Journal of Nematology 37(1):26–36. 2005.

Spatio-temporal Dynamic Heterogeneity of Nematode Abundance in a Desert Ecosystem

S. Pen-Mouratov[1] and Y. Steinberger[2]

Abstract: The abundance and distribution of natural populations of soil organisms can be influenced greatly by the types and arrangement of habitat patchiness within a landscape. Most animal populations inhabit a variety of different habitats, even within a relatively small geographic region. The aim of our research was to determine how abiotic and biotic environmental factors, including small shrub canopy, influence patchiness and the alteration of nematode populations inhabiting a small plot in a desert ecosystem. The results of our investigation showed that the aggregation of total number of nematodes, trophic groups, and nematode species in an arid region with low soil moisture content may be significantly different ($P < 0.01$), even in 10-m-square areas. Ecological indices such as λ, H', J', and SR were defined as useful for detecting changes in spatial patterns of nematodes. Only the H' index identified a difference in temporal and spatial patterns ($P < 0.01$). We conclude that the influence of different factors such as temperature, organic content, and vegetation on small plots with extreme habitat conditions was not dominant. Factors such as inter- and intra-species competition appear to play the main role in the creation of the mosaic of small plots.

Key words: desert system, ecological indices, habitat, nematodes, patchiness.

Soil organisms in terrestrial systems are distributed unevenly in time and space, and are often aggregated (Odum, 1971; Pickett and Cadenasso, 1995; Whitford, 2002). According to Wallwork (1976), the structure of vegetation can act directly as a physical factor for soil animals by impeding their mobility and providing specialized niches. Vegetation patches form at different temporal spatial scales on the landscape, thereby producing a shifting mosaic component (Ettema and Wardle, 2004; Pickett and Cadenasso, 1995).

Spatio-temporal patchiness in the soil environment is thought to be crucial for maintaining soil biodiversity and providing diverse microhabitats (because of resource partitioning) and presents a complex mosaic (Ettema et al., 2000). Patchiness of landscapes, ecosystems, and plant and animal populations have been discussed in ecological literature in recent years (Dighton et al., 2000; Garkaklis et al., 2003; Lindenmayer and Possingham, 1996; Stuart and Gaugler, 1994; Sulkava et al., 2001).

The temporal variation in habitat patch life span has an important effect on local population size (Fahrig, 1991). The abundance and distribution of soil biota populations in natural systems can be influenced greatly by the temporal types and arrangement of habitat patches within a landscape. Most animal populations inhabit a variety of different habitats, even within a relatively small geographic region (Pulliam et al., 1992). In their studies, Robertson and Freckman (1995) and Ettema et al. (2000) found that even in a homogenous wetland site, aggregation of nematode communities varied greatly by trophic function and species level. Moreover, spatial patterning is an important property of nematode communities and may differ between ecosystem types (Ettema and Yeates, 2003).

Some factors determining the activity and diversity of soil biota in arid ecosystems and the formation of patches are soil temperature, soil water potential (Steinberger and Sarig, 1993; Whitford, 1996), soil organic matter, and vegetation (Duponnois et al., 1999; Freckman and Mankau, 1986). Soil temperature, soil moisture content (Bakonyi and Nagy, 2000; Pen-Mouratov et al., 2004a), and distribution of organic matter produced in the ecosystem (Yeates and Coleman, 1982) are three of the most important factors, especially in arid and semi-arid areas (Pen-Mouratov et al., 2004b), that directly or indirectly affect the seasonal dynamics of nematode communities in soil, leading to heterogeneous distribution of soil biota in habitat. The theory of spatial heterogeneity (Robertson and Freckman, 1995; Simpson, 1964; Yeates and Bird, 1994) suggests that the more complex and heterogeneous the physical environment, the more complex and diverse will be the flora and fauna.

It has been suggested that trees (Lahav-Ginott et al., 2001; Milton and Dean, 1995; Rohner and Ward, 1999) and shrubs (Liang and Steinberger, 2001; Pen-Mouratov et al., 2003; Steinberger and Loboda, 1991) function as "keystone species" in arid and semi-arid regions, forming micro-surroundings with a higher content of moisture and soil nutrients, leading to the creation of environmental patchiness. In arid and semi-arid ecosystems, plant cover has an important effect on soil properties, which can determine the structure and function of annual plant and soil fauna communities (Gallardo, 2003).

The objective of this study was to determine how the medium scale-landscape, habitat-related abiotic constraints affect the soil nematode community in a desert ecosystem. Because soil moisture is known to be one of the most limiting and unpredictable sources of stress for the soil nematode community, we expected the total abundance, trophic structure, and ecological indices to be controlled by the spatial distribution of abiotic

---

Received for publication 1 March 2004.

[1] Researcher, Faculty of Life Sciences, Bar-Ilan University, Ramat Gan 52900, Israel.

[2] Professor and Head of Soil Ecology Laboratory, Faculty of Life Sciences, Bar-Ilan University, Ramat Gan 52900, Israel.

The authors thank M. B. Rachimbaev for his helpful comments and assistance and the staff of M. Evenari, Avdat Research Farm, for their assistance.

E-mail: steinby@mail.biu.ac.il

This paper was edited by D. A. Neher.

resources (e.g., soil moisture, organic matter), which would support Simpson's (1964) theory of spatial heterogeneity.

Material and Methods

Study area: The study was conducted in the northern Negev Desert highland at the Avdat Research Farm (30°47′ N; 34°46′ E), about 60 km south of Beer-Sheva. A 10×10-m grid was set up at a randomly selected loess plain site and divided into 1×1-m plots, producing a total of 100 plots. The area has a temperate desert climate, i.e., mild, rainy winters (5 °C to 14 °C range in January and 90 mm average winter rainfall), and hot, dry summers (18 °C to 32 °C in June). Dewfall is an additional source of moisture, occurring approximately 200 nights/year^{-1} and amounting to 35 mm/year (Evenari et al., 1982). The soil is a deep, fine-textured loessial sierozem (Alon and Steinberger, 1999).

The perennial vegetation is dominated by desert shrub association, in which the most common species are *Zygophyllum dumosum* and *Hammada scoparia* (Evenari et al., 1982).

Sampling procedure: A total of 400 soil samples from the upper (0 to 10 cm) soil layer were collected during the study period (year 2001). Soil samples were collected using a 7-cm-diam. soil auger in the early morning. The sampling location in each plot was determined using the jack-knifing method (Briggs and Knapp, 1991). Each soil sample was collected and placed in an individual plastic bag, which was then sealed and placed in an insulated box to prevent overheating during transportation to the laboratory, where the samples were kept at 4 °C until biological and chemical analysis.

Sample analysis: (i) A minimum of 5 g soil from each sample at each depth was used for soil moisture and organic matter determination. The weighed soil samples were dried at 105 °C for gravimetrical determination of soil water content, followed by organic matter determination by oxidization with dichromate in the presence of H_2SO_4, without application of external heat (Rowell, 1994); (ii) The nematodes were extracted from 100-g soil samples using the Baermann funnel procedure (Cairns, 1960), counted and preserved in formalin (Steinberger and Sarig, 1993), and identified according to order, family, and genus (if possible) using a compound microscope.

Ecological indices and statistical analysis. The characteristics of the nematode communities were described by means of the following indexes and, where appropriate expressed as the number of individuals per dry weight:

(i) Absolute abundance of individuals per 100 g^{-1} dry soil.

(ii) Abundance of omnivore-predators (OP), plant-parasitic (PP), fungal-feeding (FF), and bacterial-feeding (BF) nematodes (trophic structure) (Liang et al., 2000; Steinberger and Loboda, 1991; Steinberger and Sarig, 1993).

(iii) WI = (FF + BF)/PP (Wasilewska, 1994).

(iv) Trophic diversity, $T = 1/\sum P_i^2$, where P_i is the proportion of the *i*-th trophic group (Heip et al., 1988).

(v) Genus dominance, $\lambda = \sum P_i^2$ (Simpson, 1949).

(v) Shannon Index, $H' = -\sum P_I (\ln P_I)$, where P is the proportion of individuals in the *i*-th taxon (Shannon and Weaver, 1949).

(vii) Maturity Index $MI = \sum \upsilon_i \rho_i$, where υ_i, is the *c-p* value assigned by Bongers (1990) of the *i*-th genus in the nematode and ρ_i, the proportion of the genus in the nematode community. The *c-p* values describe the nematode life strategies and range from 1 (for colonizers and individuals tolerant to disturbance) to 5 (for persisters and individuals sensitive to disturbance.

(viii) PPI—plant-parasite index (Bongers, 1990).

(ix) Maturity index modification (∑MI), including plant-feeding nematodes (Yeates, 1994).

(x) Evenness $J' = H'/\mathrm{Ln}(S)$, where S is the number of taxa and H is Shannon index.

(xi) Species richness, $SR = (S - 1)/\ln(N)$, where S is the number of taxa and N is the number of individuals identified (Yeates and King, 1997).

The spatial patterns and spatial dynamics of nematode populations, soil moisture, and soil organic matter in time and space were assessed using both the data of earlier investigations conducted in the Negev Desert (Liang et al., 2002; Steinberger and Loboda, 1991) and values calculated according to Lakin's (1990) statistical analysis for ecological studies. According to Lakin (1990), the step-intervals (λ) were calculated as:

$$\lambda = (X_{max} - X_{min})/K$$

Where X_{max} is maximum value of individuals found in a unit sample, X_{min} is the minimum number of individuals found in the sample, and K is equal to (1 + 3.32 log N), where N = 100 represents the sample size. The lowest boundary of the first class interval (X_L) value was calculated as: $X_L = (X_{min} - \lambda/2)$. The frequency of each group is calculated, enabling construction of a distribution histogram and a space map. The histogram allows the calculation of a parabolic approximation of the frequency distribution.

Based on previous investigations (Liang et al., 2000; Steinberger and Loboda, 1991), the rate of the minimal value of soil moisture, which may affect soil biota dynamics and distribution, is 1% of the soil dry-weight moisture content, and that of soil organic matter is 0.5%. The minimal and useful value-rates, which allow determination of significant changes in nematode population dynamics, are 50 individuals/100 g^{-1} dry soil (Pen-Mouratov et al., 2004a,b).

All data were subjected to analysis of variance using an SAS model, two-way ANOVA (SAS Institute, Cary, NC). Differences obtained at a level of $P < 0.05$ were considered significant. Duncan's and Turkey's multiple-range tests were used to evaluate differences between separate means (Sokal and Rohlf, 1969).

RESULTS

Soil moisture: Mean gravimetric soil moisture content during the study period ranged between 0.4% to 8.2%, with maximal values in winter and minimal values in summer. The mean soil moisture levels exhibited significant seasonal differences ($P < 0.0001$), resulting in distinct visualization maps (Fig. 1) for each season.

The results showed a change in the spatial distribution of soil moisture patches on the 1% scaling of soil moisture content. A shift from a high heterogeneity toward a more homogeneous distribution of soil moisture occured from winter to autumn (Fig. 2A–D). In the winter, the six moisture units yielded a calculated parabolic approximation of the frequency distribution with $r^2 = 0.68$. Spring and summer seasons yielded only three main units and $r^2 = 1.0$. In autumn, the more homogeneous distribution of soil moisture yielded only two distinct units and the calculated degenerated parabola was a simple regression line.

Using Lakin's (1990) equation, the number of unit-patches obtained was 8, 9, 9, and 7, with corresponding calculated intervals of 0.60, 0.19, 0.29, and 0.19 for winter, spring, summer, and autumn, respectively (Fig. 2A′–D′). Although the number of patches was almost identical to the r^2 values obtained for the calculated parabolic exponential curve, it was found to be greater for winter ($r^2 = 0.70$) and autumn ($r^2 = 0.87$) than for spring ($r^2 = 0.52$) and summer ($r^2 = 0.46$).

Soil organic matter: The mean soil organic matter content ranged between 0.25% to 2.17%, showing relatively low spatial patchiness in each of the four seasons (Fig. 3). Defining the effectiveness of the soil organic matter in intervals of 0.5%, the four seasons yielded two defined modules. The first had only three defined intervals, with the highest value of 1.5% for winter and spring, and the second with five intervals with a maximum interval value of 2.5% for summer and autumn (Fig. 3). There was a well-defined difference ($P < 0.05$) in the patchiness pattern in the percentage of organic matter with a change throughout the seasons. There was a tendency ($P < 0.05$) for a low heterogeneity in summer to almost twice the heterogeneity in autumn. However, in all cases, the 0 to 0.5% range was the most common, occurring in over 80% of the data samples.

A parabolic exponential curve was calculated for each season for the 100 samples, using the 0.5% intervals (Fig. 4A–D). As a result, a decrease was observed in r^2 from winter to autumn, with r^2 values of 1, 1, 0.95, and 0.86 for winter, spring, summer, and autumn, respectively.

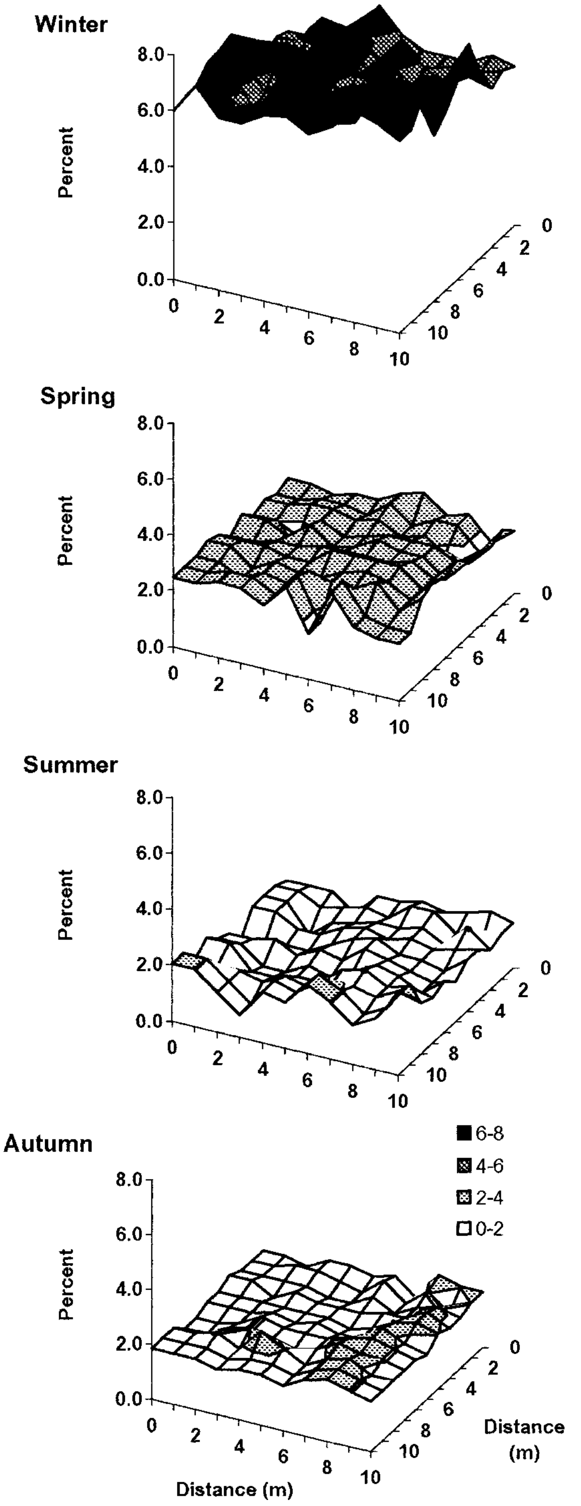

FIG. 1. Spatial distribution of soil moisture dynamics in the 10×10-m grid on a percentage dry-weight basis on 1% soil moisture calculated seasonally during the study period.

A value of 0.09 for fractional segmentation for both winter and spring was found, using the method of Lakin (1990). This value was significantly lower than the 0.19 and 0.29 segmentation units for summer and autumn, respectively (Fig. 4A′–D′). These segmentations yielded represented 12, 12, 9, and 8 unit patches

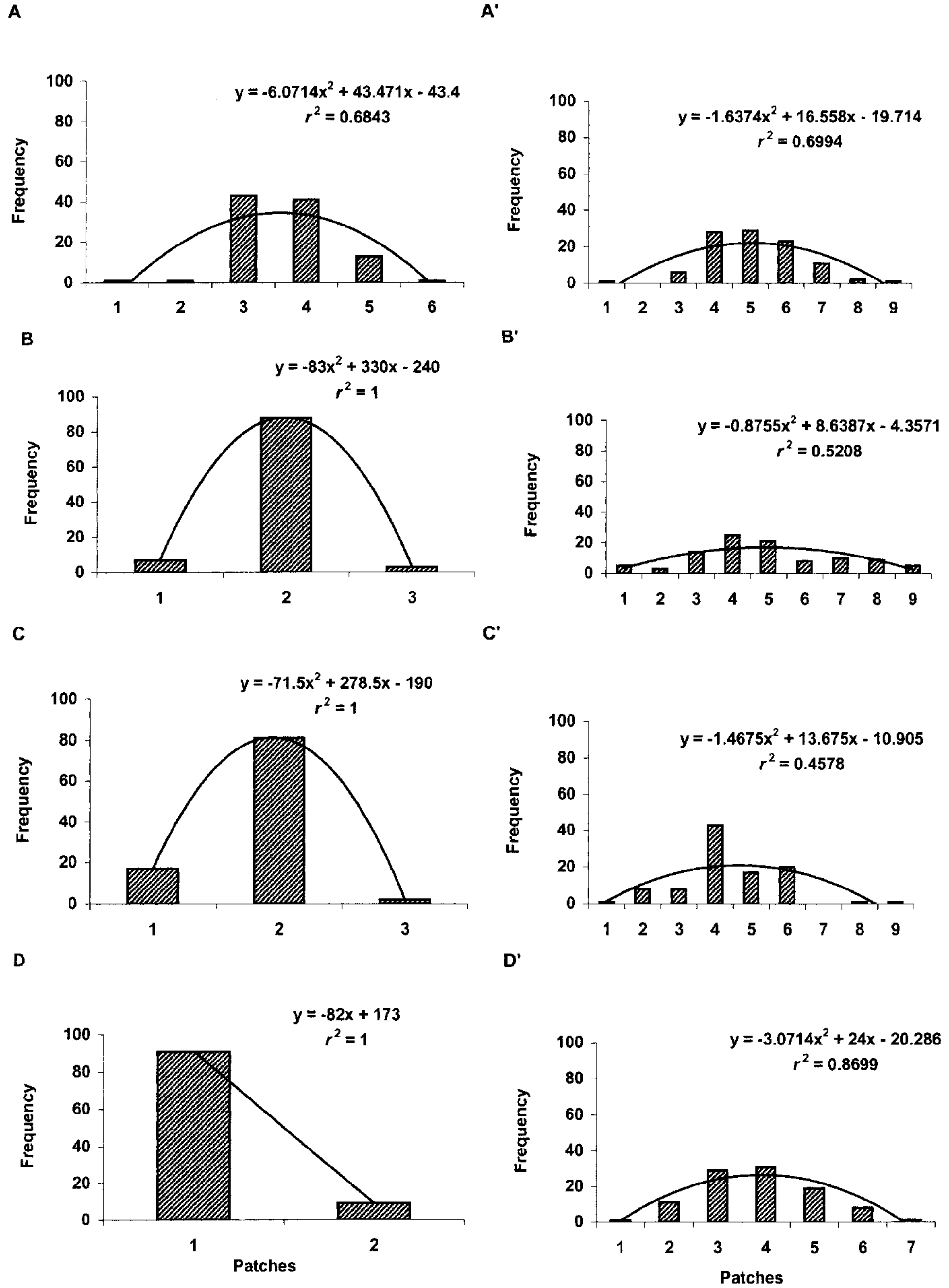

FIG. 2. Seasonal changes in the distribution of calculated soil moisture frequency with step intervals of 1% (A—winter; B—spring; C—summer; D—autumn) and calculated step intervals according to Lakin (1990) (A′—winter; B′—spring; C′—summer; D′—autumn)—with the curvilinear regressions for each season and step interval.

(Fig. 4A′–D′) with r^2 values of 0.40, 0.53, 0.56, and 0.32 for winter, spring, summer, and autumn, respectively.

Total nematodes: The total numbers of nematodes were significantly different between seasons in the observed area, reached maximum values in winter and autumn (80 ± 55 and 71 ± 47, respectively) and were minimal in spring and summer (37 ± 28 and 42 ± 29, respectively). According to previous investigations (Liang et al., 2002; Steinberger and Loboda, 1991), 50 individuals/100 g soil samples were used as the range unit for patchiness determination and calculation (Fig. 5). The total nematode density in each of the 1-m^2 units ($n = 100$) in our grid formed a contour for each season. In winter, six different intervals were observed, where the first group (0 to 50 individuals/100 g soil) representing 35% and the second group (50 to 100 individuals) representing 37% of the total population together represented 72% of the total population (Fig. 5). In winter, the r^2 calculated for the best-fit parabolic exponential curve equaled 0.91 (Fig. 6A).

Toward spring the nematode population exhibited a more homogeneous distribution. Using the 50 nema-

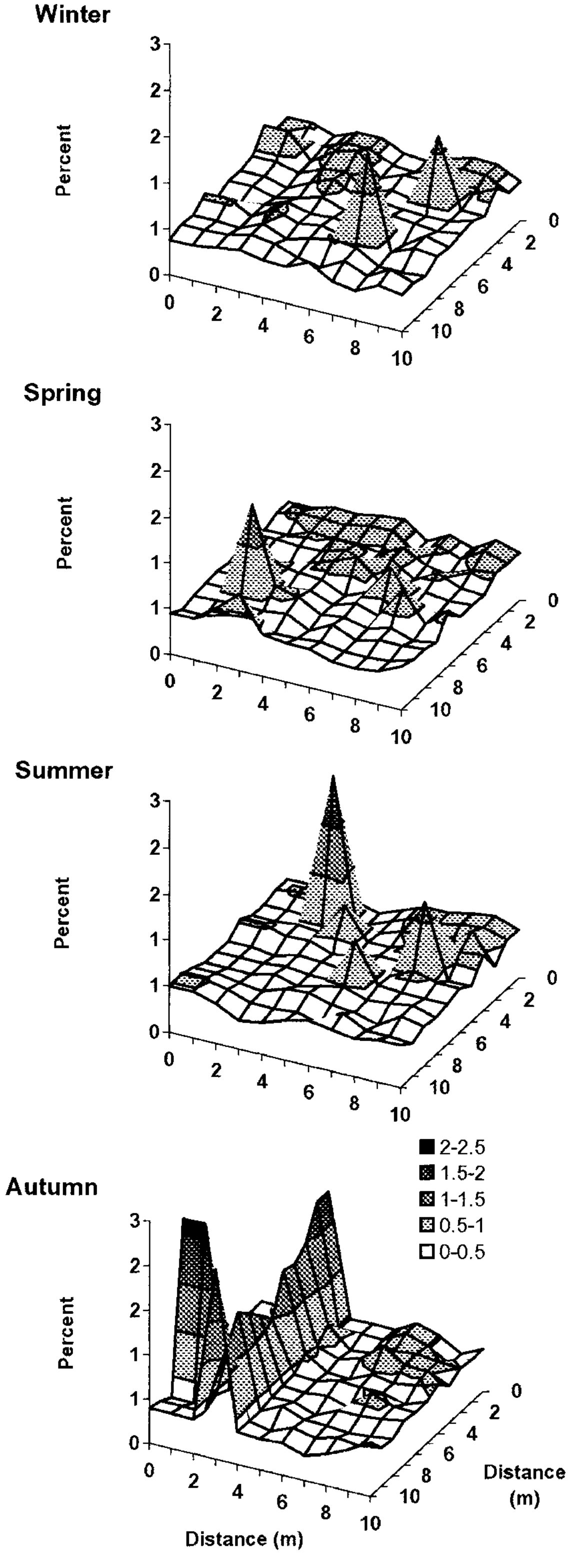

Fig. 3. Spatial distribution of soil organic matter content in the 10×10-m grid based on 0.5% organic matter calculated intervals along the study period in the different seasons.

todes/100 g soil sample in the capacity of range unit, three main groups were observed, varying from 0 to 150 individuals/100 g soil, where 74% of the entire population was represented by values ranging from 0 to 50 individuals (Fig. 5). The three patches yielded a best-fit parabolic exponential curve with $r^2 = 1.0$ (Fig. 6B).

In summer, the frequency appearance of the 0 to 50 individuals reached 72% of the total grid area, significantly changing the patchiness patterns (Fig. 5), with $r^2 = 1.0$ (Fig. 6C).

The autumn season was composed of seven patch-units with a more heterogeneous distribution. Forty-six percent of the total area in the grid was represented by a population density ranging from 50 to 100 individuals/100 g soil, followed by 34% of the total grid area with a population ranging from 0 to 50 individuals/100 g soil. Moreover, the maximal number of nematodes (ranging between 300 and 350 individuals) was observed in autumn, amounting to only 1% (Fig. 5). The parabolic exponential curve was fitted with $r^2 = 0.79$ (Fig. 6D).

Using the method of Lakin (1990), data were segmented fractionally in 9, 9, 8, and 9 units for winter, spring, summer, and autumn, respectively, yielding a patchy heterogeneous contour (Fig. 6A′–D′). The calculated intervals (Lakin, 1990) were lower by 50% to 80% ($P < 0.05$), yielding r^2 values of 0.72, 0.76, 0.48, and 0.55 for the calculated parabolic exponential best-fit curve (Fig. 6A′–D′). The change in r^2 from winter to autumn may be related to changes in population heterogeneity.

Trophic groups: All trophic groups were affected spatio-temporally and by patchiness ($P < 0.0001$) (Table 1). Plant-parasite nematodes were found to comprise 50% of the population.

Bacterivores. The number of bacteriovores varied from 0 to 71 individuals/100 g dry soil, with an annual mean of 9.2 individuals/100 g dry soil. The percentage of bacterivores in the total nematode population ranged from 14.1% to 17.8%, with a lower percentage in winter (14.1%) and summer (15.8%) and a higher percentage of the total population in spring (17.5%) and autumn (17.8%). However, the absolute mean value of individuals was 11.3, 6.5, 6.5, and 12.5 individuals/100 g dry soil in winter, spring, summer, and autumn, respectively. There was a seasonal and patchiness effect ($P < 0.0001$) on bacteriovore nematode populations (Table 1).

Fungivores. Fungi-feeding nematodes represented a higher percentage of the total population than bacterial-feeders, with an annual mean of 11.4 individuals/100 g dry soil. Throughout the seasonal sampling, fungi-feeders represented 18.0 and 16.0 percent of the total nematode population for winter and spring, respectively. An increase to 22.2% and 23.4% of the total nematode population was observed in summer and autumn. Despite the relatively low percentage of fungi-feeders in the winter rainy season, the mean number of individuals was 14.0 individuals/100 g soil, whereas there was a similar percentage in spring, with only one-third the number of fungi-feeders, a mean of 5.7 individuals/100 g soil. In the summer and autumn samples,

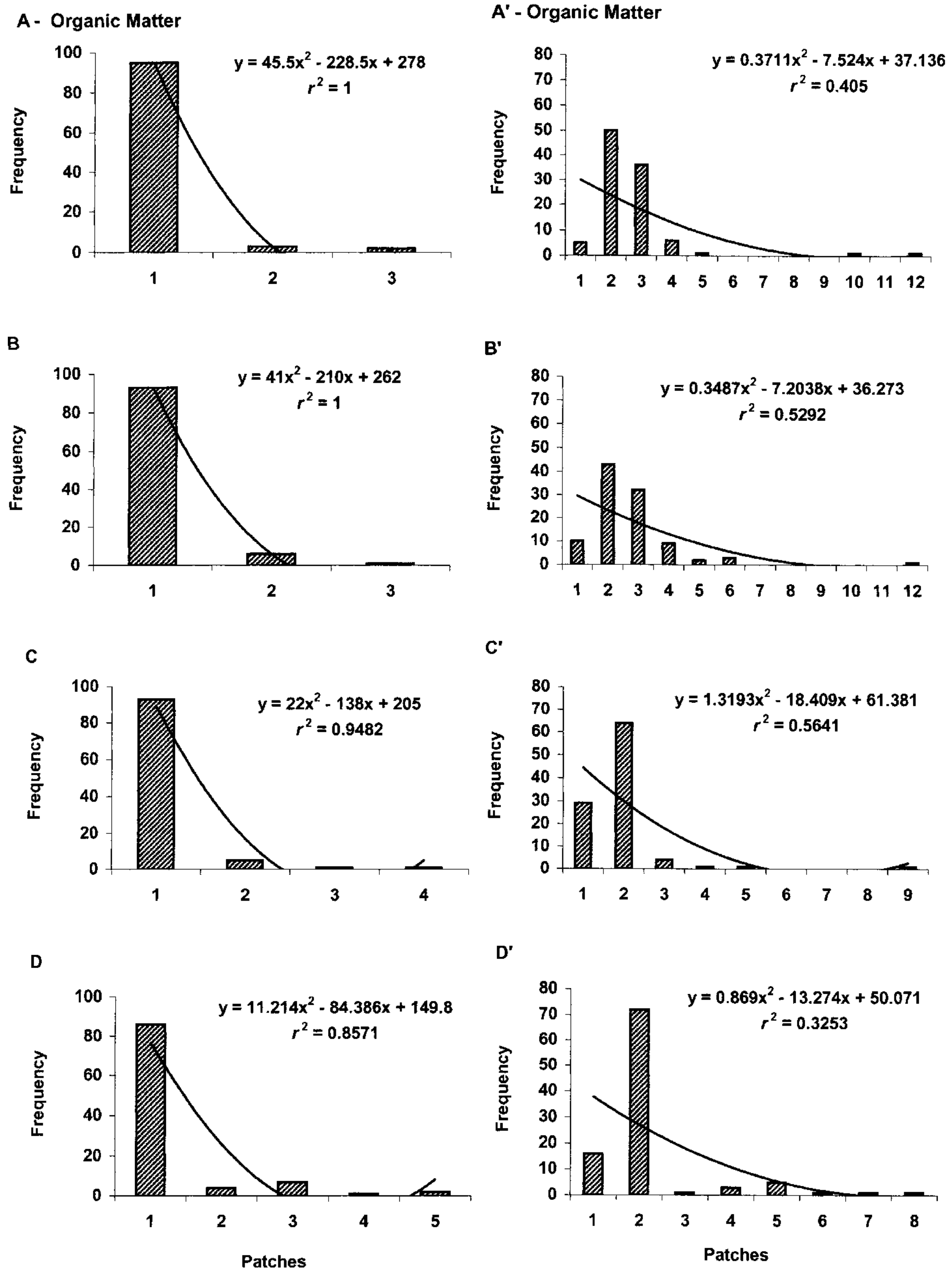

FIG. 4. Seasonal changes in the distribution of calculated soil organic matter frequency with intervals of 0.5% (A—winter; B—spring; C—summer; D—autumn) and calculated step intervals according to Lakin (1990) (A′—winter; B′—spring; C′—summer; D′—autumn)—patches and the curvilinear calculated regressions for each season and interval along the study period.

the mean value of fungi-feeders was 9.2 and 16.5 individuals/100 g dry soil, respectively, showing a change ($P < 0.05$) in the total nematode population through the season (Table 1).

Plant parasites. Plant parasites were the most numerous, representing over 50% of the total extracted soil free-living nematode population. The percentage of plant parasites in the total population was maximum in winter (58.5%) and unchanged in spring, summer, and autumn (55.2%, 56.0%, and 54.8%, respectively). However, the absolute mean value of individuals was 46.7, 20.4, 23.2, and 38.7 individuals/100 g soil in winter, spring, summer, and autumn, respectively. An effect of soil moisture ($r = 0.25$, $P < 0.0001$, $n = 400$) and percentage organic matter ($r = 0.12$, $P < 0.02$, $n = 400$) on plant-parasitic nematodes was found.

Omnivore-predators. The mean annual value of omnivore-predators nematodes amounted to 4.3 individuals/100 g dry soil. They were found to be the least dominant trophic group, with 9.4%, 11.9%, 5.9%, and 4.1% of the total extracted nematode population for winter, spring, summer, and autumn, respectively. These percentages correspond with mean values of 7.5, 4.5, 2.4, and 4.9 individuals/100 g soils for winter,

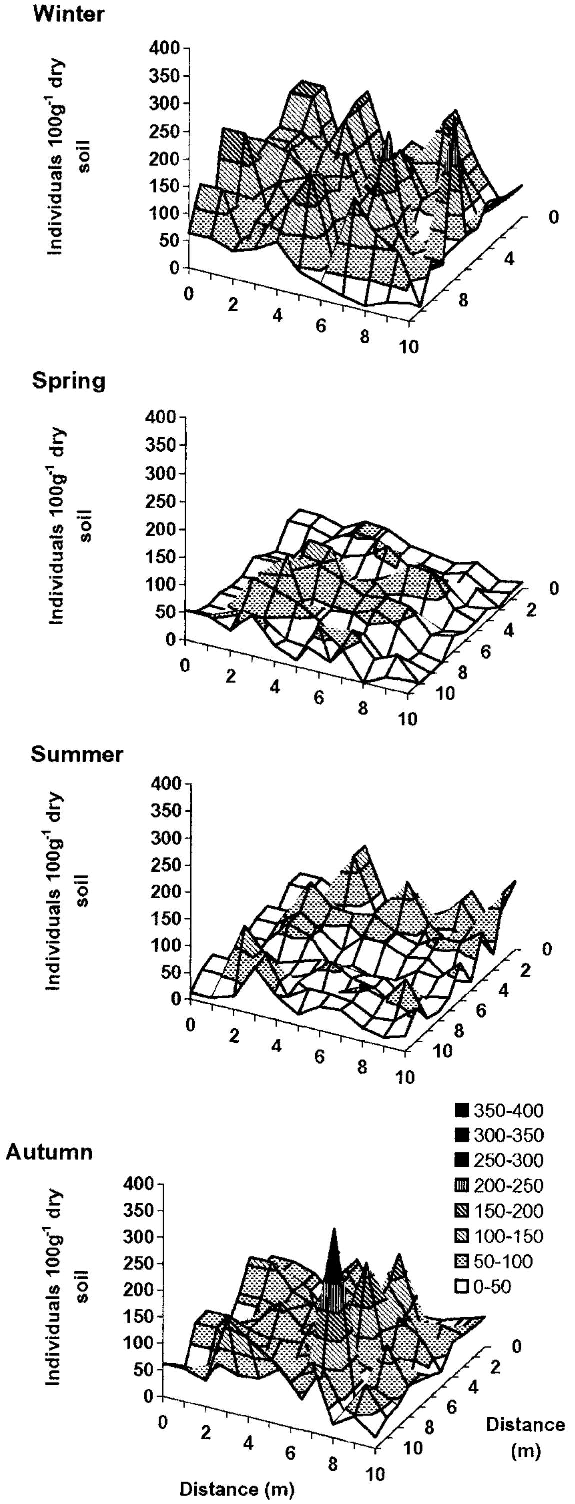

FIG. 5. Spatial distribution of total soil free-living nematode populations in the 10×10-m grid based on groups of 50 individuals calculated intervals along the study period in the different seasons.

spring, summer, and autumn, respectively. The omnivore-predators were affected ($P < 0.0001$, $n = 400$) by the changes in soil moisture availability and not organic matter content.

The most common features of the trophic groups are: (i) plant-parasite nematodes were the most numerous trophic group with the exception of patch 6 in the winter; (ii) fungi-feeders, in general, were the second most common trophic group; (iii) three patches (1, 2, 3) throughout the seasons (vertical) exhibit high similarity in trophic composition.

The number of spatial-distribution patches is similar to data obtained for the 50-unit intervals, where a wide diversity in trophic group compositions can be found with high similarity to the defined grouped patches.

Species diversity: A total of 36 genera were found in the soil samples taken throughout the study period, of which 14 taxa were found to be bacterivores, 4 taxa were fungivores, 11 were plant parasites, and 7 were omnivore-predators.

Throughout the sampling period, the number of taxa in the samples ranged between 25 and 31 for winter and spring, respectively, whereas the number of taxa in summer and autumn varied between these two values (Table 2). *Tylenchorchynchus* (plant-parasite) and *Nothotylenchus* (fungivores) species were the most abundant (25% and 15%, respectively). Among bacterivores, *Acrobeles* (4%), *Acrobeloides* (4%), *Dorylaimus* (3%), and *Nygolaimus* (3%) occurred in each of the four seasons. Of the total 36 genera, 16 were present in the soil samples taken among seasons, with no differences between seasons. However, additional analysis of our results showed significant differences in density of individual genera between pairs of seasons (Table 2). These differences could be the result of many biotic, physical, and chemical variables of the soil milieu.

Ecological indices: By studying the effect of seasonality and patchiness on different ecological indices, we found three different patterns (Table 1), described below:

(i) Both seasonality and patchiness significantly affected the nematode community in measures of trophic diversity (T), genus dominancy (λ), Shannon Index (H′), evenness (J), and richness (SR);
(ii) The nematode community was affected significantly by seasonality. This was exemplified in estimates of plant-parasite index (PPI) and maturity index modification (ΣMI); and
(iii) The ecological indices such as the maturity index (MI) and the Wasilewska index (WI) did not respond to changes in seasonality or community patchiness.

Moreover, indices that were sensitive to patch distribution were sensitive to seasonality as well, which means that abiotic-moisture availability plays an important role in nematode community distribution.

DISCUSSION

Landscapes are composed of distinct, boundaried units that are differentiated by biotic and abiotic structure and composition (Pickett and Cadenasso, 1995)

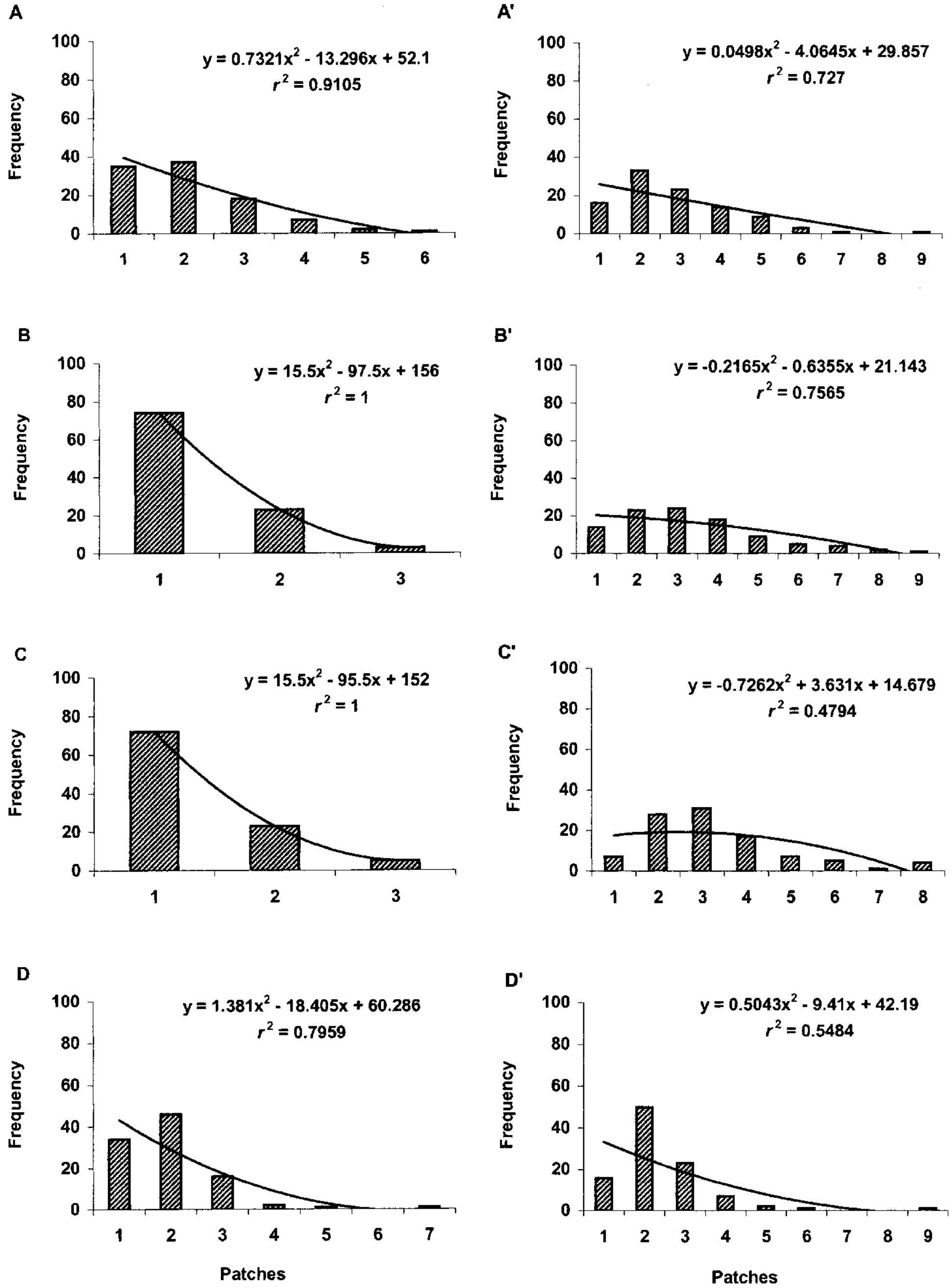

FIG. 6. Seasonal changes in the distribution of total soil free-living nematode frequency with intervals by 50 individuals as units (A— winter; B—spring; C—summer; D—autumn) and calculated intervals according to Lakin (1990) (A′—winter; B′—spring; C′—summer; D′—autumn)—patches and the curvilinear calculated regressions for each season and interval along the study period.

and can be considered an abstraction representing spatial heterogeneity at any scale. Therefore, the abundance, composition, and distribution of natural populations in space can be influenced by the types and arrangement of habitat patches within a landscape (Pulliam et al., 1992).

According to Whitford (2002), landscape units in arid lands are generally recognized by the life form and species composition of the dominant species, with plants playing a leading role in creating patches with modified microclimates. These distinct spatial patterns also result from differences in nutrients (Garner and Steinberger, 1989), which have important implications on the spatial distribution of soil biota (Smedley and Eisner, 1995). Therefore, according to Garner and Steinberger (1989), fluctuations in desert climate are extreme and organic matter is limited and scattered in "fertile islands" under shrub canopies, which undoubtedly are attractive locations for live organisms.

In our study, perennial plant cover was found on less than 5% of the entire sampling site; therefore, the study area can be defined as a shrubless loess plain site.

TABLE 1. Univariate statistics by "ANOVA" for the nematode communities during the study period (with interval units of 50 individuals between patches).

	Seasons		Patchiness of nematodes	
Variable	*F*-value	*P* value	*F*-value	*P* value
Total number of nematodes	249.3	0.0001	679.13	0.0001
Trophic structure				
BF	8.26	0.0001	19.79	0.0001
FF	30.57	0.0001	95.17	0.0001
PP	70.42	0.0001	197.57	0.0001
OP	16.61	0.0001	30.2	0.0001
Ecological indices				
WI	1.65	0.18	0.37	0.9
T	2.62	0.05	2.94	0.008
λ	3.19	0.02	6.31	0.0001
H′	15.27	0.0001	18.02	0.0001
MI	0.86	0.46	1.14	0.34
PPI	3.4	0.02	1.12	0.35
ΣMI	3.7	0.01	0.8	0.57
J′	4.34	0.01	5.13	0.0001
SR	2.67	0.05	4.25	0.0004

Indices are: (1) Total abundance: individuals 100-g^{-1} dry soil. (2) Trophic structure—BF, bacterivore; FF, fungivores; PP, plant parasites; OP, omnivores-predators. (3) Ecological indices—WI, ratio of bacterivores and fungivores to plant parasites. Td, trophic diversity; λ, dominant genus; H′, Shannon Index; MI, maturity index; ΣMI, maturity index modification; J, evenness; SR, richness. Values of $P < 0.05$ were considered significant.

TABLE 2. Mean relative abundance (%) of soil nematode taxa at different seasons during the study period.

Genus/family trophic groups	Seasons			
	Winter	Spring	Summer	Autumn
Bacterivores	14.3	18.4	15.2	18.6
1. *Acrobeles*	3.0	7.1	4.5	3.7
2. *Acrobeloides*	3.8	5.6	2.7	3.5
3. *Cervidellus*	3.4	2.1	2.3	5.1
4. *Chiloplacus*	2.9	0.9	1.9	4.2
5. *Cephalobus*	0.0	0.2	0.4	0.0
6. *Diplogaster*	0.0	0.0	0.0	0.3
7. *Eucephalobus*	0.0	0.2	0.4	0.0
8. *Mesorhabditis*	0.0	0.5	0.4	0.1
9. *Monchysterida*	0.0	0.0	0.1	0.0
10. *Pelodera*	0.0	0.0	0.4	0.0
11. *Plectus*	0.0	0.0	0.1	0.0
12. *Panagrolaimus*	0.1	0.6	0.0	0.0
13. *Rhabditis*	0.0	0.6	0.6	0.0
14. *Wilsonema*	1.1	0.6	1.4	1.7
Fungivores	17.3	13.8	21.9	23.5
15. *Aphelenchoides*	2.0	1.5	4.0	2.7
16. *Aphelenchus*	0.8	1.2	1.8	0.9
17. *Ditylenchus*	0.4	0.8	1.4	3.5
18. *Nothotylenchus*	14.1	10.3	14.7	16.4
Plant-parasites	58.6	55.1	56.8	53.9
19. *Filenchus*	0.3	0.2	0.4	0.3
20. *Heterodera*	2.0	1.4	3.1	0.9
21. *Meloidogyne*	3.7	3.8	5.0	6.4
22. *Paratylenchus*	2.2	3.3	1.5	0.7
23. *Pratylenchus*	8.2	4.4	4.5	6.4
24. *Rotylenchus*	0.0	0.3	0.3	0.1
25. *Telotylenchus*	3.4	1.2	5.7	0.2
26. *Tetylenchus*	5.1	10.0	5.7	5.5
27. *Tylenchorchynchus*	27.6	25.1	20.8	24.7
28. *Tylenchus*	5.9	4.6	9.3	8.5
29. *Xiphinema*	0.2	0.8	0.5	0.2
Omnivores-predators	9.9	12.8	6.2	4.1
30. *Discolaimus*	0.0	1.1	0.0	0.0
31. *Dorylaimellus*	2.2	1.4	1.7	1.2
32. *Dorylaimus*	4.3	3.6	2.3	1.2
33. *Eudorylaimus*	0.3	0.2	0.0	1.1
34. Leptonchidae	0.1	0.6	0.0	0.0
35. *Longidorus*	0.1	0.6	0.0	0.0
36. *Nygolaimus*	2.9	5.3	2.2	0.6

At this site, we assumed that the nematode community and structure were affected mainly by the dynamic changes in the patchiness of soil moisture availability and organic matter content. Our results were similar to those of Cadet et al. (2003), who illustrated the existence of a complex interaction between the quality of the organic matter, soil moisture, microflora, and fauna that may influence nematode trophic groups, abundance, and taxa composition.

The temporal and spatial changes in soil moisture and total nematode population yielded differences in patchiness tracery, indicating the existence of a dynamic, fast-response system to an unpredictable, multivariate environment. Nematode trophic group composition responds differently to moisture and organic matter content, demonstrating the existence of additional biotic factors (e.g., food type, source) and abiotic variables (e.g., soil chemistry, physical characteristics, aggregation).

The results obtained in this study show that the total number of nematodes and their trophic structure were found to shift on a seasonal basis toward a more heterogeneous aggregation in winter and autumn, suggesting the importance of moisture availability in spring and summer. A general overview shows that the frequency of the appearance of nematode patches decreased proportionally to the increase in the nematode density in the patches, supporting the observed difference between the winter, autumn, and spring, and summer. Similarly, Ettema et al. (2000) found a highly variable aggregation of nematode populations, where aggregation of separate species of nematodes was significant across distances of 13 m to 39 m. Moreover, their results showed that bacterivores, fungivores, and omnivore-predators exhibited a significant spatial variance in a range of 6 m to 80 m, but not plant-parasites, for which a border of variation at a distance of more than 1,200 m was not detected (Robertson and Freckman, 1995). These findings are similar to our desert site results, in which the plant-parasitic feeding group was found to maintain a relatively constant population density, whereas the other trophic groups' aggregation ability may be different significantly, even in a 10×10-m grid.

All ecological indices, except for Wasilewska's and the Maturity indices, were found to show the importance of seasonality. Only T, λ, H′, J′, and SR were useful indices for temporal as well as spatial-patch effect determination.

In spite of the relatively small study site, a distinct spatial pattern shown by different soil moisture and organic matter contents on a seasonal scale may have important implications not only on the soil free-living nematode community but also on all soil biota inhabitants. Hence, the soil properties and abiotic factors in open, arid landscapes play important roles in generating matrix-patch micro-niches similar to those observed for isolated trees in semi-arid regions (Breman and Kessler, 1995).

The results of this study show that the greater the spatial variation in soil water availability and organic matter content, the more types of microhabitats are created. The presence of a large number of microhabitats may be a key factor that determines spatial distribution patterns and presence of soil biota and supports our assumption that, even in desert soil ecosystem conditions, selection favors organisms with relatively narrow niches and specialized feeding habitats. We believe that the present investigation has increased our understanding of soil patchiness and the dynamic changes it undergoes under the influence of complex interactions between soil, climate, plants, and animals.

Literature Cited

Alon, A., and Y. Steinberger. 1999. Response of the soil microbial biomass and nematode population to a wetting event in nitrogen-amended Negev desert plots. Biology and Fertility of Soils 30:147–152.

Bakonyi, G., and P. Nagy. 2000. Temperature- and moisture-induced changes in the structure of the nematode fauna of a semiarid grassland—patterns and mechanisms. Global Change Biology 6:697–707.

Bongers, T. 1990. The maturity index: An ecological measure of environmental disturbance based on nematode species composition. Oecologia 83:14–19.

Breman, H., and J. J. Kessler. 1995. Woody plants in agroecosystems of semiarid regions. Berlin: Springer-Verlag.

Briggs, J. M., and A. K. Knapp. 1991. Estimating aboveground biomass in tallgrass prairie with the harvest method: Determining proper sample size using jackknifing and Monte Carlo simulation. Southwestern Naturalist 36:1–6.

Cadet, P., E. Pate, and N. N'Diaye-Faye. 2003. Nematode community changes and survival rates under natural fallow in the sudano-sahelian area of Senegal. Pedobiologia 47:149–160.

Cairns, E. J. 1960. Methods in nematology. Pp. 33–84 *in* J. N. Sasser, and W. R. Jenkins, eds. Nematology, fundamentals and recent advances with emphasis on plant-parasitic and soil forms. Chapel Hill, NC: University of North Carolina Press.

Dighton, J., A. S. M. Bonilla, R. A. Jimenez-Nunez, and N. Martinez. 2000. Determinants of leaf litter patchiness in mixed-species New Jersey pine barrens forest and its possible influence on soil and soil biota. Biology and Fertility of Soils 31:288–293.

Duponnois, R., K. Senghor, J. Thioulouse, and A. M. Ba. 1999. Susceptibility of several sahelian Acacia to *Meloidogyne javanica* (Treub) Chitw. Agroforestry Systems 46:123–130.

Ettema, C. H., and D. A. Wardle. 2004. The spatiotemporal patterns of nematode genera in a New Zealand forest and pasture soil. Pedobiologia 47:497–503.

Ettema, C. H., S. L. Rathbun, and D. C. Coleman. 2000. On spatiotemporal patchiness and the coexistence of five species of *Chronogaster* (Nematoda: Chronogasteridae) in a riparian wetland. Oecologia 125:444–452.

Ettema, C. H., and G. W. Yeates. 2003. Nested spatial biodiversity patterns of nematode genera in a New Zealand forest and pasture soil. Soil Biology and Biochemistry 35:339–342.

Evenari, M. E., L. Shanan, and W. Tadmore. 1982. The Negev: The challenge of a desert. Cambridge, MA: Harvard University Press.

Fahrig, L. 1991. Simulation methods for developing general landscape-level hypotheses of single-species dynamics. Pp. 417–442 *in* M. G. Turner and R. H. Gardner, eds. Quantitative methods in landscape ecology. New York: Springer-Verlag.

Freckman, D. W., and R. Mankau. 1986. Abundance, distribution, biomass, and energetics of soil nematodes in a northern Mojave Desert ecosystem. Pedobiologia 29:129–142.

Gallardo, A. 2003. Effect of tree canopy on the spatial distribution of soil nutrients in a Mediterranean Dehesa. Pedobiologia 47:117–125.

Garkaklis, M. J., J. S. Bradley, and R. D. Wooller. 2003. The relationship between animal foraging and nutrient patchiness in southwest Australian woodland soils. Australian Journal of Soil Research 41:665–673.

Garner, W., and Y. Steinberger. 1989. A proposed mechanism for the formation of "Fertile Island" in the desert ecosystem. Journal of Arid Environments 16:257–262.

Heip, C., P. M. J. Herman, and K. Soetaert. 1988. Data processing, evaluation, and analysis. Pp. 197–231 *in* R. P. Higgins and H. Thiel, eds. Introduction to the study of meiofauna. Washington, DC: Smithsonian Institution Press.

Lahav-Ginott, S., R. Kadmon, and M. Gersani. 2001. Evaluating the viability of Acacia populations in the Negev Desert: A remote sensing approach. Biological Conservation 98:127–137.

Lakin, G. F. 1990. Biometry, 4th ed. Moscow: High School for Biological Speciality of Universities.

Liang, W. J., S. Mouratov, Y. Pinhasi-Adiv, P. Avigad, and Y. Steinberger. 2002. Seasonal variation in the nematode communities associated with two halophytes in a desert ecosystem. Pedobiologia 46: 63–74.

Liang, W. J., Y. Pinhasi-Adiv, H. Shtultz, and Y. Steinberger. 2000. Nematode population dynamics under the canopy of desert halophytes. Arid Soil Research and Rehabilitation 14:183–192.

Liang, W., and Y. Steinberger. 2001. Temporal changes in nematode community structure in a desert ecosystem. Journal of Arid Environments 48:267–280.

Lindenmayer, D. B., and H. P. Possingham. 1996. Modelling the inter-relationships between habitat patchiness, dispersal capability, and metapopulation persistence of the endangered species, Leadbeater's possum, in southeastern Australia. Landscape Ecology 11: 79–105.

Milton, S. J., and W. R. J. Dean. 1995. How useful is the keystone species concept, and can it be applied to Acacia erioloba in the Kalahari Desert? Zeitschrift für Okologie und Naturschutz 4:147–156.

Odum, E. P. 1971. Fundamentals of ecology, 3rd ed. Philadelphia: W. B. Saunders Company.

Pen-Mouratov, S., X. L. He, and Y. Steinberger. 2004a. Spatial distribution and trophic diversity of nematode populations under *Acacia raddiana* along a temperature gradient in the Negev Desert ecosystem. Journal of Arid Environments 56:339–355.

Pen-Mouratov, S., M. Rakhimbaev, G. Barness, and Y. Steinberger. 2004b. Spatial and temporal dynamics of the nematode populations under *Zygophyllum dumosum* in an arid environment. European Journal of Soil Biology 40:31–46.

Pen-Mouratov, S., M. Rakhimbaev, and Y. Steinberger. 2003. Seasonal and spational variation in nematode communities in the Negev Desert ecosystem. Journal of Nematology 35:157–166.

Pickett, S. T. E., and M. L. Cadenasso. 1995. Landscape ecology: Spatial heterogeneity in ecological systems. Science 296:331–334.

Pulliam, H. R., J. B. Dunning, and J. G. Liu. 1992. Population-dynamics in complex landscapes: A case study. Ecological Applications 2:165–177.

Robertson, G. P., and D. W. Freckman. 1995. The spatial-distribution of nematode trophic groups across a cultivated ecosystem. Ecology 76:1425–1432.

Rohner, C., and D. Ward. 1999. Large mammalian herbivores and the conservation of arid acacia stands in the Middle East. Conservation Biology 13:1162–1171.

Rowell, D. L. 1994. Soil science: Methods and applications. London: Longman Group UK Ltd.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Urbana, IL: University of Illinois Press.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:668.

Simpson, G. G. 1964. Species density of North American recent mammals. Systematic Zoology 13:57–73.

Smedley, S. R., and T. Eisner. 1995. Sodium uptake by puddling in a moth. Science 270:1816–1818.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry: Principles, practices, and statistics in biological research. San Francisco, CA: W. H. Freeman and Co.

Steinberger, Y., and I. Loboda. 1991. Nematode population dynamics and trophic structure in a soil profile under the canopy of the desert shrub *Zygophyllum dumosum*. Pedobiologia 35:191–197.

Steinberger, Y., and S. Sarig. 1993. Responses by soil nematode populations in the soil microbial biomass to a rain episode in the hot, dry Negev Desert. Biology and Fertility of Soils 16:188–192.

Stuart, R. J., and R. Gaugler. 1994. Patchiness in populations of entomopathogenic nematodes. Journal of Invertebrate Pathology 64: 39–45.

Sulkava, P., V. Huhta, J. Laakso, and E.-R. Gylen. 2001. Influence of soil fauna and habitat patchiness on plant (*Betula pendula*) growth and carbon dynamics in a microcosm experiment. Oecologia 129: 133–138.

Wallwork, J. A. 1976. The distribution and diversity of soil fauna. London: Academic Press.

Wasilewska, L. 1994. The effect of age of meadows on succession and diversity in soil nematode communities. Pedobiologia 38:1–11.

Whitford, W. G. 1996. The importance of the biodiversity of soil biota in arid ecosystems. Biodiversity and Conservation 5:185–195.

Whitford, W. G. 2002. Ecology of desert systems. New York: Academic Press.

Yeates, G. W. 1994. Modification and qualification of the nematode maturity index. Pedobiologia 38:97–101.

Yeates, G. W., and A. F. Bird. 1994. Some observations on the influence of agricultural practices on the nematode faunas of some South Australian soils. Fundamental and Applied Nematology 17: 133–145.

Yeates, G. W., and D. C. Coleman. 1982. Role of nematodes in decomposition. Pp. 55–80 *in* D. W. Freckman, ed. Nematodes in soil ecosystems. Austin, TX: University of Texas.

Yeates, G. W., and K. L. King. 1997. Soil nematodes as indicators of the effect of management on grasslands in the New England Tablelands (NSW): Comparison of native and improved grasslands. Pedobiologia 41:526–536.