

Seasonal and Spatial Variation in Nematode Communities in a Negev Desert Ecosystem¹

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Abstract: Seasonal and spatial variation in soil nematode communities was investigated in a field study conducted on a loessial plain in the northern Negev Desert, Israel. Soil samples from 0- to 50-cm depths were collected seasonally during 2001 under the canopy of *Atriplex halimus* and *Hammada scoparia*, and between shrubs (control). Total population abundance ranged from 8 to 887 individuals per 100 g soil, represented by 32 genera from 16 families. Significant temporal and vegetation effects were elucidated using most ecological indices applicable to express nematode community composition. Of those indices computed, only the Shannon index, the modified maturity index, and genus dominance distinguished differences in vertical distribution.

Key words: desert, distribution, ecology, halophyte, nematode.

Deserts are most precisely defined by productivity and climate. Life forms in a desert ecosystem share a common problem of survival in an environment where the availability of water is uncertain. In response to this problem, adaptive similarities between the different groups often diminish. Water and organic matter in the desert soil system are in constant motion along vertical gradients, creating dynamic fluctuations in soil water availability and plant debris. Such movement along the root surfaces will influence the spatial distribution of soil biota, especially those biotic components related to energy, nutrients, and food sources (bacteria and fungi).

Water infiltrates the soil during rainfall, moving below the root zone to underground storage. The temporal and spatial heterogeneity of soil-water availability certainly facilitates coexistence among many soil biotas. In desert ecosystems, where biological processes are regulated by rainfall (Noy-Meir, 1973), it is reasonable to assume that the diversity of microhabitats will be determined by the soil-water system, which is also influenced by climatic factors. Thus, the diversity of soil microhabitats along the soil profile will facilitate the use of this limited resource by soil animals.

Nematodes are ubiquitous inhabitants of soil systems (Bernard, 1992; Dropkin, 1989) due to their extreme abundance, adaptation, contribution to soil biota biomass, large number of species, and functionality among multiple trophic groups. Soil moisture availability has been found to be one of the most significant ecological factors directly affecting nematode abundance and community composition. It is dependent indirectly upon plant debris for energy and nutrients via feeding activity (Freckman and Mankau, 1986; Small, 1987;

Steinberger et al., 2001; Steinberger and Loboda, 1991; Yeates et al., 2002). Therefore, we assume that soil moisture and organic matter will affect the relative abundance and spatio-temporal patterns of nematode colonization and succession.

The physical and chemical components of soil, as well as the salinity of underground water, determine the nature of vegetation in the Negev Desert (Evenari et al., 1982). Desert plants have developed different strategies for exploiting scarce water resources (Evenari et al., 1976). The scattered occurrence of halophyte vegetation, and mechanisms of salt resistance in those plants, result in “islands of salinity” under the plant canopies (Sarig and Steinberger, 1994). These plants absorb salts through their root systems, translocating them to the leaves and redepositing them on the soil surface (Weisel, 1973). Perennial plants in desert ecosystems provide a multitude of microniches, mediating temperature and moisture regimes and supplying organic matter, especially in the root zone. In spite of spatial variability of moisture in a desert landscape, root growth in loessial plain soils reaches a depth of only 0.4 to 0.6 m, as a result of shallow water infiltration. Roots may reach a depth of 1 to 3 m in sandy or rocky soils (Danin, 1983). Because root proliferation of desert plants is correlated positively with exploitation of water resources, spatial-temporal variability in moisture should have an important effect on nematode community composition, abundance, and diversity.

These fluctuations in abiotic parameters between the wet winter and dry summer desert environment suggest that the “window of activity” for soil free-living nematodes at different depths and seasons is affected by the plant rhizosphere and physiological adaptations. Soil moisture was more favorable for nematode activity at all the depths in autumn and summer than in winter and spring, perhaps because of the input of dew, which may have a moderating effect (Evenari et al., 1982; Liang et al., 2002; Steinberger et al., 19898). Contrasting patterns of water movement through the soil profile and organic matter accumulation in upper layers could be a mechanism for defining spatio-temporal changes in total abundance.

The objective of this study was to determine the spa-

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tial and temporal relationship between abundance, activity, and diversity of the soil nematode communities and fluctuations in abiotic factors including soil moisture, organic matter, and salinity under the canopy of *Hammada scoparia* (Pomel) Iljin and the saltbush *Atriplex halimus* L., two typical halophyte shrubs of the Negev Desert highlands.

MATERIALS AND METHODS

Sampling site: Soil samples were collected from the loessial plain near Sede Boker (30°52'N, 34°47'E) in the northern Negev Desert, Israel. The annual rainfall ranges from 34 to 187 mm with a mean of 98 mm, with all rainfall occurring during the winter months (November–April). Dew occurs on an average of 200 nights per year, providing additional precipitation of about 35 mm (Evenari et al., 1982). Mean monthly temperatures vary from 6 °C in January to 25 °C in August. Average daily relative humidity reaches 60 to 70% in winter and 40 to 50% in summer. The plants characteristic of the site are *H. scoparia*, *Artemisia herba-alba*, and *A. halimus*

(Danin, 1983). *Hammada scoparia* is much more abundant at the site than the other shrubs.

Methods: Four replicate soil samples (200 g each) were collected with a corer at random from under the canopies of *A. halimus* and *H. scoparia* or from open spaces between shrubs (control) in each of the four seasons: winter (January), spring (April), summer (July), and autumn (September) in 2001. Samples were collected in 10-cm increments to a depth of 50 cm. Samples from each depth increment were placed in individual plastic bags and transported to the laboratory in a cooler to avoid excessive heat during summer periods. All soil samples were sieved (2-mm mesh) to remove root fragments and other organic debris. Subsamples from each replicate soil sample were removed to determine soil moisture, total organic matter, soil salinity (by electrical conductivity), and free-living soil nematodes.

Soil analysis: Soil chemical properties were measured for each 10-cm increment for a total of 5 depths per core. A 3-g subsample from each of four replicates of each site was weighed and dried at 105 °C for gravi-

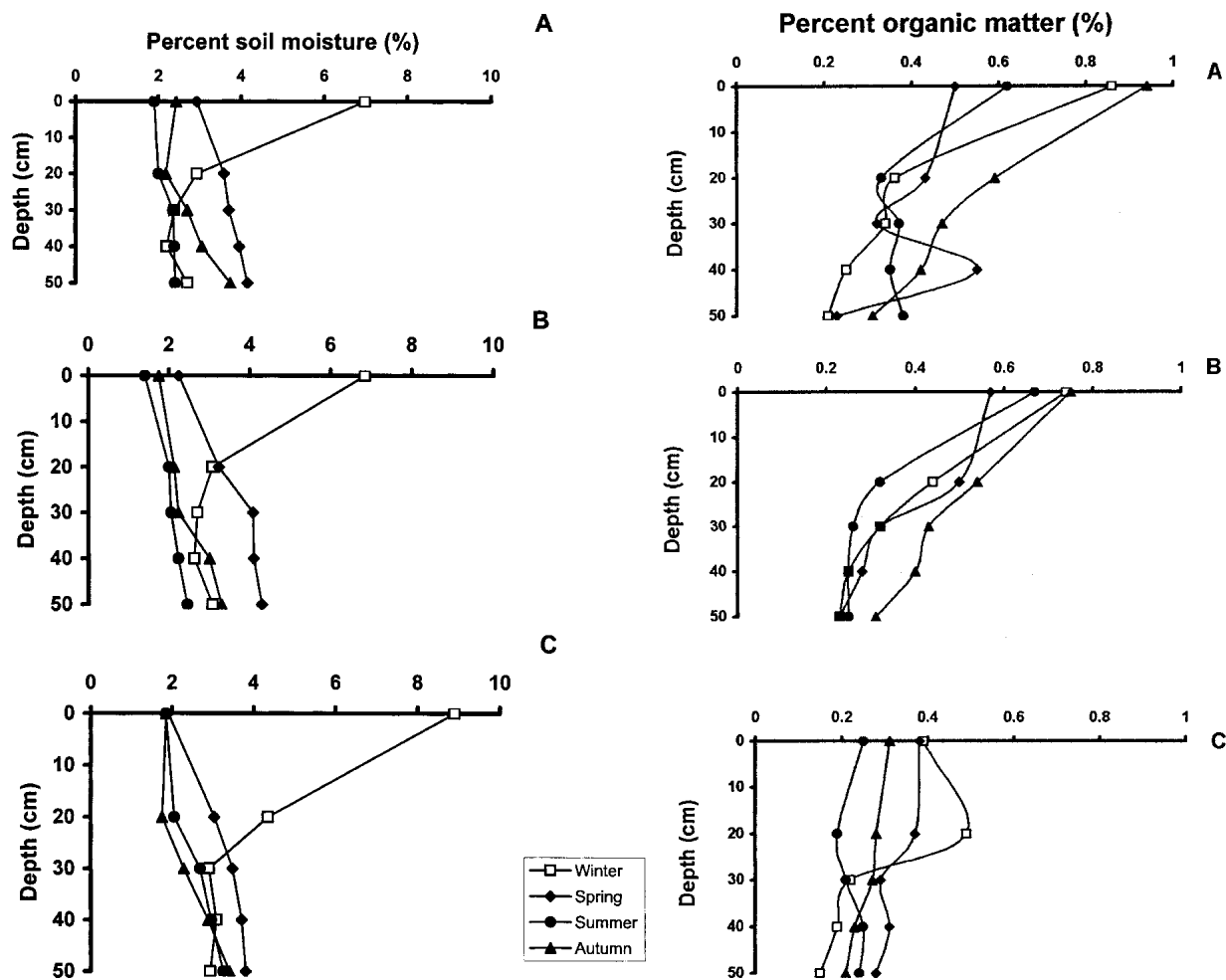


FIG. 1. Changes in soil moisture and organic matter under *A. halimus* (A), *H. scoparia* (B), and control (C) (□ - winter, ♦ - spring, ● - summer, ▲ - autumn).

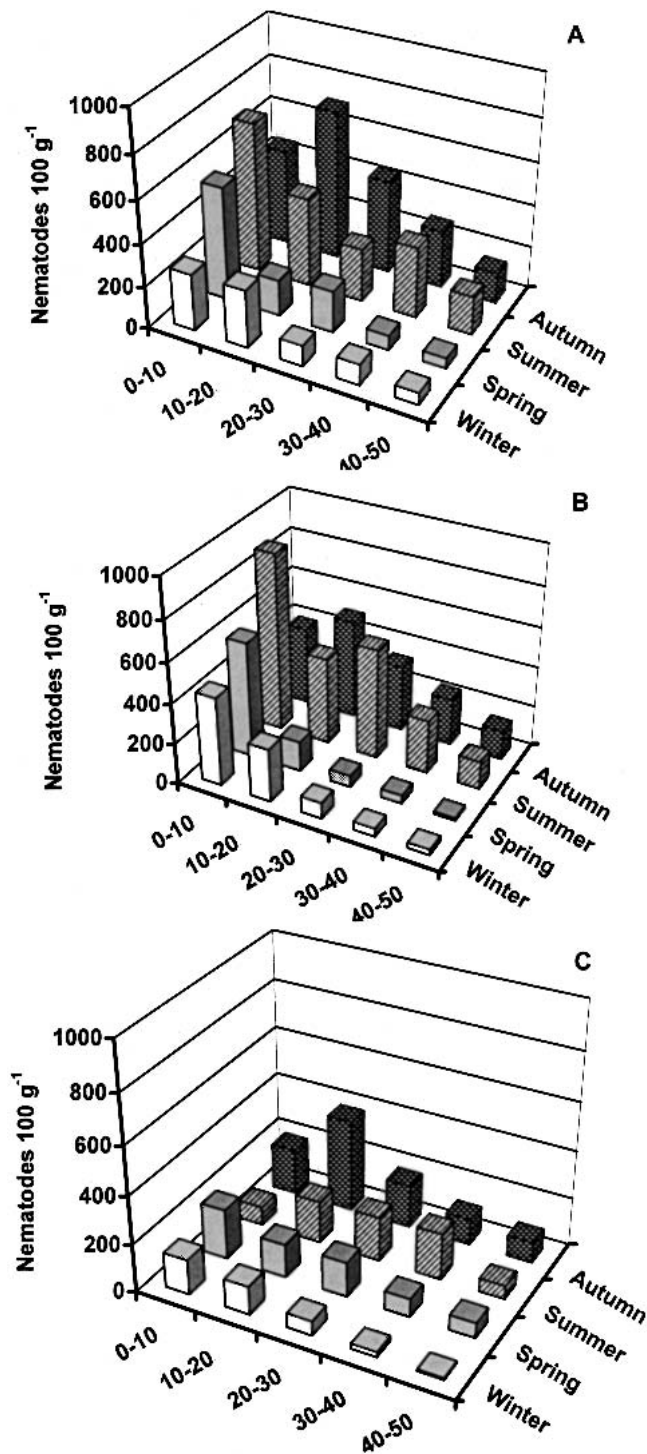


FIG. 2. Changes in the total number of nematodes under *A. halimus* (A), *H. scoparia* (B), and control (C) at different depths during different seasons.

metrical determination of moisture expressed as a percentage of dry weight. Soil organic matter was determined using the modified chromate combustion method of Rowell (1994) and Xie and Steinberger (2001).

Nematode extraction: One hundred grams from each replicate sample were used for nematode extraction

using the Baermann funnel method (Steinberger and Loboda, 1991). After extraction, the nematode population was preserved in a 5% formalin solution for further analysis, and the total number of individuals in each sample was determined. All available nematodes in each sample were identified to order, family, and genus using a compound microscope. Trophic groups were classified as bacterivores, fungivores, plant-parasites, and omnivores-predators according to known feeding habitats or stoma and esophageal morphology (Steinberger and Sarig, 1993; Yeates et al., 1993).

The characteristics of the nematode communities were described by means of the following indexes: (I) absolute abundance of individuals per 100 g dry soil; (II) trophic structure [numbers of bacterivores (BF), fungivores (FF), plant-parasites (PP), omnivores-predators (OP)] (Liang et al., 2000; Steinberger and Loboda, 1991; Steinberger and Sarig, 1993); (III) ratio of fungivores plus bacterivores to plant-parasites (WI), where $WI = (FF + BF)/PP$ (Wasilewska, 1994); (IV) fungivore/bacterivore ratio (F/B), which indicates the relative organic matter decomposition pathway in detrital food webs, a smaller ratio being associated with faster rates of decomposition (Twinn, 1974); (V) trophic diversity (T) describes the diversity of functional groups, where $T = 1/\sum Pi^2$ and Pi is the proportion of the i -th trophic group in the nematode community (Heip et al., 1988); (VI) Shannon index (H'), a species diversity

TABLE 1. Univariate analysis of variance (ANOVA) for soil moisture, organic matter, and soil nematodes under the canopy of two shrub species and in controls for a four-season period (January 2000–November 2001).

Index	Vegetation		Season		Depth	
	F-test	P value	F-test	P value	F-test	P value
Soil moisture	2.07	N.S.	78.13	0.0001	10.97	0.0001
Organic matter	17.33	0.0001	3.05	0.0300	23.00	0.0001
Total nematode abundance	12.53	0.0001	11.31	0.0001	16.56	0.0001
1. Trophic structure						
BF	15.16	0.0001	16.30	0.0001	14.36	0.0001
FF	5.91	0.0030	5.91	0.0007	6.17	0.0001
PP	6.43	0.0020	5.81	0.0008	9.31	0.0001
OP	4.78	0.0100	2.55	N.S.	6.60	0.0001
2. Ecological indices						
WI	10.05	0.0001	8.70	0.0001	0.94	N.S.
F/B	1.50	N.S.	0.24	N.S.	1.52	N.S.
T	0.56	N.S.	0.28	N.S.	1.07	N.S.
H'	13.62	0.0001	14.03	0.0001	3.69	0.0065
MI	6.96	0.0012	6.80	0.0002	1.31	N.S.
ΣMI	1.39	N.S.	0.69	N.S.	2.92	0.0300
λ	3.13	0.0500	5.44	0.0010	1.08	N.S.
J'	12.01	0.0001	11.86	0.0001	3.00	0.0200
SR	4.47	0.0130	6.01	0.0006	0.55	N.S.

Indices are: Total abundance: individuals per 100 g dry soil. (1) Trophic structure—BF, bacterivores; FF, fungivores; PP, plant-parasites; OP, omnivores-predators. (2) Ecological indices—WI, ratio of bacterivores and fungivores to plant-parasites; F/B, fungivores/bacterivores ratio; T, trophic diversity; H' , Shannon index; MI, maturity index; ΣMI , modified maturity index; λ , genus dominance; J' , evenness; SR, richness.

N.S. = not significant at $p > 0.05$.

measure, which gives more weight to rare species, $H' = (-\sum P_i [\ln P_i])$, where p is the proportion of individuals in the i -th taxon (Shannon and Weaver, 1949); (VII) maturity index (MI), a measure based on the life-history strategy characteristics of nematode taxa (Bongers, 1990; Freckman and Ettema, 1993); (VIII) modified maturity index (ΣMI), including plant-feeding nematodes (Yeates, 1994); (IX) genus dominance (λ), which was used to assess dominance in all nematode genera in the sample, $\lambda = \sum P_i^2$, where P_i is the proportion of the i -th taxon (McSorley and Frederick, 1996; Simpson, 1949); (X) Evenness (J'), where $J' = H' / \text{maximum}$, $H' = H' / \log_e s$ (McSorley and Frederick, 1996; Pielou, 1975; Yeates and Bird, 1994); and (XI) specific 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). Data were analyzed by analysis of variance, with abundance as a dependent variable and depth, location, and season as independent variables. Mean comparisons were tested using a

Duncan multiple-range test. All statistical procedures were performed using Statistical Analysis System (SAS) software. Significance was defined as an α of 0.05.

RESULTS

Soil moisture and organic matter: The winter rainfall was 80.3 mm, of which 46.3 mm fell before the winter sampling. Approximately 83% of the annual rainfall occurred between October and February. This rainfall pattern was reflected in the soil moisture profiles (Fig. 1A,B,C), which show a sharp increase in winter, with no significant differences between the two shrub habitats. However, moisture was greater between shrubs (8.9%) than under either *A. halimus* or *H. scoparia* at the 0- to 10-cm layer (6.8 and 6.9%, respectively) ($p < 0.001$). Moreover, soil moisture content in the upper (0-10 cm) and the deepest (40-50 cm) layers was greater than at the 10- to 40-cm depth ($p < 0.05$; $df = 180$).

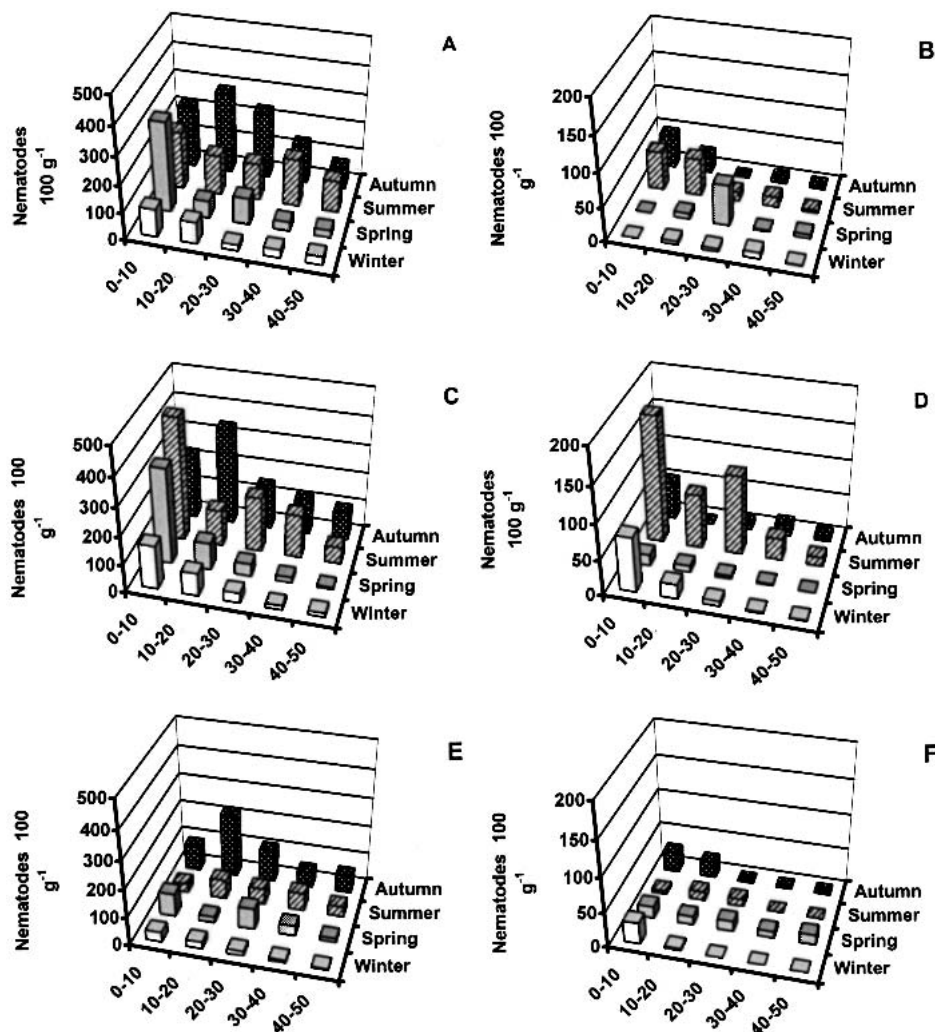


FIG. 3. Distribution of bacterivore (BF) (A,C,E) and fungivore (FF) (B,D,F) nematode trophic groups in soil under *A. halimus* (A,B), *H. scoparia* (C,D), and inter-shrub or vegetation-free (E,F) at the different depths.

Soil organic matter in the two top layers (0–10 and 10–20 cm) under shrubs was greater than between shrubs (Fig. 1A,B) ($p < 0.001$). No differences in organic matter in the deeper layers were apparent ($p < 0.05$). The greatest value of 0.95% was observed at the 0- to 10-cm layer in autumn beneath *A. halimus*, while the same layer contained only 0.53% organic matter in spring ($p < 0.01$) (Fig. 1A,B,C). In contrast, seasonal differences ranged from 0.75 to 0.58% and 0.28 to 0.38% beneath *H. scoparia* and between shrubs, respectively. At the 40- to 50-cm depth, minimum values of organic matter content were 0.23, 0.25, and 0.15% for *A. halimus*, *H. scoparia*, and between shrubs, respectively (Fig. 1A,B,C).

Total nematode abundance: Mean total abundance of nematodes ranged between 8 and 887 individuals per 100 g dry soil (Fig. 2A,B,C). Time, depth, and plant species affected total nematode abundance significantly

($p < 0.0001$) (Table 1). Total numbers of nematodes under *A. halimus* reached maximum values of 704 individuals in the 0- to 10-cm layer during the hot, dry summer period. In the 40- to 50-cm layer, mean numbers were 75% less than in the 0- to 10-cm layer, with 181 individuals per 100 g soil. This was the largest population observed for any season at the 40- to 50-cm depth. The trend in winter and spring followed that of summer, with fewer individuals at all depths (Fig. 2). In autumn, the trend of abundance increased, with 702 individuals per 100 g dry soil at the 10- to 20-cm depth, 36% greater than the 452 individuals per 100 g in the 0- to 10-cm layer in the *A. halimus* rhizosphere. The pattern under *H. scoparia* was similar to that under *A. halimus* for all seasons. The mean total number of nematodes reached a maximum of 887 individuals per 100 g dry soil in the upper layer during summer (Fig. 2), and decreased (84%) to 139 individuals at the 40-

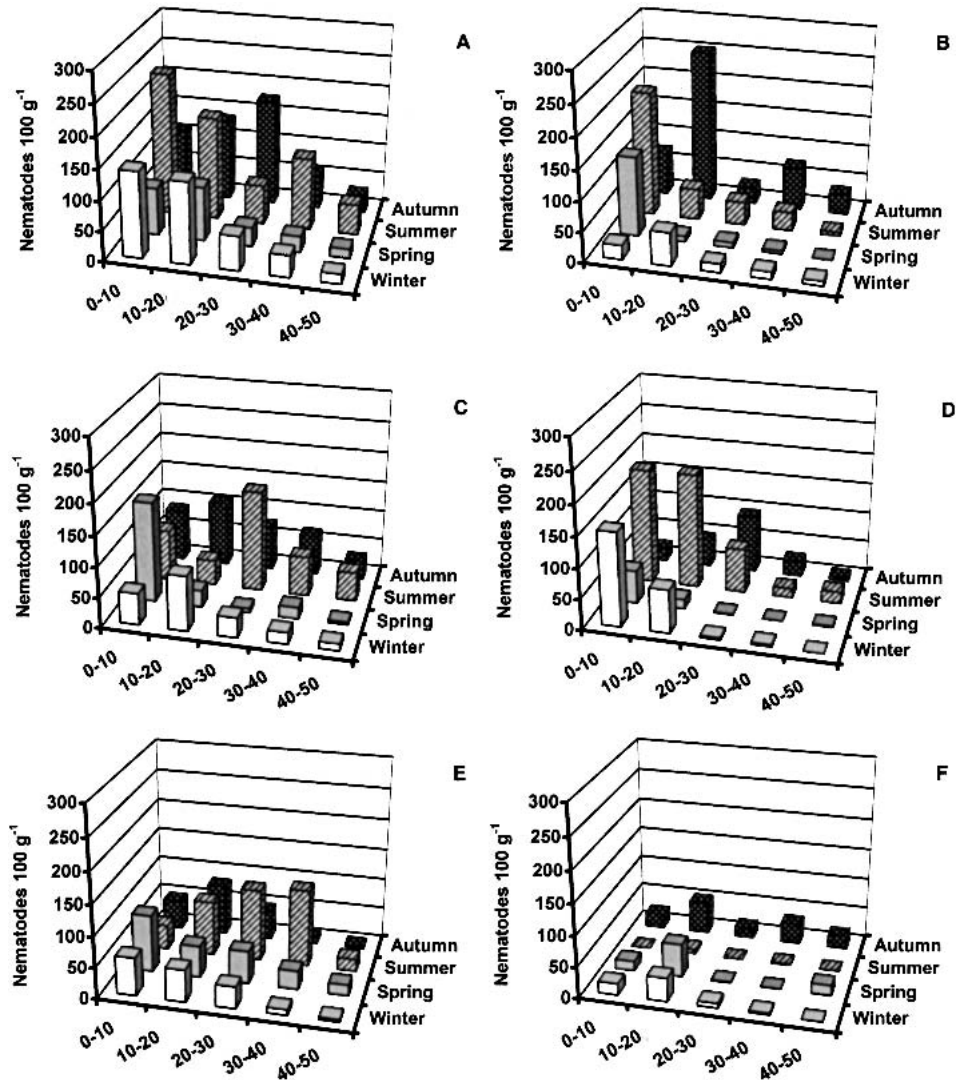


FIG. 4. Distribution of plant-parasites (PP) (A,C,E) and omnivore-predator (OP) (B,D,F) nematode trophic groups under *A. halimus* (A,B), *H. scoparia* (C,D), and control (E,F) at the different sampling layers during the study period.

50-cm depth. A similar pattern was observed between shrubs, where mean abundance ranged from 383 to 8 individuals per 100 g dry soil. Generally, nematode abundance was greater under than between shrubs ($F = 15.2$; $p < 0.0001$). However, no significant differences were found between the vegetation types ($p > 0.05$) during the study period.

Trophic groups: Bacterivorous nematodes were most abundant in the upper layer (0–10 cm) in spring under *A. halimus*, in summer under *H. scoparia*, and in autumn between shrubs (Fig. 3A,C,E). Bacterivores exhibited a similar pattern to that of total nematodes, with mean maximum abundance of 324, 437, and 225 individuals per 100 g dry soil under *A. halimus*, *H. scoparia*, and control, respectively. Treatment, season, and depth significantly affected bacterivore population abundance under shrubs and in control ($p < 0.0001$) (Table 1).

Abundance of fungivores in the 0- to 10-cm depth under *H. scoparia* in summer reached a mean maximum of 177 individuals per 100 g dry soil (Fig. 3D). The maximum mean fungivore values obtained under *A. halimus* and in the control soil were found to be three to five times lower than under *H. scoparia* (Fig. 3B,F,D). However, fungivore and bacterivore numbers exhibited similar trends. Differences in abundances were observed under and between shrubs, between seasons and depth ($p < 0.001$) (Table 1).

Figure 4 illustrates changes in plant-parasite and omnivore-predator abundance during the four seasons and at the different depths. Two main features related to the plant-parasite population can be observed: in each treatment, the greatest abundance of population was present during the summer and autumn seasons, and a relatively high population was present uniformly at all depths. Total number of individuals, and the distribution pattern among the different depths and seasons, varied between *A. halimus* and the other two treatments ($p < 0.05$, $df = 180$).

Omnivore-predator populations were relatively abundant in the 0- to 10-cm and 0- to 20-cm layers under the shrubs, and declined in abundance at greater depths (Fig. 4B,D,F). Maximum values of omnivores-predators were observed in autumn under both *A. halimus* and between shrubs. In contrast, omnivores-predators were most abundant in summer under *H. scoparia* (Fig. 4D) ($p < 0.01$). Numbers of omnivores-predators remained relatively constant throughout the seasons (Table 1).

Nematode taxa: A total of 32 genera in 6 families were identified in all samples taken from the 0- to 50-cm depths. *Tylenchorchynchus*, *Acrobeles*, *Acrobeloides*, and *Cervidellus* were the most abundant taxa in the soil samples taken from beneath the plants and from the open space between shrubs (vegetation-free area). Their mean relative abundance was 23%, 13%, 8%, and 11% of the nematode community, respectively. Throughout the study period, the relative abundance of *Tylenchorchynchus* was greater between shrubs (35%) and un-

TABLE 2. Univariate analysis of variance (ANOVA) for nematode species under the canopy of two shrub species and in controls for a four-season period (January 2000–November 2001).

Index	Vegetation		Season		Depth	
	F-test	P value	F-test	P value	F-test	P value
Total nematode abundance	12.53	0.0001	11.31	0.0001	16.56	0.0001
Bacterivores						
<i>Acrobeles</i>	9.87	0.0001	24.30	0.0001	0.83	N.S.
<i>Acrobeloides</i>	1.95	N.S.	19.21	0.0001	2.65	0.0350
<i>Cephalobus</i>	1.52	N.S.	8.54	0.0001	0.20	N.S.
<i>Cervidellus</i>	7.31	0.0009	15.10	0.0001	2.59	0.0380
<i>Chiloplacus</i>	3.15	0.0450	26.66	0.0001	0.73	N.S.
<i>Diploscapter</i>	0.80	N.S.	1.25	N.S.	0.09	N.S.
<i>Eucephalobus</i>	1.00	N.S.	1.00	N.S.	1.00	N.S.
<i>Heterocephalobus</i>	1.17	N.S.	1.33	N.S.	0.58	N.S.
<i>Mesorhabditis</i>	11.75	0.0001	16.04	0.0001	2.73	0.0310
<i>Rhabditis</i>	6.95	0.0012	3.25	0.0230	2.13	N.S.
<i>Wilsonema</i>	0.78	N.S.	2.78	0.0430	1.67	N.S.
Fungivores						
<i>Aphelenchoides</i>	0.38	N.S.	2.05	N.S.	2.26	N.S.
<i>Aphelenchus</i>	0.45	N.S.	3.07	0.0300	1.96	N.S.
<i>Ditylenchus</i>	1.18	N.S.	0.58	N.S.	1.27	N.S.
<i>Nothotylenchus</i>	3.95	0.0210	3.87	0.0100	1.55	N.S.
Plant-parasites						
<i>Filenchus</i>	0.71	N.S.	2.04	N.S.	0.72	N.S.
<i>Heterodera</i>	1.17	N.S.	1.33	N.S.	0.58	N.S.
<i>Meloidogyne</i>	5.51	0.0048	1.07	N.S.	1.37	N.S.
<i>Pratylenchus</i>	0.23	N.S.	13.36	0.0001	0.18	N.S.
<i>Telotylenchus</i>	1.00	N.S.	0.90	N.S.	1.07	N.S.
<i>Tetylenchus</i>	4.76	0.0096	0.43	N.S.	1.16	N.S.
<i>Tylenchorchynchus</i>	4.13	0.0200	7.09	0.0002	7.06	0.0001
<i>Tylenchus</i>	1.13	N.S.	1.01	N.S.	3.88	0.0048
<i>Trichodorus</i>	0.00	0.0000	0.00	0.0000	0.00	0.0000
Omnivores-predators						
<i>Discolaimus</i>	0.55	N.S.	2.02	N.S.	2.77	0.0300
<i>Dorylaimus</i>	1.00	N.S.	1.00	N.S.	1.00	N.S.
<i>Eudorylaimus</i>	0.95	N.S.	2.23	N.S.	5.28	0.0005
<i>Leptonchus</i>	0.78	N.S.	2.19	N.S.	0.44	N.S.
<i>Mononchus</i>	0.00	0.0000	0.00	0.0000	0.00	0.0000
<i>Nyngolaimus</i>	2.46	N.S.	1.80	N.S.	5.77	0.0002

N.S. — not significant.

der *A. halimus* (28%) than under *H. scoparia* (24%). In contrast, relative abundances of *Cervidellus* were greater under *H. scoparia* (14%) than *A. halimus* (10%) and between shrubs (11%).

Nine of 30 genera were affected by plant cover treatment ($p < 0.05$). Twelve genera were affected by season ($p < 0.05$), and only eight were affected by depth ($p < 0.05$). The abundance of only three genera (*Cervidellus*, *Mesorhabditis*, and *Tylenchorchynchus*) was affected by all three variables (treatment, season, and depth) ($p < 0.05$) (Table 2).

Ecological indices: The ratio of bacterivores and fungivores to plant-parasites (WI) was influenced by treatment and sampling period but not by soil layer ($p < 0.0001$) (Fig. 5; Table 1). Maximum numbers of nematodes under *A. halimus* were observed during autumn regardless of sampling depth. In contrast, smaller abundances were present in spring and summer in the two upper soil layers (Table 1). A different pattern was ob-

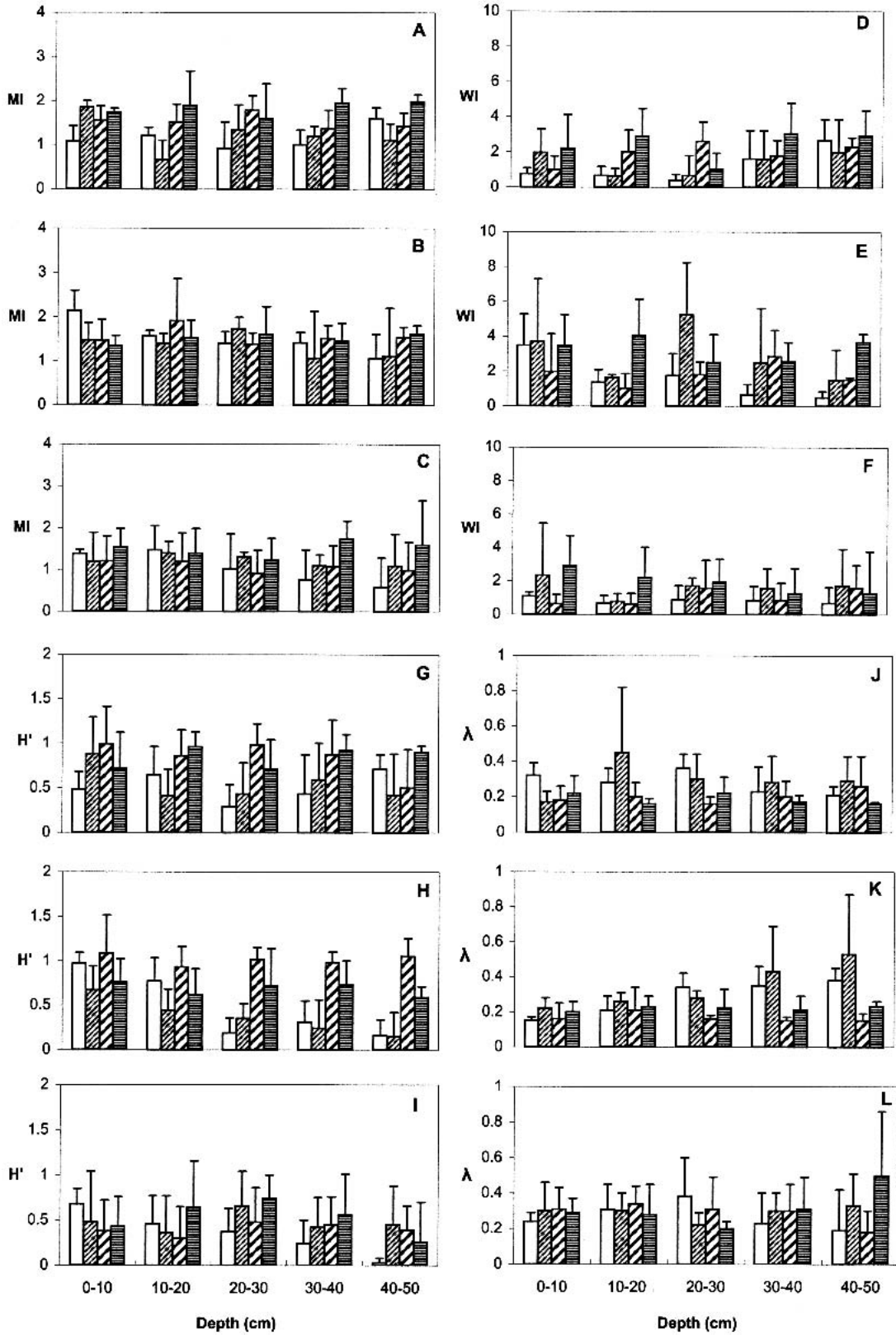


FIG. 5. Variations in ecological indices (MI maturity index; WI ratio of bacterivores and fungivores to plant-parasites; H' Shannon Index; λ genus dominance) at the 0- to 50-cm soil layer under *A. halimus* (A,D,G,J), *H. scoparia* (B,E,H,K), and control (C,F,I,L) throughout the different seasons (□ winter, ▨ spring, ▩ summer, and ▪ autumn). Bars represent means, and error bars represent one standard deviation.

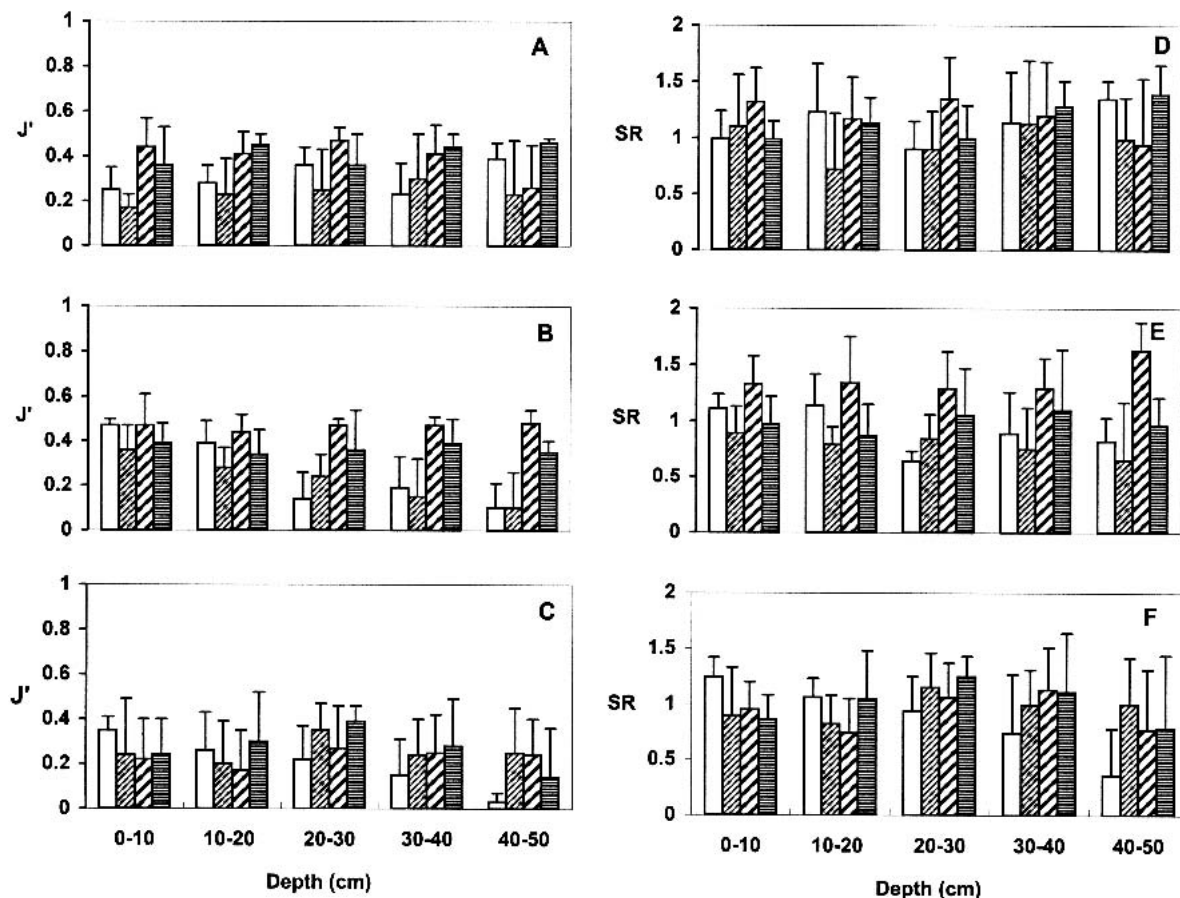


FIG. 6. Variations in ecological indices (J' , evenness; SR, richness) at the 0- to 50-cm soil layer under *A. halimus* (A,D), *H. scoparia* (B,E), and control (C,F) throughout the different seasons (\square winter, diagonal lines spring, cross-hatched summer, horizontal lines autumn). Bars represent means, and error bars represent one standard deviation.

tained under *H. scoparia*, where relatively greater numbers occurred in the upper layers during all seasons. Greatest numbers of nematodes at the 10- to 20-cm depth occurred in autumn ($p < 0.05$), whereas greater numbers at the deeper 20- to 30-cm layer occurred in spring. Between vegetation, significant differences were observed among depths in all seasons except winter.

The fungivore-to-bacterivore ratio (F/B) was not affected by plant cover or by temporal and spatial sampling (Table 1). Mean values of the F/B ratio under *A. halimus*, *H. scoparia*, and in the control samples ranged between 0.1 and 0.2. No differences were observed between treatments, seasons, and depths ($p > 0.05$) (Table 1). However, slight fluctuations were observed through time and space.

Values of trophic diversity (T) under *A. halimus*, *H. scoparia*, and control samples ranged between 0.6 and 1.4, with a maximum mean value of 1.1 for all seasons and depths. No significant differences ($p > 0.05$) were observed between plant cover treatments, seasons, or depths (Table 1).

Values of the Shannon index (H') (Fig. 5; Table 1) exhibited similar trends between *A. halimus* and *H. scoparia* samples. H' values were greater under *A. halimus* and *H. scoparia* than in the control samples ($p < 0.05$, n

= 240), and values obtained for winter and spring (0.4) were smaller than in summer and autumn (0.7).

Evenness (J'), which is determined from the diversity index (H'), varied among vegetation treatments, with greater values observed beneath *A. halimus* and *H. scoparia* than inter-shrub samples ($p < 0.0001$) (Fig. 6; Table 1). Values were greater in summer and autumn than in the wet, winter and spring seasons ($p < 0.0001$). Values of J' in the 0- to 10-cm depth were greater than in the other depths throughout the study period ($p < 0.02$).

Values of maturity index (MI) were more similar under than between plants ($p < 0.05$, $df = 180$) (Fig. 5; Table 1). Samples taken in autumn had greater MI values than those of the other three seasons ($p < 0.05$). Modified maturity index (ΣMI) values did not differentiate vegetation treatment or vary through time, as did MI (Table 1).

Generic dominance (λ) in the inter-shrub samples exhibited greater values than samples taken under *A. halimus* ($p < 0.05$) (Table 1; Fig. 5). Differences were observed between seasons, with maximum values observed in spring and minimum values in summer ($p < 0.001$, $n = 240$). Generally, index values did not vary with depth.

Richness (SR) under *A. halimus* was greater than with inter-shrub samples, reaching maximum values in summer ($p < 0.01$). Composition was relatively constant with depth ($p < 0.05$) and variable seasonally ($p < 0.05$).

DISCUSSION

Annual mean abundance of total nematodes beneath the two shrubs was several magnitudes more abundant than between shrubs. Maximum values under shrubs were about 900 individuals per 100 g soil in contrast to 8 individuals per 100 g soil in vegetation-free zones. These values are similar to those reported by Steinberger and Loboda (1991) and Liang et al. (2000) for *Z. dumosum*, and lower than in data reported by Freckman and Mankau (1986) in the Mojave Desert. Bacterivores were the most abundant trophic group during the study period, followed by plant-parasites. The least abundant trophic group was fungivore-feeders, and the relatively low number of omnivores-predators in this study are supported by Liang et al. (2000, 2002). The Negev Desert is considered a "hot desert," making it less stable than the Mojave Desert, which has a more abundant omnivore-predator population and is known as a "cold desert," as reported by Freckman and Mankau (1986).

The values obtained for WI ranged from 0.7 to a maximum of 8.5, which is in the range reported by Wasilewska (1994) and Liang et al. (2002) for meadow and desert communities. The fungivore/bacterivore ratio (F/B) reflects the structure of the microflora community, which is known to be the primary decomposers directly affecting organic matter decomposition and nutrient cycling (Hendrix et al., 1986; Ingham et al., 1985). This value was found to be 50% of the 0.47 level found in the same desert for *Z. dumosum* in the upper soil (0–10 cm) layer (Liang et al., 2002) and 20% of the values obtained in a Mediterranean agroecosystem (Liang et al., 2001).

Trophic diversity (T) describes the diversity of functional groups within the nematode populations. The values obtained in this study (0.6–1.7) were less than the value (2.14) reported by Liang et al. (2000) for different plants in sandy soil in the northern Negev Desert at Bira-Sluge.

The Shannon diversity index (H') gives more weight to rare species, where greater values indicate greater diversity. The H' values in this study showed significant seasonal, spatial, and plant-cover effects. Values of H' ranged from 0.99 to 0.29 under *A. halimus*, 1.1 to 0.16 under *H. scoparia*, and 0.03 to 0.74 in the open spaces between shrubs. The values reported in this study were smaller than those reported by Yeates and King (1997) for native and improved grasslands (2.36 and 1.43, respectively) in samples taken at a 30-cm depth, and were lower compared to data reported by Liang et al. (2000, 2002) in a desert system.

Evenness (J'), which is determined from the diversity index (H'), showed similar results, with significant differences in nematode faunas under the different treatments affected by temporal and spatial variables. However, the values obtained were found to be low compared to results reported by Yeates and King (1997) for native grassland and by Price and Siddiqi (1994) for rainforests in Cameroon.

The maturity index (MI) can reflect the degree of disturbance of the soil ecosystem as described by Bongers (1990) and Bongers et al. (1997). Changes in nutrient status appear as a decrease in MI values, and our results show that nutrient availability is affected mostly by vegetation type and seasonality, not by soil depth profile. According to Yeates (1994), (ΣMI) led us to a different conclusion, with emphasis on the vertical distribution effect rather than on the temporal or plant cover contribution.

Genus dominance (λ) was found in the range of 0.09 to 0.87, which greater than the range of 0.09 to 0.36 and 0.10 to 0.22 obtained by Yeates and Bird (1994) and McSorley and Frederick (1996), respectively. In our study, species richness (SR) was less than 2.0, compared to the range of 1.49 to 5.02 obtained by Yeates and Bird (1994) in an agroecosystem, and values reported for a study undertaken in North America by McSorley and Frederick (1996) ranged between 3.48 to 4.25 in an agroecosystem.

In conclusion, significant temporal and vegetation cover effects were elucidated in most of the indices during the study period. However, only three (H' , ΣMI , and J') out of nine indices distinguished any vertical distribution of the nematode communities. In the ecological indices examined, the Shannon index (H') and genus dominance (λ) were found to be the most sensitive in our case to the spatial-vertical and temporal variations as related to vegetation cover. In this desert environment, where "window activity unpredictability" is one of the most important features, sparse data appear on the nematode community, although it plays an important role in the energy and nutrient cycle. Maturity Index, and not ΣMI , values elucidate the importance of abiotic factors by coupling between organic matter and moisture availability, as suggested.

The results of the present study largely confirm previous results reported in the literature. However, they demonstrate that the addition of the vertical parameter, which reflects gradual changes in moisture availability, was not distinguishable by most nematode community indices.

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