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

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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 10m-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 intraspecies 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; Sukkava 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 (Dupponnois 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

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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 (Eve-nari et al., 1982). The soil is a deep, fine-textured loess-sial 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* (Eve-nari 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 oxidation with dichromate in the presence of H₂SO₄, 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/ΣPᵢ², where Pᵢ is the proportion of the i-th trophic group (Heip et al., 1988).

(v) Genus dominance, λ = ΣPᵢ² (Simpson, 1949).

(vi) Shannon Index, H’ = −ΣPᵢ(logPᵢ), where P is the proportion of individuals in the i-th taxon (Shannon and Weaver, 1949).

(vii) Maturity Index MI = Συᵢᵢ, where υᵢᵢ is the c-p value assigned by Bongers (1990) of the i-th genus in the nematode and ρᵢ is 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 (ΣMI), including plant-feeding nematodes (Yeates, 1994).

(x) Evenness J = H’/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:

\[ \lambda = \frac{(X_{\text{max}} - X_{\text{min}})}{K} \]

Where \(X_{\text{max}}\) is maximum value of individuals found in a unit sample, \(X_{\text{min}}\) 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 (\(X_\lambda\)) value was calculated as: \(X_\lambda = \left(X_{\text{min}} - \lambda/2\right)\). 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 occurred 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.

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. 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-m² 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-
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 bacterivores 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,
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,
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 ($\lambda$), 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 ($\sum MI$); 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).
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.

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.
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, Etema 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 $F$, $\lambda$, $H'$, $J'$, 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.

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