial biomass (µg C g dry soil^{-1})				CLPP (µg CO_2-C g dry soil^{-1} h^{-1})				qCO_2 (µg CO_2-C g^{-1} biomass-C h^{-1})			
	Eastern patch		Western patch		Eastern patch		Western patch		Eastern patch		Western patch	
	0-10 cm	0-10 cm	0-10 cm	0-10 cm	0-10 cm	10-20 cm	0-10 cm	10-20 cm	0-10 cm	10-20 cm	0-10 cm	10-20 cm
1A	57.21	96.48	149.52**	44.26	3.46	17.65	28.27	27.10	0.30	0.30	0.31	0.30**
1B	11.92**	7.71	8.03	44.39**	21.11**	24.13	13.47	9.23	0.30	0.29***	0.29**	0.30
1C	38.46	174.57	83.73	20.64	23.14	28.39	17.97	8.66	0.30	0.30***	0.30**	0.30
1D	83.49**	46.75	244.82**	1.94	9.24	6.38	34.74	18.73	0.30	0.30	0.31	0.25**
1E	117.06**	147.46	198.87	40.03**	11.30	15.56	14.92	4.61	0.30	0.30***	0.31	0.30
1F	17.22**	10.49	50.72	51.57	23.65**	28.83	17.86	6.19	0.30	0.30***	0.29	0.30
2A	56.20	4.06	5.97**	5.04	14.23	28.89	22.34	28.11	0.30	0.28	0.13	0.28**
2B	131.54**	75.15	5.29	75.78**	13.03**	21.84	15.88	8.02	0.31	0.30***	0.11**	0.30
2C	223.95	5.01	5.16	6.59	12.15	21.04	17.01	19.08	0.31	0.28***	0.11**	0.29
2D	12.07**	109.53	5.81**	6.85	22.27	22.11	24.01	20.01	0.30	0.30	0.13	0.29**
2E	44.74**	3.60	98.47	28.39	32.97	20.55	8.54	33.39	0.30	0.27***	2.27	0.30
2F	72.03**	3.87	7.78	21.52	44.85**	24.37	21.01	8.65	0.30	0.28***	0.17	0.30
3A	62.53	201.06	4.79**	73.45	19.79	18.47	19.35	17.52	0.30	0.30	0.10	0.30**
3B	59.57**	77.55	115.05	67.90**	12.26**	21.89	8.71	9.85	0.30	0.30***	2.31**	0.30
3C	52.38	2.82	131.58	54.51	29.94	25.35	11.09	14.54	0.30	0.27***	3.03**	0.30
3D	45.29**	43.83	6.45**	2.06	22.89	4.22	20.20	21.37	0.30	0.30	0.11	0.25**
3E	16.16**	5.49	22.98	21.58**	23.25	20.69	3.23	20.31	0.30	0.29***	0.52	0.30
3F	165.27**	6.34	66.27	20.42	18.40**	23.18	9.69	2.28	0.31	0.29***	1.52	0.30
4A	133.52	83.12	6.90**	91.51	40.20	19.76	22.50	14.85	0.31	0.30	0.15	0.30**
4B	70.69**	5.91	60.93	52.69**	13.10**	26.96	9.40	14.28	0.30	0.29***	1.40**	0.30
4C	202.30	5.80	4.76	78.50	19.31	23.08	22.77	8.88	0.31	0.29***	0.10**	0.30
4D	13.41**	60.51	63.02**	97.98	25.26	15.54	9.64	20.93	0.30	0.30	1.45	0.31**
4E	121.94**	28.46	193.64	47.96**	17.25	14.44	13.36	20.12	0.31	0.30***	4.47	0.30
4F	11.74	50.24	67.94	6.84	22.62**	10.65	12.60	27.20	0.30	0.30***	1.56	0.28
5A	69.79	98.66	289.30**	32.69	10.18	9.18	26.12	4.93	0.30	0.30	0.31	0.30**
5B	15.99**	5.58	63.15	14.86**	24.29**	22.65	16.47	4.16	0.30	0.29***	0.30**	0.30
5C	58.86	51.28	161.69	1.77	15.77	11.46	26.18	20.42	0.30	0.30***	0.31**	0.25
5D	70.14**	38.27	241.90**	2.46	28.23	5.03	10.48	22.44	0.30	0.30	0.31	0.26**
5E	93.22***	3.76	41.39	54.13**	23.12	12.40	21.12	14.34	0.30	0.28***	0.30	0.30
5F	14.68**	6.71	5.33	81.10	22.27**	20.37	17.06	12.95	0.30	0.28***	0.28	0.30
6A	222.90	26.75	18.18**	9.73	16.35	25.50	25.37	6.44	0.31	0.30	0.41	0.29**
6B	167.41**	31.36	54.20	86.09**	9.44**	4.33	12.76	18.06	0.31	0.30***	1.36**	0.30
6C	36.05	3.09	50.34	161.22	26.71	20.63	10.45	26.54	0.30	0.27***	1.16**	0.31
6D	12.31**	3.68	40.12**	52.01	25.30	17.23	4.05	16.90	0.30	0.27	0.92	0.30**
6E	65.92**	102.49	24.10	8.24**	38.72	11.11	26.11	21.28	0.30	0.30***	0.55	0.29
6F	17.62**	28.6	12.65	108.79	18.83**	13.87	21.25	14.96	0.30	0.30***	0.28	0.30

** p<0.01; *** p<0.001

Changes in the community-level physiological profile (CLPP in percentage) of the four detected carbon groups (aromatic acids, carboxylic acids, amino acids, and carbohydrates) represented by 14 different substrates are presented in Figure 2A, B, C, D.

Based on the data obtained in the present study, we may elucidate that, the distributions of the four utilized substrates groups, at both sites and both soil layer at the eastern and western sites are follows: carboxylic acids > aromatic carboxylic acids > amino acids > carbohydrates.

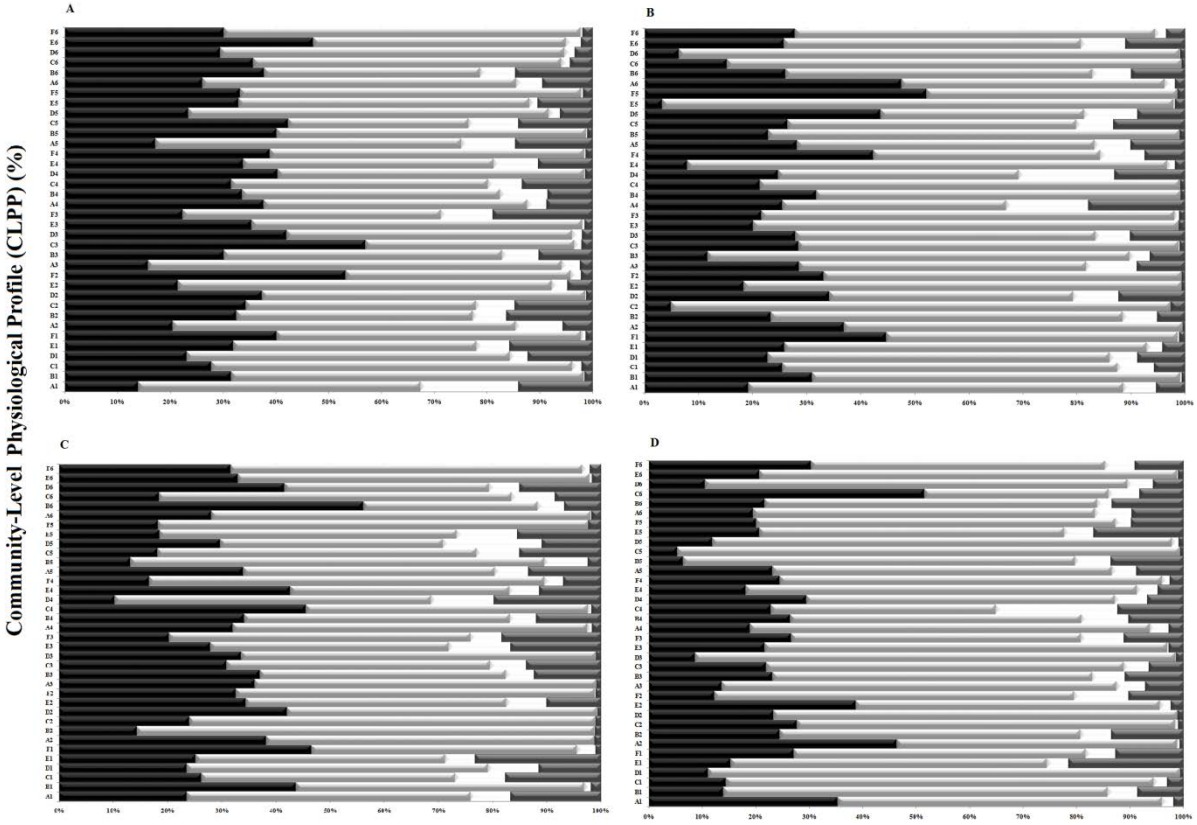

Figure 2. CLPP (%) in the eastern and western sites: **A**- 0-10 cm soil layer in the eastern site; **B**- 10-20 cm soil layer in the eastern site; **C**- 0-10 cm soil layer in the western site; and **D**- 10-20 cm soil layer in the western site. ■- Aromatic carboxylic acids; ■- Carboxylic acids; □- Carbohydrates; ■- Amino acids.

Discussion

In the present study, the multi-scale analysis of the spatial distribution of soil microbial community revealed several different scales of organization, horizontally, ranging from 2 m to 10 m within the patches and vertically with two soil layers. The abiotic parameters exhibit similar patterns between the patches were the SM was found to be higher in the upper soil layer in comparison to the deeper soil layer at both sampling sites. A similar pattern was found for OM - were the western patch exhibited relatively higher organic matter in both layers in comparison to the eastern site patch. These two abiotic parameters are known as key factors for biotic activity (14, 15, 16). The mean values of biotic variables (microbial biomass, CO_2 evolution, CLPP) obtained for the eastern-site patch were higher than those in the western-site patch, except for CO_2 evolution in the 10-20 cm soil layer of the western site patch, which established an opposite trend. Moreover, a negative correlation was found between abiotic and biotic parameters in both site patches: the upper soil-surface layer exhibited higher biotic activity in comparison to the deeper soil layer. Based on the above, we assume that these biotic factors were triggered by the patchiness and the differences in vegetation cover.

qCO_2 undoubtedly provides a useful measure of microbial efficiency (2, 19). Our data related to qCO_2 distribution were found in accord with the literature data: an increase in qCO_2 brings a reduction in microbial efficiency. High qCO_2 and low microbial efficiency (microbial biomass and CO_2 evolution) were obtained for the western patch. Based on all obtained data, we assume that the richness of the microbial communities in both layers within the site patches, as well as the spatial distribution of the microbial communities

between the patches, can be due to the distribution of abiotic factors, as well as the relative effect of the vegetation cover. Data obtained in the present study revealed that the overall microbial community structures on horizontal patterns are more similar among the samples within a site than among those taken between sites, since the geochemical and physical environments appear to be more similar in the former than in the latter case. It was also shown that there is variability in vertical patterns for the microbial community in these sandy soil ecosystems. As our attention in the present study focused on comparison between the spatial structure of microbial communities and environmental properties the results yield new response targeting interest on how biota communities develop in soil systems, and which factors may be important in management of soil-ecosystem. The selection of tillage system has important role in managing agroecosystems. Soil moisture saved through reduced tillage systems may be important in years with below- average rainfall. Soil organic matter tends to stabilize at a certain level for a specific tillage system used in fields with a particular soil texture. It is important to mention that sandy soils with similar particle size distribution but due to differences in mineralogy of the clay sized fraction that represents not more than a few percent of the soil mass, show very different physical properties and in sandy soils unlike other soils, the elementary fabric is easily affected by tillage practices. If greater porosity can be produced through tillage operations, the stability of these systems is very weak and compaction by wheels or other actions can in return produce a dense structure with adverse physical properties. This leads to a decrease in the water retention properties and hydraulic conductivity, an increase in the resistance to penetration and sensitivity to surface crusting. Thus, compaction results from a variation of the structure at all scales, i.e. from the macroscopic to microscopic scales. More generally, sandy soils, more than other soils, require careful management in an environmentally friendly manner. Indeed, even if most physical degradation processes are more easily reversible in sandy soils than in other soils, the physical fertility of these soils is weak. These soils require very little tillage operations in the wrong way to produce significant adverse consequences for plant development and consequently for crop yield and environment, that is the reason that microbial community can be used for the management in this type of ecosystems.

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References

1. Agnelli, A., Ascher, J., Corti, G., Ceccherini, M., Nannipieri, P. and Pietramellara G., (2004): Distribution of microbial communities in a forest soil profile investigated by microbial biomass, soil respiration and DGGE of total and extracellular DNA. Soil Biol. Biochem. 36:859–868.
2. Anderson, J. and Domsch K., (1978): A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biol. Biochem. 10:215–221.
3. Bell, R. and Seng V., (2007): The management of the agro-ecosystems with sandy soils, FAO corporate document repository:298-304.
4. Berg, N. and Steinberger, Y., (2008): Role of perennial plants in determining the activity of the microbial community in the Negev Desert ecosystem. Soil Biology & Biochemistry 40: 2686-2695.

5. Campbell, C.D., Chapman, S.J., Cameron, C.M., Davidson, M.S., Potts, J.M., (2003): A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. Applied and Environmental Microbiology 69: 3593–3599.
6. Danin, A., (2005): The sandy areas of Caesarea, a rare situation of alpha and beta diversity linked by plant succession. Isr. J. Plant Sci. 53:247–252.
7. Danin, A., Yaalon, D., (1982): Silt plus clay sedimentation and decalcification during plant succession in sands of the Danin / Diversity and plant succession in the sandy areas of Caesarea Mediterranean coastal area of Israel. Isr. J. Earth Sci. 31:101–109.
8. Fierer, N., Schimel, J., and Holden, P., (2003): Variations in microbial community composition through two soil depth profiles. Soil Biol. Biochem. 35:167–176.
9. Kemnitz, D., Kolb, S., and Conrad, R., (2007): High abundance of Crenarchaeota in a temperate acidic forest soil. FEMS Microbiol. Ecol. 60:442–448.
10. Koller, D., Sachs, M., Negbi, M., (1964): Germination regulating mechanisms in some desert seeds. VIII Artemisia monosperma. Plant. Cell Physiol. 5:85–100.
11. LaMontagne, M., Schimel, J. and Holden, P., (2003): Comparison of subsurface and surface soil bacterial communities in California grassland as assessed by terminal restriction fragment length polymorphisms of PCR amplified 16S rRNA genes. Microb. Ecol. 46:216–227.
12. Lindstrom E., and Langenheder S, (2011): Local and regional factors influencing bacterial community assembly. Environmental Microbiol Rep 4:1-9.
13. Rahel, F., (1990): The hierarchical nature of community persistence - a problem of scale. Am. Nat. 136:328-344.
14. Saleska, S. R., Harte, J. and Torn, M. S. (1999). The effect of experimental ecosystem warming on CO_2 fluxes in a montane meadow. Glob. Change Biol. 5: 125-141.
15. Savin, M. C., Gorres, J. H., Neher, D. A. and Amador, J. A. (2001). Biogeophysical factores influencing soil respiration and mineral nitrogen content in an old field soil. Soil Biol. Biochem. 33: 429-438.
16. Steinberger, Y. and Sarig, S. (1993). Responses by soil nematode populations in the soil microbial biomass to a rain episode in the hot, dry Negev Desert. Biol. Fertil. Soils. 16: 188-192.
17. Tobin, K., Onstott, T., DeFlaun, M., Colwell, F., and Fredrickson, J., (1999): In situ imaging of microorganisms in geologic material. J. Microbiol. Methods 37:201–213.
18. Torsvik, V., and Ovreas, L., (2002): Microbial diversity and function in soil: from genes to ecosystems. Curr. Opin. Microbiol. 5:240–245.
19. Wardle, D.A., and Ghani, A., (1995): A critique of the microbial metabolic quotient (qCO_2) as a bioindicator of disturbance and ecosystem development. Soil Biol. Biochem. 12:1601–1610.
20. Zhang, C., Palumbo, A., Phelps, T., Beauchamp, J., Brockman, F., Murray, C., Parsons, B., and Swift, D., (1998): Grain-size and depth constraints on microbial variability in coastal plain subsurface sediments. Geomicrobiology 15:171–185.