Zoological Studies **51**(7): 1018-1026 (2012)

Zoological Studies

Forest Fire Modifies Soil Free-Living Nematode Communities in the Biriya Woodland of Northern Israel

Stanislav Pen-Mouratov[1], Orit Ginzburg[1], Walter G. Whitford[2], and Yosef Steinberger[1,*]

[1]*The Mina & Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat-Gan 52900, Israel*

[2]*USDA-ARS Jornada Experimental Range, MSC 3JER, New Mexico State University, Las Cruces, NM 88003, USA*

(Accepted July 23, 2012)

Stanislav Pen-Mouratov, Orit Ginzburg, Walter G. Whitford, and Yosef Steinberger (2012) Forest fire modifies soil free-living nematode communities in the Biriya woodland of northern Israel. *Zoological Studies* **51**(7): 1018-1026. We hypothesized that differential tree damage caused by fire in a Mediterranean conifer forest would reduce soil free-living nematode abundances and species diversity and affect the nematode community's trophic structure. Nematode communities were examined in soil samples collected from 4 subsites according to damage caused by the fire: all trees completely burned; burned trees with some live canopy foliage; burned trees removed by salvage logging, and a patch of unburned forest. Abundances of 2 bacterium-feeding nematode genera (*Cephalobus* spp. and *Acrobeloides* spp.) were higher in burned forest soils than in unburned forest soils. Other species of bacteria-feeding nematodes were less abundant in burned forest soils than in unburned forest soils. There was no effect of fire on the abundances of fungus-feeding nematodes. Eight of 13 species of omnivore-predator nematode genera were more abundant in unburned forest soils than in burned forest soils. Only 2 omnivore-predators with very low abundances were found in soils of the burned forest but were absent from unburned forest soils. Fire resulted in a lower trophic diversity, lower generic diversity, and lower generic richness in burned forest soils than in unburned forest soils. The fungivore-bacterivore ratio was similar in burned and unburned areas. Maturity indices were lower in burned than in unburned forest soils. The reported increased abundance of bacterium-feeding nematodes 6 wk after the fire remained consistent in burned forest soils 2 yr post-burn in this study. Other short-term changes in nematode communities did not persist in this study during the 2nd year post-burn. http://zoolstud.sinica.edu.tw/Journals/51.7/1018.pdf

Key words: Bacteria-feeding nematodes, Diversity, Fungivores, Omnivore-predators, Plant-parasitic nematodes.

Fire is an important part of the evolutionary history of most forest ecosystems in the world (Covington and Moore 1994, Conard et al. 2001). The effects of fire on ecosystems are complex, ranging from reductions or elimination of aboveground biomass to impacts on belowground physical, chemical, and biological properties (Neary et al. 1999). Biological properties of the soil are more sensitive to heat than are chemical and physical soil characteristics (DeBano et al. 1998). Moreover, environmental factors may affect various aspects of living organisms, from the community structure level to the morphological level and on to genetic levels (Yeates 1982, Jones et al. 2006, Ben Naceur et al. 2012). Fire is often extremely patchy, depending on local fuel loads, and the wind strength and direction, which results in large patches of unburned, moderately burned, and intensely burned areas, leading to a mosaic pattern of post-fire soils with modified biotic and abiotic processes (Visser 1995, Smith et al. 2005).

Forest fires are integral and important ecological factors in Mediterranean ecosystems that lead to changes in landscape stability and evolutionary transformations (Pausas and Vallejo 1999, Andréu et al. 2004). Pausas (2004) reported

*To whom correspondence and reprint requests should be addressed. Tel: 972-3-5318571. Fax: 972-3-7384058.
E-mail:yosef.steinberger@biu.ac.il

that in the Mediterranean basin, there has been a steady increase in the number of forest fires over the past century.

Numerous studies focused on elucidating the effects of fires on the forest vegetation composition and structure (Stocks 1991, Peckham et al. 2008), and on changes in the physical and chemical properties of soils (Hernandez et al. 1997, DeBano 2000). Studies on the effects of fire on other biota, especially the soil biota, are less numerous and frequently report conflicting results.

Free-living soil nematodes are abundant multicellular animals that participate in fundamental ecological processes in the soil, such as decomposition and nutrient cycling (Freckman 1988, de Goede and Bongers 1994, Bongers and Ferris 1999). Free-living soil nematodes are sensitive to ecosystem disturbances, including forest fires (Yeates 1982, Freckman and Virginia 1997, Yeates et al. 1999, Certini 2005). They also possess several attributes that make them excellent indicators for evaluating soil conditions (Freckman 1988, Neher 2001).

Previous studies that examined forest-fire impacts on the free-living soil-nematode community reported contradictory conclusions, ranging from confirmation of forest-fire's effects on the nematode community (Bloemers et al. 1997) to a refutation of such effects (Fenster et al. 2004). It was found that over time, fire does not significantly affect nematode abundance and diversity (Matlack 2001), but in the short term (6 wk after a fire), the total number of bacterium-feeders (BFs; *Acrobeloides*) and omnivore-predators (OPs) increased, while the number of fungus-feeding (FF; *Aphelenchoides*) nematodes declined, and root parasites remained unchanged (McSorley 1993).

Given the lack of clear and generalizable results on the effects of fire on the soil biota and soil processes, it is important to evaluate both the qualitative and quantitative effects of fire on the soil biota in forests in different bioclimatic regions. Since fire is a frequent disturbance in Mediterranean-region forests, studies of the effects of fire on the soil biota and soil processes are needed in order to manage forests in areas with Mediterranean climates. Therefore, we conducted a research program designed to examine differences in free-living soil-nematode communities in post-fire patches that had experienced different burn intensities compared to an unburned forest.

MATERIALS AND METHODS

Study site

The study area is located in the Biriya Forest of northern Israel. This area has a typical Mediterranean climate, with mild, rainy winters and hot, dry summers. The mean annual rainfall is 700 mm, almost exclusively all falling in winter (Dec.-Feb.). The mean maximum daily temperature in the hot season is 30°C (in Aug.), and it is 9°C in winter (in Jan.). The topography is hilly, with several steep slopes.

Vegetation at the site is primarily composed of pines (*Pinus halepensis* and *P. brutia*) and cedars (*Cedrus atlantica* and *C. brevifolia*) that were planted over the past 50 yr. Most of the area is now a mature forest. However, some new planting was carried out following a severe snowstorm in 1992. The forest is grazed by cattle and browsed by wild herbivores such as deer. The soils are of the pale Rendzina type (Xerorthents), derived from chalk and limestone (with an 88% $CaCO_3$ content), but are all highly weathered and characterized by a relatively low nutrient content (0.09% N and 1.14% organic C) (Dan and Koyumdjiski 1979, Ravikovitch 1981).

In July 2006, fire damaged an area of approximately 200 ha. Due to the patchy nature of the fire and the variable effectiveness of the efforts to extinguish the flames, there were different levels of damage to trees. The extent and intensity of fire damage to the forest were assessed by the extent of fire damage to trees. Burned areas were classified by visible damage to trees: areas with all trees totally burned and burned patches where tree canopies remained alive. In Mar. and July 2007 (following salvage-logging operations), sampling plots were marked, and soil samples were collected as described in Ginzburg and Steinberger (2012a b). The study sites represented 3 different post-fire forest conditions combined with salvage-logging operations: 1) burned forest, with all burned trees removed (BTR); 2) burned forest, with burned trees not removed (BFA); 3) burned area, with trees with live canopies not removed (BDT); and 4) control (forest area that was not burned) (CON). Salvage logging was conducted mechanically with minimum soil disturbance. The slash was left in piles to decompose.

Soil sampling

We initiated sampling in Nov. 2007 after autumn rains and 16 mo post-burn. Winter samples were collected in Feb. 2008, spring samples in May 2008, and summer samples in July 2008, 24 mo post-burn. In total, 144 soil samples from the upper 10 cm were collected after all litter was removed. Due to some heterogeneity in the study area, we collected 12 samples each from the BFA and BDT sites, 8 samples from the BTR site, and 4 from the CON site. Sample replicates, each weighing 0.5 kg, were collected seasonally in individual bags from 9 strips that had experienced different degrees of forest conflagration. In total, 36 soil samples (9 strips, 4 samples per strip, with 5-m spacing between samples) were randomized and stratified in relation to tree trunks. Each soil sample was immediately placed in an insulated container and taken to the laboratory. Soil samples were kept in cold storage at 4°C until being processed. Before the biological and chemical analyses, samples were sieved (through a 2-mm mesh size) to remove root particles and other organic debris.

Laboratory analysis

The following analyses were performed on each soil sample. Soil moisture was determined gravimetrically as the percentage dry mass by drying the samples to a constant weight at 105°C. Soil organic matter was measured by a modified method of Rowell (1994). Nematodes were extracted from 100 g of fresh soil samples using the Baermann funnel procedure (Cairns 1960) and were preserved in formalin. Nematodes from each sample were identified to order, family, and genus using a compound microscope. Nematodes were classified into the following trophic groups according to known feeding habitats or stoma and esophageal morphology (Yeates et al. 1993): (1) BFs; (2) FFs; (3) plant parasites (PPs); and (4) OPs. The total number of nematodes was counted and adjusted to 100 g dry soil.

Characteristics of the nematode communities were determined using the following indices: (1) absolute abundance of individuals adjusted to 100 g of dry soil (TNEM); (2) abundance of OP, PP, FF, and BF nematodes (trophic structure) (Steinberger and Loboda 1991); (3) fungivore/bacterivore (FB) ratio, FB = FF/BF (Twinn 1974); (4) trophic diversity (TD), $TD = 1/\sum Pi^2$, where Pi is the proportion of the ith trophic group (Heip et al. 1988); (5) Simpson's dominance index (D), $D = \sum Pi^2$ (Simpson 1949); (6) Shannon-Weaver index (H'), $H' = -\sum PiI (\ln PiI)$, where P is the proportion of individuals in the ith taxon (Shannon and Weaver 1949); (7) maturity index (MI), $MI = \sum \upsilon í fi/n$, where υί, is the c-p value assigned by Bongers (1990 1999) to the ith genus of nematode, fi is the frequency of family i in the sample, and n is the total number of individuals in the sample (Neher and Darby 2005) (c-p values describe nematode life strategies, and range from 1 (colonizers, tolerant of disturbance) to 5 (persisters, sensitive to disturbance)); (8) modified maturity index (MMI), which includes plant-feeding nematodes (Yeates 1994); (9) 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); and (10) Sørensen-Czekanowski dissimilarity index (ISC) = $[1 - (2\Sigma \min (x_i, y_i)/(\Sigma x_i + \Sigma y_i))] \times 100$, where min is the minimum value of the number of individuals of the most abundant species in the 2 compared sites, x_i is the total number of individuals at the 1st site, and y_i is total number of individuals at the 2nd site (Magurram 1988).

Statistical analysis

All data were subjected to a statistical analysis of variance (ANOVA) using the SAS model with Duncan's multiple-range test, Pearson correlation coefficients, and a CANOCO redundancy analysis (ter Braak and Prentice 1996, ter Braak and Smilauer 2002) and were used to evaluate differences between separate means. Differences at the level of $p < 0.05$ were considered statistically significant.

RESULTS

The intensity of burns as indicated by tree death had less of an effect on soil nematodes than salvage harvesting of the burned trees. Plots where trees had been harvested had lower soil moisture in winter and summer than in other burned areas (Table 1). Nematode abundances were significantly lower in soils of tree-harvested plots than in unburned plots in spring and summer. There was no difference in nematode abundances between soils of the burned plots with standing trees and unburned plots (Table 1). Soil nematodes were most abundant during the rainy seasons (autumn and winter) and least abundant in summer near the end of the dry season.

Neither fire nor salvage logging had any negative effect on FF nematodes. BF nematodes were less abundant in salvage-logged areas and in the unburned forest than in the other burned areas, except probably in winter. PP and OP nematode numbers were significantly reduced in all burned areas compared to their numbers in the unburned forest (Table 1).

Two genera of BF nematodes (*Acrobeloides* spp. and *Cephalobus* spp.) were more abundant in soils of the burned forest with more intact trees

Table 1. Seasonal fluctuations in soil moisture (SM), organic matter (OM), average number of nematodes (TNEM), and average numbers of bacterium-feeding nematodes (BF), fungus-feeding nematodes (FF), plant-parasitic nematodes (PP), and omnivore-predator nematodes (OP) ± standard deviation. Numbers of nematodes and trophic groups are per 100 g of soil. Significant differences are indicated by different letters ($p < 0.05$)

Season	Location	SM (%)	OM (%)	TNEM
Autumn	Burned trees, dead	27.2 ± 8.4[a]	2.49 ± 0.6[a]	3139 ± 3644[ba]
	Burned, live foliage	28.5 ± 6.2[a]	2.76 ± 0.7[a]	6332 ± 5765[a]
	Burned, salvage logged	21.1 ± 6.3[a]	2.36 ± 0.3[a]	485 ± 601[b]
	Unburned forest	23.4 ± 3.8[a]	2.53 ± 0.7[a]	3448 ± 1188[ba]
Winter	Burned trees, dead	27.4 ± 6.4[a]	1.93 ± 0.2[b]	1453 ± 1622[a]
	Burned, live foliage	23.9 ± 3.2[ba]	2.00 ± 0.2[b]	888 ± 744[a]
	Burned, salvage logged	20.5 ± 5.1[b]	2.40 ± 0.7[a]	1057 ± 1029[a]
	Unburned forest	25.1 ± 0.4[ba]	1.93 ± 0.1[b]	838 ± 189[a]
Spring	Burned trees, dead	4.26 ± 0.6[b]	2.39 ± 0.4[ba]	503 ± 505[ba]
	Burned, live foliage	4.21 ± 0.9[b]	2.59 ± 0.6[ba]	655 ± 730[ba]
	Burned, salvage logged	4.79 ± 1.2[b]	2.32 ± 0.1[b]	251 ± 197[b]
	Unburned forest	6.20 ± 1.4[a]	2.85 ± 0.6[a]	935 ± 710[a]
Summer	Burned trees, dead	3.01 ± 0.9[cb]	2.69 ± 0.6[a]	346 ± 453[ba]
	Burned, live foliage	3.20 ± 0.7[b]	3.03 ± 0.8[a]	367 ± 337[ba]
	Burned, salvage logged	2.31 ± 0.5[c]	3.00 ± 1.0[a]	106 ± 125[b]
	Unburned forest	4.23 ± 0.7[a]	3.44 ± 0.8[a]	657 ± 388[a]
Year	Location	$p < 0.01$	NS	$p < 0.02$
	Season	*$p < 0.0001$*	*$p < 0.0001$*	*$p < 0.0001$*

Season	Location	BF	FF	PP	OP
Autumn	Burned trees, dead	2307 ± 2258[ba]	792 ± 1421[a]	0 ± 0[b]	41 ± 141[b]
	Burned, live foliage	5043 ± 5017[a]	1184 ± 1558[a]	36 ± 69[b]	69 ± 144[b]
	Burned, salvage logged	419 ± 504[b]	59 ± 105[a]	7 ± 13[b]	0 ± 0[b]
	Unburned forest	683 ± 445[b]	122 ± 152[a]	2209 ± 1420[a]	435 ± 110[a]
Winter	Burned trees, dead	1020 ± 1096[a]	234 ± 521[a]	95 ± 95[b]	105 ± 112[a]
	Burned, live foliage	558 ± 496[a]	28 ± 50[a]	46 ± 68[b]	256 ± 432[a]
	Burned, salvage logged	627 ± 1013[a]	104 ± 193[a]	73 ± 78[b]	254 ± 262[a]
	Unburned forest	217 ± 113[a]	76 ± 63[a]	274 ± 441[a]	272 ± 169[a]
Spring	Burned trees, dead	456 ± 489[a]	33 ± 48[a]	1 ± 3[b]	13 ± 18[b]
	Burned, live foliage	595 ± 723[a]	17 ± 21[a]	17 ± 31[b]	34 ± 80[b]
	Burned, salvage logged	201 ± 166[a]	12 ± 13[a]	20 ± 27[b]	20 ± 22[b]
	Unburned forest	326 ± 281[a]	44 ± 51[a]	104 ± 156[a]	494 ± 434[a]
Summer	Burned trees, dead	201 ± 301[a]	35 ± 55[a]	30 ± 67[b]	80 ± 162[ba]
	Burned, live foliage	256 ± 229[a]	49 ± 47[a]	21 ± 53[b]	40 ± 85[b]
	Burned, salvage logged	101 ± 128[a]	4 ± 9[a]	1 ± 2[b]	1 ± 2[b]
	Unburned forest	251 ± 161[a]	31 ± 18[a]	177 ± 130[a]	199 ± 149[a]
Year	Location	$p < 0.005$	NS	$p < 0.0001$	$p < 0.0001$
	Season	*$p < 0.0001$*	*$p < 0.0001$*	*$p < 0.0001$*	*$p < 0.003$*

SM, soil moisture; OM, organic matter; TNEM, total number of nematodes (100 g^{-1} dry soil); BF, bacterial-feeding; FF, fungal-feeding; PP, plant-parasitic; OP, omnipore-predators. BFA, burned forest area with all trees burned completely; BDT, burned trees with dead tree trunks remaining; BTR, burned trees with trunks removed from the damaged area; CON, control unburned area. Significant differences ($p < 0.05$) between sampling sites are indicated by different uppercase letters.

than in unburned forest soils and soils of salvage-logged plots. Genera of BF nematodes that were more abundant in soils of unburned plots than in burned plots were *Achromadora* spp., *Acrobeles* spp., and *Metateratocephalus* spp. (Table 2). There were no differences in abundances of FF

Table 2. Nematode genera dispersion (no. of individuals (ind.)/100 g dry soil) at the study area during the study period

TG	Genera	Sampling locations				*P* <
		BFA	BDT	BTR	CON	
BF	Achromadora	7.2b	9.7b	0.4b	43.5a	0.067
	Acrobeles	7.9ba	15.0ba	0.3b	24.6a	ns
	Acrobeloides	242.5ba	461.2a	73.0b	30.4b	0.0008
	Alaimus	NF	NF	NF	3.6	0.03
	Anaplectus	5.2a	2.4a	NF	NF	ns
	Cephalobus	585.3ba	903.5a	226.3b	73.4b	0.01
	Cervidellus	8.3a	1.1a	0.2a	NF	ns
	Chiloplacus	12.4a	144.8a	15.1a	10.1a	ns
	Chronogaster	NF	NF	NF	2.6	0.03
	Diploscapter	5.1	NF	NF	NF	ns
	Eucephalobus	63.6a	6.0a	2.5a	15.0a	ns
	Eumonhystera	0.8	NF	NF	NF	ns
	Heterocephalobus	4.0ba	0.5b	NF	8.6a	0.004
	Metateratocephalus	7.4b	18.2b	2.8b	71.8a	0.0001
	Monhystera	2.9a	18.2a	NF	12.4a	ns
	Panagrolaimus	3.4a	7.5a	0.3a	NF	ns
	Panagrobelus	NF	NF	NF	9	0.0002
	Plectus	19.1a	13.6a	14.6a	24.6a	ns
	Rhabditis	8.4a	0.5a	NF	NF	ns
	Mesorhabditis	NF	0.6ba	NF	2.4b	ns
	Teratocephalus	NF	2.2b	NF	19.0a	0.002
	Tylocephalus	5.6a	2.7a	NF	10.4a	ns
	Wilsonema	7.0a	5.5a	1.7a	8.1a	ns
FF	Aprutides	1.9a	NF	NF	2.6a	ns
	Aphelenchoides	20.7a	11.0a	26.7a	10.4a	ns
	Aphelenchus	213.5a	271.2a	14.8a	52.5a	ns
	Ditylenchus	0.1a	3.4a	2.9a	NF	ns
	Nothotylenchus	NF	NF	0.3b	2.6a	0.04
	Paraphelenchus	35.7a	31.0a	NF	NF	ns
	Tylencholaimus	1.5a	2.3a	NF	NF	ns
	Leptonchus	NF	0.5	NF	NF	ns
PP	Basiria	NF	NF	NF	5.7	0.03
	Bitylenchus	NF	0.4	NF	NF	ns
	Coslenchus	0.5b	NF	4.0b	34.7a	0.0001
	Filenchus	16.2b	18.0b	14.2b	556.6a	0.0001
	Heterodera	NF	2.7	NF	NF	ns
	Longidorella	0.4	NF	NF	NF	ns
	Longidorus	1	NF	NF	NF	ns
	Malenchus	3.3b	1.4b	NF	88.3a	0.0001
	Meloidogyna	6.5a	1.4a	2.0a	nf	ns
	Pratylenchus	2.7a	NF	NF	2.4a	ns
	Pungetus	NF	1	NF	NF	ns
	Tylenchorhynchus	NF	8.9a	2.7a	2.6a	ns
	Tylenchus	0.3a	0.4a	2.2a	0.6a	ns
	Xiphinema	0.5	NF	NF	NF	ns
OP	Aporcelaimus	20.9b	19.2b	8.6b	60.7a	0.056
	Aporcelaimellus	1.5b	0.6ba	0.9b	6.5a	0.0001
	Axonhium	NF	NF	0.5	NF	ns
	Discolaimus	0.5	NF	NF	NF	ns
	Dorylaimus	1.1a	2.9a	NF	3.2a	ns
	Dorylaimoides	1.6c	11.1cb	20.9b	44.2a	0.0002
	Epidorylaimus	1.2a	2.7a	NF	5.7a	ns
	Eudorylaimus	9.4b	39.3ba	23.6b	82.8a	0.057
	Mesodorylaimus	NF	13.3b	4.0b	56.3a	0.0003
	Microdorylaimus	4.4b	2.5b	NF	12.7a	0.02
	Mononchus	4.1a	0.5a	NF	3.2a	ns
	Nygolaimus	1.0b	1.1b	0.7b	5.6a	0.079
	Thonus	NF	0.1b	0.4b	7.6a	0.0006

TG, trophic group; BF, bacterium-feeding; FF, fungus-feeding; PP, plant-parasitic; OP, omnivore-predators; NF, not found; ns, not significantly different; BFA, burned forest area with all trees completely burned; BDT, burned trees with dead tree trunks remaining; BTR, burned trees with trunks removed from the damaged area; CON, control unburned area.

nematodes between burned and unburned plots. Two genera of FF nematodes (*Paraphelenchus* spp. and *Tylencholaimus* spp.) were found only in areas with burned trees that were not salvage-logged. One genus of FF nematodes (*Ditylenchus* spp.) was found only in burned areas but not in the unburned forest.

Three genera of PP nematodes (*Coslenchus* spp., *Filenchus* spp., and *Malenchus* spp.) were more abundant in unburned forest soils than in burned forest soils. Several genera of PP nematodes were found in low numbers only in burned areas, and were absent from unburned forest soils (Table 2).

Eight of the 13 species of OP nematode genera were more abundant in unburned forest soils than burned forest soils. Only 2 OPs at very low abundances were found in soils of burned forest but were absent from unburned forest soils (Table 2).

Fire in the conifer forest resulted in lower trophic diversity, lower generic diversity, and lower generic richness in burned forest soils than unburned forest soils (Table 3). The FB ratio was similar in burned and unburned areas. The maturity indices were predictably lower in burned than unburned forest soils. The low dominance index for nematode communities in unburned forest soils indicates relatively equal abundances of dominant genera (Tables 2, 3).

Abundances of FF, PP, and OP nematode trophic groups were correlated with soil moisture primarily in dry soils in summer, while abundances of BF and FF nematodes were correlated with soil moisture only in autumn. The only correlations with soil organic matter were OPs in spring and summer. Ecological indices were correlated with soil moisture only in spring and summer (Table 4).

Table 3. Ecological indices of soil nematode communities (FB, fungivore-bacterivore ratio; TD, trophic diversity; D, dominance index; H', generic diversity index; MI, maturity index; MMI, modified maturity index; SR, species richness) in soils of burned forest with all trees dead (BFA), burned forest with some live foliage (BDT), burned forest, salvage logged (BTR), and unburned forest (CON)

Locations	FB	TD	D	H'	MI	MMI	SR
BFA	0.16	1.58	0.47	1.11	1.12	2.2	0.65
BDT	0.15	1.61	0.41	1.28	1.28	2.33	0.81
BTR	0.32	1.55	0.48	1	1	2.26	0.61
CON	0.18	2.49	0.22	1.93	3.39	2.9	1.29

Table 4. Correlation coefficients of the average number of nematodes (TNEM), bacterium-feeder (BF), fungus-feeder (FF), plant-parasite (PP), omnivore-predator (OP). Ecological indices: FB, fungivore/bacterivore ratio; TD, trophic diversity; D, dominant index; H', Shannon index; MI, maturity index; MMI, modified maturity index; SR, richness. Soil properties: soil moisture (SM) and soil organic matter (OM)

Season index	Autumn		Winter		Spring		Summer	
	SM (%)	OM (%)	SM (%)	OM (%)	SM (%)	OM (%)	SM (%)	OM (%)
TNEM	0.64***	0.33*	NS	NS	NS	NS	0.45**	NS
Trophic structure								
BF	0.62***	NS	NS	NS	NS	NS	NS	NS
FF	0.48**	NS	NS	NS	NS	NS	0.42**	NS
PP	NS	NS	NS	NS	NS	NS	0.57***	NS
OP	NS	NS	NS	0.40*	0.52**	0.49**	0.54***	NS
Ecological indices								
FB	0.36*	NS	NS	0.64***	NS	NS	NS	NS
TD	NS	NS	NS	NS	0.37*	NS	0.76***	NS
D	NS	NS	NS	NS	-0.34*	NS	-0.74***	NS
H'	NS	NS	NS	NS	0.41**	NS	0.79***	NS
MI	NS	NS	NS	NS	NS	NS	0.65***	NS
MMI	NS	NS	NS	NS	NS	NS	0.63***	NS
SR	NS	NS	NS	NS	0.36*	NS	0.75***	NS

* p <0.05, ** p < 0.01, *** p < 0.001, correlation coefficient significant.

The most dissimilar soil-nematode communities were from soils of burned dead-tree plots and burned-tree live-canopy plots. However, the dissimilarity comparisons of the nematode communities of burned plots and unburned controls were essentially the same for all comparisons (Table 5).

DISCUSSION

This study clearly shows that fire in a coniferous forest in a Mediterranean region reduced abundances and affected the taxonomic composition of soil-nematode communities at 1-2 yr post-burn. A burned coniferous forest in this region had a reduced taxonomic diversity of soil-nematode communities, and the soil-nematode community was structurally a dis-climax community. The effects of wildfire on soil nematodes in this forest support findings of Bloemers et al. (1997) and contradict those of Fenster et al. (2004), who reported that forest fires had no effect on the free-living soil-nematode community. Results of our study also showed that post-fire management practices exacerbated some of the fire effects on nematode communities. Salvage logging exposed the soil to direct solar radiation resulting in accelerated drying of the soils. In areas where trees were killed by fire and left standing or removed by salvage logging, higher solar radiation stimulated germination and the establishment of tree seedlings and herbaceous plants.

The trophic structure of the nematode community was more sensitive to forest-fire impacts on soils than was nematode abundances.

Table 5. Czekanowski-Sorensen indices of dissimilarity between nematode communities (NCs) in soils of a burned forest with all trees dead (BFA), burned forest with some live foliage (BDT), burned forest with salvage logging (BTR), and unburned forest (CON)

Comparison	NC
BFA:BDT	29.38
BFA:BTR	55.24
BDT:BTR	63.13
BFA:CON	70.35
BDT:CON	73.53
BTR:CON	68.29

BF nematodes (*Acrobeloides* spp. and *Cephalobus* spp.) that were more abundant in burned forest soils than in soils of the unburned forest probably responded to the higher microbial biomass that developed because of greater available nutrients and organic carbon in post-fire soils (Rutigliano et al. 2007). Moreover, results obtained from the same place (Ginzburg and Steinberger 2012a) showed that an increase in total soluble nitrogen (TSN) in burned areas may limit microbial activity during the 1st year after a wildfire, and it had recovered to the previous, pre-fire condition in the 4th year, when plant regeneration assured proliferation of the microbial community. These 2 species of BFs were dominant in burned forest soils, and that dominance accounted for the lower diversity indices. In addition, it was reported that fire affects fungi more than bacteria (Vasquez et al. 1993, Bååth et al. 1995), thus the higher numbers of BF nematodes in burned forest soils. However, since there were no significant differences in abundances of FF nematodes among burned and unburned forest soils in this study, it is apparent that the fire had either no significant effect on soil fungi and FF nematodes or had only a short-term effect that lasted for less than 1 yr.

While PP and OP nematodes were more abundant in unburned forest soils, some genera of plant parasites were found only in soils of the unburned forest. These genera may have colonized roots that were still alive but that were stressed by the loss of nutrients from the fire-killed canopy. Overall, PP and OP nematodes were sensitive to the effects of fire. This is consistent with the conclusions of Bongers and Ferris (1999), who found that these trophic groups were sensitive to ecological perturbations.

Most of the temporal differences in nematode communities in post-burn and unburned forest soils were apparently due to seasonal rainfall patterns of the region. Differences in ecological indices of nematode communities from burned and unburned forest soils remained the same for the year and seasons of this study. Since this study was initiated more than 1 yr after the wildfire had occurred, the patterns reported here are those resulting from longer-term residual effects of the fire. McSorley (1993) reported that numbers of BFs (*Acrobeloides* spp.) and OPs increased within 6 wk after a fire. McSorley also reported a decrease in FF (*Aphelenchoides* spp.) nematodes, but no change in abundances of PP nematodes. Some of the short-term effects of fire reported by McSorley (1993) extended through 2 yr post-burn. *Acrobeloides* spp. numbers remained higher in burned areas, with more intact trees than in unburned forest soils. However, numbers of FF *Aphelenchoides* spp. in burned forest soils did not differ from those in unburned forest soils. Thus, the deleterious effect of fire on those FFs was either short-term or did not occur as a result of the fire.

In conclusion, wildfire in conifer forests in a Mediterranean climatic region had several long-term effects on soil-nematode communities. These effects appeared to be mediated through changes in food resources of different nematode taxa. The most significant differences were marked increases in the abundances of 2 genera of BF nematodes (*Cephalobus* spp. and *Acrobeloides* spp.) and reduced numbers of PP nematodes. Since BF nematodes are important regulators of decomposition and mineralization rates, it appears that the recovery of soil biological function following a fire will take more than 2 yr.

Acknowledgments: The authors wish to express their appreciation to Dr. M. Sternberg and Mr. A. Oren for their useful comments that significantly improved this paper. Special thanks to Ms. S. Victor for her useful remarks and to Ms. G. Barness for technical assistance.

REFERENCES

Andréu V, O González, J Campo, E Gimeno-Garcia, JL Rubio. 2004. Evolution of hydrological properties of a Mediterranean forest soil seven years after forest fires. Geophys. Res. Abstract **6**.

Bååth E, A Frostegård, T Pennanen, H Fritze. 1995. Microbial community structure and pH response in relation to soil organic-matter quality in wood-ash fertilized, clear-cut or burned coniferous forest soils. Soil Biol. Biochem. **27:** 229-240.

Ben Naceur H, A Ben Rejeb Jenhani, MS Romdhane. 2012. Impacts of salinity, temperature, and pH on the morphology of *Artemia salina* (Branchiopoda: Anostraca) from Tunisia. Zool. Stud. **51:** 453-462.

Bloemers GF, M Hodda, PJD Lambshead, JH Lawton, FR Wanless. 1997. The effects of forest disturbance on diversity of tropical soil nematodes. Oecologia **111:** 575-582.

Bongers T. 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia **83:** 14-19.

Bongers T. 1999. The Maturity Index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. Plant Soil **212:** 13-22.

Bongers T, H Ferris. 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. **14:** 224-228.

Cairns EJ. 1960. Methods in nematology. *In* JN Sasser, WR Jenkins, eds. Nematology, fundamentals and recent advances with emphasis on plant parasitic and soil forms. Chapel Hill, NC: Univ. of North Carolina Press, pp. 33-84.

Certini G. 2005. Effects of fire on properties of forest soils: a review. Oecologia **143:** 1-10.

Conard SG, T Hartzell, MW Hilbruner, GT Zimmerman. 2001. Changing fuel management strategies - the challenge of meeting new information and analysis needs. Int. J. Wildland Fire **10:** 267-275.

Covington WW, MM Moore. 1994. Southwestern ponderosa forest structure - changes since Euro-American settlement. J. For. **92:** 39-47.

Dan J, H Koyumdjiski. 1979. The classification of Israel soils by the committee on soil classification in Israel. Special publication no. 137. Bet Dagan, Israel: Division of Scientific Publications, The Volcani Center.

de Goede RGM, T Bongers. 1994. Nematode community structure in relation to soil and vegetation characteristics. Appl. Soil Ecol. **1:** 29-44.

DeBano LF. 2000. The role of fire and soil heating on water repellency in wildland environments: a review. J. Hydrol. **231:** 195-206.

DeBano LF, DG Neary, PF Folliott. 1998. Fire's effects on ecosystems. New York: J. Wiley.

Fenster M, C Ferrick, M Scott. 2004. Fall burning does not affect nematode density or carbon and nitrogen levels in Iowa oak forest soils. Tillers **5:** 9-12.

Freckman DW. 1988. Bacterivorous nematodes and organic matter decomposition. Agric. Ecosyst. Environ. **24:** 195-217.

Freckman DW, RA Virginia. 1997. Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. Ecology **78:** 363-369.

Ginzburg O, Y Steinberger. 2012a. Effects of forest wildfire on soil microbial-community activity and chemical components on a temporal-seasonal scale. Plant Soil doi: 10.1007/s11104-012-1243-2.

Ginzburg O, Y Steinberger. 2012b. Salvage logging versus natural regeneration post-fire practices in a forest: soil chemical and microbial aspects. Open J. Ecol. **2:** 29-37.

Heip C, PMJ Herman, K Soetaert. 1988. Data processing, evaluation and analysis. *In* RP Higgins, H Thiel, eds. Introduction to the study of meiofauna. Washington, DC: Smithsonian Institution Press, pp. 197-231.

Hernandez T, C Garcia, I Reinhardt. 1997. Short-term effect of wildfire on the chemical, biochemical and microbiological properties of Mediterranean pine forest soils. Biol. Fertil. Soils **25:** 109-116.

Jones KL, TC Todd, JL Wall-Beam, JD Coolon, JM Blair, MA Herman. 2006. Molecular approach for assessing responses of microbial-feeding nematodes to burning and chronic nitrogen enrichment in a native grassland. Mol. Ecol. **15:** 2601-2609

Magurram AE. 1988. Ecological diversity and its measurement. Princeton, NJ: Princeton Univ. Press.

Matlack GR. 2001. Factors determining the distribution of soil nematodes in a commercial forest landscape. For. Ecol. Manage. **146:** 129-143.

McSorley R. 1993. Short-term effects of fire on the nematode community in a pine forest. Pedobiologia **37:** 39-48.

Neary DG, CC Klopatek, LF DeBano, PF Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. For. Ecol. Manage. **122:** 51-71.

Neher DA. 2001. Role of nematodes in soil health and their use as indicators. J. Nematol. **33:** 161-168.
Neher DA BJ, Darby. 2005. Computation and application of nematode community indices: general guidelines. *In* E Abebe, ed. Freshwater nematodes: ecology and taxonomy. Wallingford, UK: Centre for Agricultural Bioscience International (CABI), pp. 211-222.
Pausas JG. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). Climatic Change **63:** 337-350.
Pausas JG, VR Vallejo. 1999. The role of fire in European Mediterranean ecosystems. *In* E Chuvieco, ed. Remote sensing of large wildfires in the European Mediterranean basin. Berlin: Springer, pp. 3-16.
Peckham SD, DE Ahl, SP Serbin, ST Gower. 2008. Fire-induced changes in green-up and leaf maturity of the Canadian boreal forest. Remote Sens. Environ. **112:** 3594-3603.
Ravikovitch S. 1981. The soils of Israel: formation, nature and properties, 1st ed. Tel Aviv: Hakibbutz Hameuchad Publishing House. (in Hebrew)
Rowell DL. 1994. Soil science: methods and applications. London: Longman Group UK.
Rutigliano FA, A De Marco, R D'Ascoli, S Castaldi, A Gentile, AV De Santo. 2007. Impact of fire on fungal abundance and microbial efficiency in C assimilation and mineralisation in a Mediterranean maquis soil. Biol. Fertil. Soils **44:** 377-381.
Shannon CE, W Weaver. 1949. The mathematical theory of communication. Urbana, IL: Univ. of Illinois Press.
Simpson EH. 1949. Measurement of diversity. Nature **163:** 668.
Smith JE, D McKay, G Brenner, J McIver, JW Spatafora. 2005. Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. J. Appl. Ecol. **42:** 526-535.
Steinberger Y, 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.
Stocks BJ. 1991. The extent and impact of forest fires in northern circumpolar countries. *In* J Levine, ed. Global biomass burning. Cambridge, MA: MIT Press, pp. 197-203.
ter Braak CJF, IC Prentice. 1996. A theory of gradient analysis. *In* CJF ter Braak, ed. Unimodal models to related species environment. Wageningen, The Netherlands: DLO-Agricultural Mathematics Group, pp. 138-271.
ter Braak CJF, P Smilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (vers. 4.5). Wageningen, The Netherlands and Ceské Budejovice, Czech Republic: Biometrics.
Twinn DC. 1974. Biology of plant litter decomposition. London and New York: Academic Press.
Vasquez FJ, MJ Acea, T Carballas. 1993. Soil microbial populations after wildfire. FEMS Microbiol. Ecol. **13:** 93-104.
Visser S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol. **129:** 389-401.
Yeates GW. 1982. Variation in pasture nematode populations over thirty-six months in a summer dry silt loam. Pedobiologia **24:** 329-346.
Yeates GW. 1994. Modification and qualification of the nematode maturity index. Pedobiologia **38:** 97-101.
Yeates GW, KL 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.
Yeates GW, T Bongers, RGM De Goede, D Freckman, SS Georgieva. 1993. Feeding habits in soil nematode families and genera - an outline for soil ecologists. J. Nematol. **25:** 315-331.
Yeates GW, DA Wardle, RN Watson. 1999. Responses of soil nematode populations, community structure, diversity and temporal variability to agricultural intensification over a seven-year period. Soil Biol. Biochem. **31:** 1721-1733.