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ORIGINAL PAPER

The impacts of a wildfire in a semiarid grassland on soil nematode abundances over 4 years

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Abstract

Fire is the most common disturbance in arid regions and is expected to become more common in many areas as a result of climate change. In this study, I followed the impacts of a wildfire on soil nematode abundances and soil moisture and organic matter (SOM) content in a semiarid grassland for 4 years, using paired burned and unburned sites. I also used a laboratory microcosm experiment to determine the capacity of nematodes to recover under favorable conditions and the importance of surface litter in their recovery. Immediately following the fire, bacterivorous, fungivorous, and herbivorous nematodes in burned sites were 49, 73, and 76% less abundant than in unburned reference sites. Although microbivores recovered rapidly in the microcosm experiment, this recovery was dependent on surface litter, which was reduced by 86% in burned sites in the field. The recovery of microbivores took more than 3 years in the field, and herbivores did not recover during the study period. It is not clear why herbivores did not recover in the field, given that plants seemed to, but it may be related to longer generation times or slower dispersal. Burned sites also had 22% less SOM than unburned sites over the study period and lower soil respiration and pH 14 and 21 months, respectively, after the fire. Soil moisture was lower in burned sites for at least 14 months. The slower recovery of nematode abundances in the field, compared to microcosms, may be related to the exacerbation of moisture limitation at burned sites in this semiarid region. Changes in fire regime may, therefore, have widespread impacts on soil food webs and processes in semiarid climates.

Keywords Functional group · Microcosm · Soil organic matter · Soil respiration · Fire · Climate change

Introduction

Fires are expected to become more common in Western North America and other arid regions, as a consequence of climate change (Flannigan et al. 2005; Melillo et al. 2014), and have the potential to act as feedback to climate change if they alter the amount of C stored in terrestrial systems (Amiro et al. 2001; Mack et al. 2011). Many soil properties are affected by fires, including pH, hydrophobicity, and nutrient and organic matter contents (Certini 2005). Soil food webs are a critical component of terrestrial ecosystems and regulate the cycling of both C and mineral nutrients in soils (Hunt et al. 1987; de Vries et al. 2013). The diversity and abundance of soil organisms, both microbes and fauna, are negatively impacted by fires (Pressler et al. 2019). The response of soil food webs to fire is therefore important in understanding how ecosystem processes are likely to respond to changing fire regimes. For example, Brennan et al. (2009) found that fires reduced decomposition rates and increased the influence of soil fauna on the decomposition rate. The timescale over which soil food webs recover from fires may also help predict thresholds for fire frequency above which soil ecosystem processes are negatively impacted.

The impacts of fires on soil fauna are understudied relative to other factors that affect soil fauna (Zaitsev et al. 2016), and Pressler et al. (2019) identified the impacts of fires on soil fauna as an area needing additional research. Nematodes are important regulators of soil microbial communities, increasing nutrient cycling (Hunt et al. 1987; Zhu et al. 2018), microbial productivity (Mikola and Setälä 1998), and plant growth (Setälä and Huhta 1991). Soil nematodes have long been used

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as indicators of soil food web condition, because nematodes are represented in all of the major channels of the soil food web (e.g., bacterial, fungal channels, and direct root feeders) and multiple trophic levels (Yeates et al. 1993; Bongers and Bongers 1998). Their abundances and composition also provide insights into microbial groups that are more expensive or time-consuming to directly measure (Ritz and Trudgill 1999).

Previous research on forest soils affected by fires has generally found reduced nematode diversity, but increased abundances of bacterial-feeding nematodes, between 66% (Butenko et al. 2017) and 640% (Pen-Mouratov et al. 2012) higher than unburnt reference sites. This is likely in response to increases in bacterial abundance or productivity (Butenko et al. 2017). Fungivores and plant-feeding nematodes generally decrease following fires, although their responses are much more variable (Pen-Mouratov et al. 2012; Butenko et al. 2017). There is very little data on higher trophic levels of nematodes, but Renčo and Čerevková (2015) found that predaceous nematodes largely disappeared following a wildfire and had not recovered after 8 years. A recent meta-analysis found that across all functional groups, nematode abundances in published studies decreased 88% (Pressler et al. 2019).

There is less research on the responses of nematodes to fire in grasslands, and grassland studies have focused on controlled burns rather than wildfires. In these studies, microbe and plant-feeding nematodes have generally increased in response to burning (Todd 1996; Yeates and Lee 1997; Jones et al. 2006; Soong et al. 2017), but their responses have been smaller and more variable. Additionally, most of these studies (with the exception of Yeates and Lee 1997) come from a single site, which receives annual controlled burns (Konza Prairie Biological Station, KS, USA). It is therefore unclear if the different responses of nematodes to controlled burns, as opposed to wildfires, are due to the nature of the fire (unpredictable and wild vs. annual and controlled) or differences in the ecosystems studied (forests vs. grasslands).

This study used a wildfire in a semiarid grassland to address the following questions: (1) What are the immediate impacts of fire on soil nematodes in a semiarid system? (2) What is the timescale of their recovery? (3) How do functional groups differ in terms of their response to and recovery from the fire? My study site, Fishtrap Recreation Area (FRA), receives less than half the annual precipitation of Konza Prairie Biological Station, making it considerably more arid than previous studies of nematode responses to fire. I sampled soil nematodes at burned sites, along with paired unburned reference sites, for 4 years following a wildfire. I also collected data on soil moisture, SOM, soil respiration, and aboveground plant biomass in order to understand factors that might be affecting nematode recovery. Because fungi are generally more negatively affected by fires than bacteria (Bååth et al. 1995; Certini 2005; Pressler et al. 2019), I predicted that bacterial-feeding nematodes would recover from the fire more rapidly than fungivores and that herbivorous nematode recovery would occur with plant recovery. I paired this observational field study with a lab microcosm experiment to look at the importance of surface plant litter for nematode recovery. Surface litter helps soils retain moisture and can provide C for soil microbes, so I predicted nematodes would recover more quickly with litter.

Methods

Site description

Fishtrap Recreation Area (FRA) is located in eastern Washington State, USA, in Spokane and Lincoln Counties (47.35°N 117.80°W). FRA is within the channeled scablands, which have young, shallow soils as a result of scouring by ice age floods. It has a dry-summer continental climate, with warm, dry summers and cold, wet winters. The mean annual precipitation is 320 mm, and the mean annual temperature is 8 °C (Western Regional Climate Center n.d.). Precipitation occurs mainly in winter. The growing season is relatively short, occurring between the thawing of the ground in spring and the drying out of the soil in midsummer (about 4 to 5 months). Wildfires occur primarily from midsummer to early fall, with a peak in August and September. The channeled scablands include grasslands and shrublands, with scattered wetlands and stands of *Pinus ponderosa*. This study included only sites with grassland vegetation. The recreation area is managed by the Bureau of Land Management (BLM). The Watermelon Hill Fire was set accidentally on July 19, 2014, in FRA and contained 5 days later after burning between 3770 and 4620 ha (Bureau of Land Management 2014; Monitoring Trends in Burn Severity 2014). The burn severity of the Watermelon Hill Fire was evaluated by Monitoring Trends in Burn Severity, which uses pre- and post-fire Landsat images to categorize burn severity on the basis of changes in vegetation (Eidenshink et al. 2007). Over two thirds of the area affected by the Watermelon Hill Fire experienced a low severity burn and moderate severity burn accounted for most of the remainder (Monitoring Trends in Burn Severity 2014).

Field sampling

I first sampled sites in southern FRA (“Farmer’s Landing,” FL) on September 11, 2014, and sites in eastern FRA (“Damage Creek,” DC) on September 15, 2014. Within each of these areas, I selected three pairs of burned and unburned patches of grassland (for twelve sites in six pairs total, Table 1). At each site, I collected three subsamples of soil. Each subsample was at least 3 m from any other subsample and consisted of 200–600 g of soil collected from the top

Table 1 Area and soil properties of the sites included in this study

Site	Treatment	Area (m^2)	Distance between paired sites (m)	Clay (%)	Silt (%)	Sand (%)	Texture description	pH	SOM (g kg^{-1})	total N (g kg^{-1})
FL #1	unburned	460	125	13.7 ± 5.5	58.2 ± 7.1	28.1 ± 3.8	Silt loam	6.7 ± 0.5	92 ± 37	3.1 ± 1.3
FL #1	burned	1390		9.6 ± 2.0	61.3 ± 5.5	29.1 ± 3.8	Silt loam	6.3 ± 0.1	40 ± 9	1.4 ± 0.3
FL #2	unburned	540	10	11.8 ± 1.3	43.2 ± 5.4	45.0 ± 6.5	Loam	6.7 ± 0.1	40 ± 10	1.6 ± 0.4
FL #2	burned	230		10.8 ± 2.6	59.2 ± 10.8	30.0 ± 10.6	Silt loam	6.4 ± 0.3	44 ± 14	1.6 ± 0.3
FL #3	unburned	510	40	11.4 ± 1.7	58.0 ± 2.9	30.5 ± 1.5	Silt loam	6.7 ± 0.5	105 ± 23	4.1 ± 0.6
FL #3	burned	1550		9.8 ± 1.1	59.1 ± 5.3	31.1 ± 4.3	Silt loam	6.5 ± 0.1	49 ± 17	2.1 ± 0.9
DC N	unburned	830	35	9.1 ± 1.4	45.6 ± 3.4	45.4 ± 4.7	Loam	7.1 ± 0.1	90 ± 25	3.0 ± 0.8
DC N	burned	620		8.8 ± 0.5	61.6 ± 2.0	29.6 ± 1.6	Silt loam	6.5 ± 0.1	116 ± 2	4.1 ± 0.3
DC W	unburned	830	15	12.7 ± 0.1	55.1 ± 2.4	32.2 ± 2.3	Silt loam	8.0 ± 0.2	113 ± 5	5.0 ± 0.4
DC W	burned	820		8.5 ± 3.4	61.9 ± 7.6	29.6 ± 6.1	Silt loam	8.0 ± 0.2	98 ± 24	4.0 ± 1.4
DC S	unburned	930	25	8.0 ± 3.7	60.4 ± 2.5	31.6 ± 6.2	Silt loam	7.5 ± 0.1	135 ± 30	6.5 ± 1.5
DC S	burned	1650		10.6 ± 1.3	56.4 ± 1.9	33.0 ± 1.3	Silt loam	7.4 ± 0.2	119 ± 14	5.3 ± 0.9

FL Farmer's Landing, *DC* damage creek. Distance between paired sites reports the approximate distance from each unburned site to its paired burned site. For soil properties, mean ± SD (*N* = 3) is reported for each site. Soil analyses were performed on soil from the April 2016 sampling

10 cm. Surface litter and vegetation were removed prior to collecting soil, which was stored in a cold room (8 °C) after collection until processing. Soil was then sieved using a 6.3-mm sieve to remove coarse roots and rocks. I determined gravimetric soil moisture of subsamples by drying 14-g (± 7 g) wet soil to constant mass at 50 °C and estimated organic matter content of soils by ashing dried soils at 450 °C for 2 hours.

From each subsample, 16 g (±8 g) of field moist soil were used to extract nematodes using Baermann funnels (Baermann 1917). Subsamples were pooled together before analysis, such that each data point includes nematodes extracted from 30 to 56 g of soil. Nematodes were extracted over 2 days at room temperature and then stored at 8 °C until sorting. I counted and sorted nematodes in two steps. I first counted the total number of nematodes in each sample under a dissecting microscope (40X). The nematode samples were then centrifuged at 78×*g* for 6 min to concentrate the nematodes into a pellet. I then identified a subsample of the nematodes (10% of the total or 30 nematodes, whichever was greater) to functional group under a compound microscope (100X) following the categories of Yeates (1999). The functional groups identified were bacterivore, fungivore, plant associate, plant feeder, omnivore, and predator. Plant associates and plant feeders responded similarly so were pooled together as herbivores. I used the abundance of functional groups in the subsample to estimate their abundance in the original sample. All nematode abundances were expressed as nematodes per g dry soil.

I resampled the sites for nematodes, soil moisture, and soil organic matter in spring 2015 (FL on April 9 and DC on April 15), 2016 (FL on April 7 and DC on April 12 and 16), and 2018 (both FL and DC on May 23). In spring 2015 and 2016, I also collected samples of aboveground plant biomass by clipping and collecting all plant biomass aboveground within three 0.0625-m^2 quadrats at each site. These samples were sorted into live and dead (or senescent) plant biomass in the lab, dried to constant mass, and weighed. I measured soil respiration in the field at these sites in fall 2015 (FL on September 10 and DC on September 11) and spring 2016 (FL on April 7 and DC on April 12 and 19) using an LI-6400 infrared gas analyzer (Li-Cor Inc., Lincoln, NE, USA).

I performed additional analyses on soil samples collected in April 2016 in order to evaluate the validity of site pairing. Soil pH was measured using an EcoSense pH10A probe on a 1:2 soil to DI water extraction (Robertson et al. 1999). Total soil N was determined by the University of California Stable Isotope Facility using an elemental analyzer interfaced with a continuous flow isotope ratio mass spectrometer. I measured soil texture using a micro-pipette method modified from Miller and Miller (1987). Dried 4-g soil samples were passed through a 2-mm sieve, ground to a powder, reacted with 10% H_2O_2, (Aqua Solutions Inc., Deer Park, TX, USA), and dried again. Samples were then added to 35 mL of 5% sodium hexametaphosphate (Gilson Company Inc., Lewis Center, OH, USA) solution and left on a rocker table for 24 h. Then each sample was shaken vigorously, allowed to sit for 1 min, after which a 5-mL pipette sample was taken from a depth of 2.5 cm (containing silt and clay particles). Each sample then sat for 2 h, after which another 5-mL pipette sample was taken from the same depth (now containing primarily clay particles). These 5 mL were dried and weighed. I sieved the remaining samples with a 75-μm sieve to retain the sand fraction, which was then dried and ashed (at 450 °C for 2 hours) to remove residual organic matter. Blanks were used to account for the weight of sodium hexametaphosphate residue, and organic matter (weight lost during either the reaction with H_2O_2 or ashing) was subtracted from the total sample weight prior to calculations. Sand, clay, and silt percentages were then calculated as:

$$\%\mathrm{sand} = \left(\frac{\mathrm{sand(g)}}{\mathrm{totalsoil(g)}}\right) \times 100$$

$$\%\mathrm{clay} = \left(\frac{\mathrm{claypipettesample(g)}}{\mathrm{clay} + \mathrm{siltpipettesample(g)}}\right)\left(\frac{\mathrm{totalsoil(g)} - \mathrm{sand(g)}}{\mathrm{totalsoil(g)}}\right) \times 100$$

$$\%\mathrm{silt} = 100\% - (\%\mathrm{clay} + \%\mathrm{sand})$$

Microcosm construction

I conducted a laboratory microcosm experiment using soil collected from FRA in September 2014. The factors in the experiment were burned or unburned (2 levels), grass litter added or not added (2 levels), and days until microcosm sampled (3 levels 20, 40, or 60 days). These factors were fully crossed, for a total of 12 treatment combinations. All six pairs of sites were represented in all treatments, and these acted as replication within the microcosm experiments (6 replicates of 12 treatment combinations). I used each of two soil subsamples from each site (out of three collected from the field) to make six microcosms. The two soil subsamples I used were the subsamples with the highest and the median total nematode abundance from each site, and these provided within site replication in the microcosm experiment. These subsamples were chosen, rather than the subsample with the lowest nematode abundance, to ensure microcosms had a sufficient initial abundance of nematodes for their populations to persist through the experiment.

Soil microcosms consisted of polystyrene vials (93-mm height X 23-mm inner diameter) to which I added 10-g (±0.25 g) field moist soil. Because of the low soil moisture at the time that soils were collected, all microcosms received 1.8 g of water at the beginning of the experiment, and the entire experiment was sprayed with water as needed during the experiment to keep the soil surface moist. Half of the microcosms received 0.1 g of *Festuca idahoensis* litter, cut into approximately 5–10-mm lengths (collected from FRA on September 15, 2014). A third of the microcosms were assigned to each of three sampling times: 20, 40, or 60 days. After all soil, water, and litter were added, I compacted the soil in all microcosms to a density of 1.1 g/mL (±0.05 g/mL). Microcosms were randomly arranged in a clear plastic box and placed in a growth chamber at 15 °C with a 12-h light and 12-h dark cycle.

Microcosms were destructively sampled for nematodes at 20, 40, or 60 days by placing all soil and litter from the sampled microcosms into Baermann funnels for 2 days to extract nematodes. The process of extracting, counting, and sorting nematodes from microcosms was the same as the process for field samples.

Data analysis

For the field study, all subsamples from the same site and sampling date were averaged together prior to analysis. Statistical analyses of soil texture, pH, and total N were performed in SYSTAT 13 (SYSTAT Software Inc., San Jose, CA, USA). For each soil property, I used the correlation between the unburned sites and their paired burned sites to evaluate how well matched unburned and burned sites were. I also used paired t tests to look for differences between burned and unburned sites among these variables.

All other statistical analyses were performed in R (R Core Team 2018). I used linear mixed models using the R package lme4 (Bates et al. 2015) to analyze the abundance of nematode functional groups, as well as soil moisture, organic matter, respiration, and aboveground live and dead plant biomass. I used type III ANOVAs with burn status (i.e., burned vs. unburned), sampling date, and the interaction of burn status and date included as fixed factors, and site included as a random factor. To assess the recovery of nematode functional groups, I used linear regression, with the difference in abundance between paired burned and unburned sites as the dependent variable and months since the fire as the independent variable. When this regression was significant, recovery was estimated by solving for the time since fire at which the difference would equal zero. I also used linear regression to look at how the abundance of nematode functional groups was affected by soil moisture across the entire field study (i.e., pooling all sampling dates).

For the microcosm experiment, I used type III ANOVAs with burn status, days elapsed (20, 40, or 60), and substrate (grass litter added or not added) as fixed factors, along with all of their two-way and three-way interactions, and site as a random factor. All data, for both the field study and microcosm experiment, were log transformed prior to analysis. All data collected during this study are available from the corresponding author on reasonable request.

Results

Field study

Soil texture was relatively similar across sites (Table 1). Most of the sites had silty loam soil, but two had loam soil. All sites had relatively low clay content (8.0–13.7%). The % clay, silt, and sand did not differ between burned and unburned sites ($P = 0.23$, $P = 0.11$, and $P = 0.19$, respectively) and were not correlated between paired burned and unburned sites ($P = 0.32$, $P = 0.27$, $\mathrm{P} = 0.32$, respectively). Soil pH was strongly correlated between paired burned and unburned sites ($P < 0.001$, $r = 0.97$), but burned sites had lower pH (7.1 for unburned sites compared to 6.8 for burned, $P = 0.016$). Total soil N was also correlated between paired burned and unburned sites ($P = 0.039$, $r = 0.76$) but did not significantly differ between burned and unburned sites (Table 1, $P = 0.14$).

Overall, unburned sites had higher soil moisture than burned sites (Fig. 1a, Table 2, $P = 0.003$). Soil moisture was higher in the spring (April and May) than the fall (September) throughout the study ($P < 0.001$). Although there was no interaction between burn status and date ($P = 0.78$), the 95% confidence intervals for soil moisture in burned and unburned sites did not overlap through September 2015 but did in 2016 and 2018. Soil organic matter was 21.7% lower in burned sites than unburned sites (Fig. 1b, Table 2, $P < 0.001$). A marginally significant effect of date on SOM ($P = 0.065$) appears driven by a decline in unburned sites after September 2014. Soil respiration was 39% lower in burned sites 14 months after the fire (Fig. 2a, Table S1, $P = 0.005$). Respiration increased 58% between September 2015 and the following spring ($P < 0.001$) and that increase was larger at the burned sites (Burn status X Date interaction, $P = 0.048$), such that burned and unburned sites had comparable rates of soil respiration in April 2016. Live aboveground plant biomass did not differ between burned and unburned sites in the spring following the fire (April 2015) or 1 year later (Fig. 2b, Table S1, $P =$ 0.48). The fire reduced aboveground litter by 86% in burned sites, relative to unburned sites, 9 months after the fire (Fig. 2c, Table S1, $P < 0.001$). A year later (April 2016), aboveground litter had increased 186% in the burned sites but remained unchanged in the unburned sites (Burn status X Date interaction, $P = 0.002$).

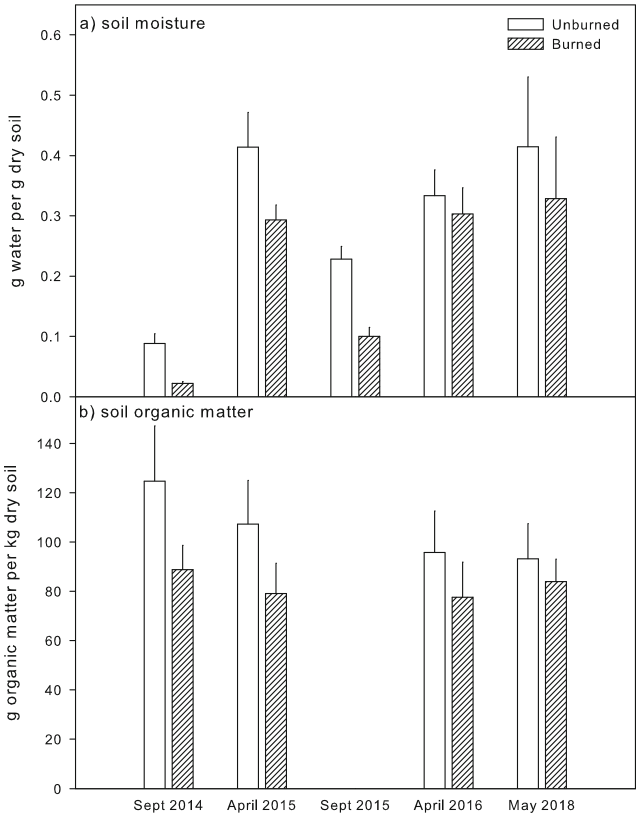


Fig. 1 Gravimetric soil moisture (**a**) and soil organic matter (**b**, estimated using loss-on-ignition) at burned and unburned sites from September 2014 (2 months after the fire) to May 2018. Height of bars shows the mean of six sites, and error bars show one standard error. Soil organic matter was not measured in September 2015

Table 2 The effects of burn status (burned or unburned), sampling date, and their interaction on gravimetric soil moisture and soil organic matter content in the field

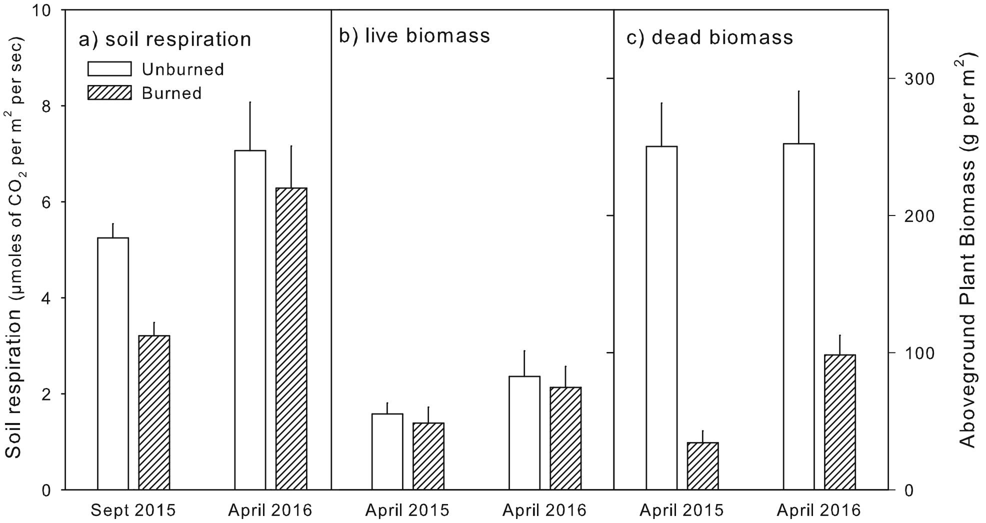
Source	Soil moisture			Soil organic matter		
	df	F	p	df	F	p
Burn status	1	9.88	0.003	1	14.40	< 0.001
Date	4	20.50	< 0.001	3	2.64	0.065
Burn status X Date	4	0.44	0.78	3	0.77	0.52
Error	45			35		

The degrees of freedom differed between variables because variables were sampled different numbers of times during the study. Soil moisture was sampled in September 2014, April 2015, September 2015, April 2016, and May 2018; soil organic matter was not sampled in September 2015. Site was included as a random factor in the ANOVAs

The most abundant trophic group of nematodes was generally the bacterivores, which were 49% less abundant in burned sites 2 months after the fire (Fig. 3a) and were 22% less abundant in burned sites over the entire study (Table 3, $P = 0.019$). Bacterivorous nematodes were also more abundant in spring samplings than they had been in September 2014 (Date, $P < 0.001$), regardless of whether the site had burned. The difference in mean bacterivore abundance between paired burned and unburned sites decreased over time ($P = 0.013$, $R^2 = 0.248$). The regression of the difference in bacterivore abundance and time since fire (difference = − 0.027 * months since fire + 1.103) predicted that bacterivores recovered after 40 months (i.e., in November 2017).

Fungivorous nematodes showed larger declines at burned sites but recovered over a similar time period. Burned sites had 73% fewer fungivores in September 2014 (Fig. 3b) and 31% fewer fungivores over the entire study (Table 3, $P < 0.001$). Like bacterivores, fungivores were more abundant in spring samplings than they had been in September 2014 (Date, $P < 0.001$). There was a significant interaction between Date and Burn status for fungivores ($P = 0.007$) because of high densities of fungivores in unburned sites in April 2015, when densities at the burned sites were still relatively low. The difference in mean abundance between paired burned and unburned sites decreased with time since the fire ($P < 0.001$, $R^2 = 0.502$). Although the overall mean fungivore abundances appeared comparable between burned and unburned sites in April 2016 (Fig. 3b), the regression of the difference in fungivore abundance between paired sites and time since the fire (difference = − 0.041 * months since fire + 1.551) did not

Fig. 2 Soil respiration (**a**) and aboveground biomass of (**b**) live and (**c**) dead plants at burned and unburned sites in April or September 2015 and April 2016. Means (of $N = 6$) ± 1 SE



predict full recovery until September 2017 (i.e., 38 months after the fire). Both bacterivore and fungivore abundances were strongly related to soil moisture over the entire field study ($R^2 = 0.27$ and 0.33, respectively, $P < 0.001$ for both, Table S2).

Herbivorous nematodes were the most abundant trophic group in unburned sites in September 2014 but were the most consistently impacted by the fire (Table 3, $P < 0.001$). Herbivores were 76% less abundant in burned sites 2 months after the fire and 60% less abundant in burned sites over the entire study (Fig. 3c). Although herbivorous nematodes were more abundant in May 2018 than they had been in September 2014 (Date, $P = 0.036$), the difference in abundance between paired burned and unburned sites did not decrease over time (regression, $P = 0.21$), and there was no interaction between Date and Burn status in the overall analysis (Table 3, $P = 0.88$). Herbivores were the only functional group of nematodes whose abundance did not seem strongly related to soil moisture; the regression of herbivore abundance and soil moisture was only marginally significant (Table S2, $P = 0.083$) and explained very little of the variation in herbivore abundance ($R^2 = 0.064$).

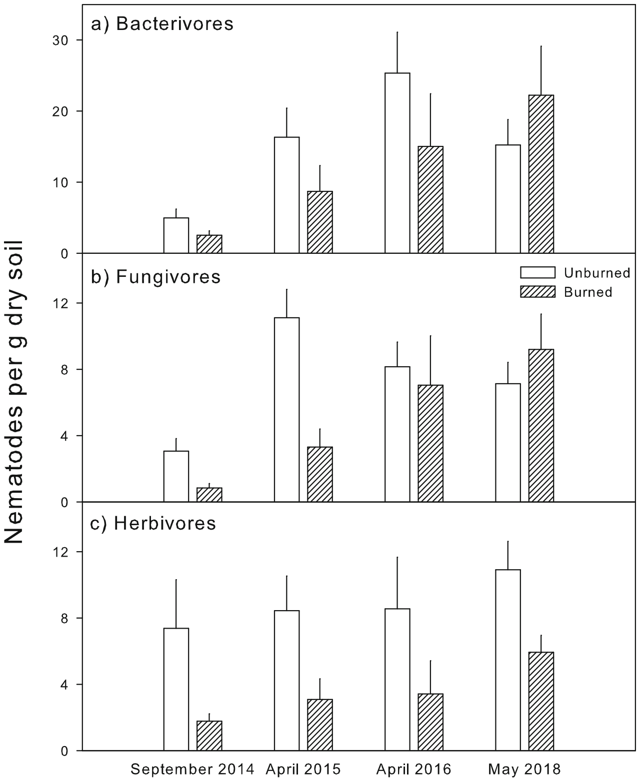


Fig. 3 The abundance of nematodes in burned and unburned sites from September 2014 (2 months after the fire) until May 2018. Means (of $N = 6$) ± 1 SE

Only a single predaceous nematode was found during this study. Omnivores were found in many samples but at such low abundances that they may not have been adequately sampled. Omnivores and predators were therefore omitted from all analyses.

Microcosm experiment

Bacterivorous and fungivorous nematodes increased in abundance in the microcosm experiment by 4.9 and 14.7-fold, respectively, in the first 20 days (relative to field densities, Fig. 4a and b), and were more abundant in the microcosms for most of the experiment than they had been throughout the field study. Bacterivores were more abundant in unburned soils than burned soils (Table 4, $P < 0.001$) and increased in abundance when grass litter was added (Table 4, Substrate X Days interaction, $P = 0.026$). At day 60, the abundance of bacterivores in burned soil with grass litter added was comparable to unburned soil with grass litter, although they remained at lower abundance in burned soil without the addition of litter ($P < 0.001$). Fungivorous nematodes increased in abundance between day 20 and day 60 but only in burned soils with grass litter added (Table 4, Burn status X Substrate X Days

Table 3 The effects of burn status, sampling date, and their interaction on the abundance of nematodes in the field

Source	df	Bacterivores F	Bacterivores p	Fungivores F	Fungivores p	Herbivores F	Herbivores p
Burn status	1	6.06	0.019	14.30	< 0.001	20.62	< 0.001
Date	3	11.41	< 0.001	17.19	< 0.001	3.18	0.036
Burn status X Date	3	2.06	0.12	4.79	0.007	0.23	0.88
Error	35						

Samples were collected on September 2014, April 2015, April 2016, and May 2018. Site was included as a random factor in the ANOVAs

interaction, $P = 0.037$). Like bacterivores, fungivores were more abundant in unburned soils in day 20, but by day 60, fungivores in burned soils with added grass litter had reached comparable abundance. Herbivorous nematodes were still at abundances comparable to the field after 20 days (Fig. 4c). Herbivores subsequently increased in abundance throughout the experiment (Table 4, $P = 0.003$) and were more abundant in unburned soils ($P < 0.001$) but did not respond to the addition of litter substrate.

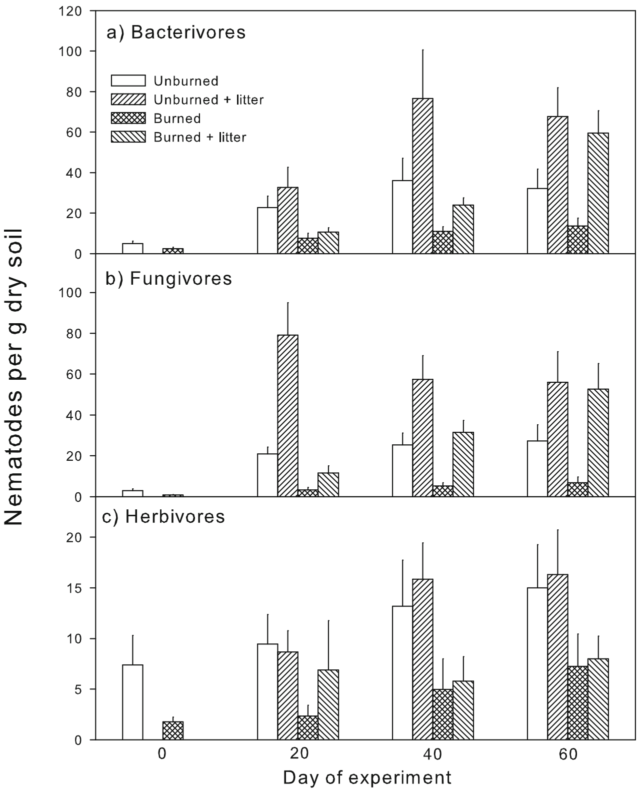


Fig. 4 The abundance of nematodes in the microcosm experiment, using soil from burned and unburned sites, after 0, 20, 40, and 60 days. "+litter" microcosms received grass litter on the surface of the soil. Field abundances from September 2014 were used in this graph as initial (day 0) abundances, but the field study did not include litter addition. Means (of $N = 12$) ± 1 SE. *P* values for pairwise comparisons of all significant factors and interactions are shown in Tables S3–S5

Discussion

Pairing of burned and reference sites

The absence of pre-data is a challenge in studying the impacts of wildfires. Most ecologists therefore use reference sites to infer the pre-burn condition of burned sites, but it is difficult to show that such reference sites were initially similar to burned sites. In this study, I evaluated the pairing of burned and unburned sites using additional soil properties (soil pH, total N, and soil texture) measured 21 months after the fire. Soil pH generally increases following fires (Certini 2005), but decreases have been observed in lower intensity fires (Pereira et al. 2017). Soil pH was lower in burned sites in my study, but the correlation between soil pH in burned sites and in their paired unburned site was highly significant. I found a similar correlation for total N. Soil texture variables (% clay, silt, and sand) were not correlated between paired sites, but all sites were fairly similar in texture. Following sites through time can also provide additional confirmation that the initial differences between burned and reference sites were caused by the fire. In my study, the differences between burned and unburned sites

Table 4 The effects of burn status, substrate, days elapsed, and their interactions on the abundance of nematodes in the microcosm experiment

Source	df	Bacterivores F	Bacterivores p	Fungivores F	Fungivores p	Herbivores F	Herbivores p
Burn status (B)	1	46.57	< 0.001	86.23	< 0.001	45.73	< 0.001
Substrate (S)	1	34.87	< 0.001	84.60	< 0.001	2.57	0.11
Days (D)	2	11.82	< 0.001	4.08	0.019	6.01	0.003
B X S	1	1.74	0.19	5.47	0.021	0.58	0.45
B X D	2	1.67	0.19	7.40	< 0.001	0.25	0.78
S X D	2	3.74	0.026	0.69	0.50	0.073	0.93
B X S X D	2	0.43	0.65	3.39	0.037	0.021	0.98
Error	127						

The microcosm experiment used soil collected in the field in September 2014, and was sampled after 20, 40, or 60 days had elapsed. Substrate refers to the effect of adding grass litter. Site was included as a random factor in the ANOVA decreased over time. This is consistent with the recovery over time of sites that were initially similar to their reference sites but is not what would be expected if the initial differences between burned and unburned sites represented pre-existing site differences.

Impacts of the fire on microbivorous nematodes

Abundances of both bacterivorous and fungivorous nematodes were substantially reduced in burned sites, and they took about 3 years to recover. In contrast to previous studies (e.g., McSorley 1993; Pen-Mouratov et al. 2012; Čerevková et al. 2013), no functional groups seemed to benefit from the fire at any point during this study. Nematodes experience high mortality during fires, with abundances declining more than 90% following experimental burning (Villegas and Bastow, *unpublished data*). Since free-living soil nematodes have generation times on the order of 3–14 days (Vancoppenolle et al. 1999), however, recovery could occur much more rapidly than was seen at FRA, if conditions were suitable. This was seen in the microcosm experiment, in which temperature and moisture were suitable and consistent, and microbivorous nematodes recovered by day 60. Surface litter was necessary for the recovery of bacterivores and fungivores in the microcosm experiment; however, litter was largely removed from burned sites by the fire. Plant litter may be important for microbivorous nematodes because they feed on saprotrophic microbes. Soong et al. (2017) found that nematodes incorporated C from isotopically labeled grass litter and that the addition of such litter increased nematode abundances. Surface litter also helps soil retain moisture, and both fungivore and bacterivore abundances were positively correlated with soil moisture in the field. Burned sites were drier than unburned sites through at least September 2015, 14 months after the fire. Fires reduce moisture retention of soils through at least three mechanisms: by increasing the water repellency of soil, by reducing SOM, and by reducing surface litter (Certini 2005). There was only 39% as much surface litter at burned sites as unburned 21 months after the fire, and it would likely have taken another 2 years to accumulate to pre-fire levels. This is similar to the timescale over which microbivores were predicted to have recovered but longer than timescale over which soil moisture seemed to recover. This may mean that surface litter is also important in the recovery of soil nematodes for trophic reasons or that soil moisture at burned sites remained lower during unsampled times of the year (e.g., summer or fall after 2015).

Fungi are thought to be more sensitive to fire than bacteria (Bååth et al. 1995; Pressler et al. 2019), and bacterivorous nematodes are generally considered more disturbance-adapted than fungivores (Bongers and Ferris 1999). It is therefore surprising how similarly fungivores and bacterivores responded to the Watermelon Hill Fire, in terms of both their decrease in abundance and the timescale of their recovery. McSorley (1993); Pen-Mouratov et al. (2012); Čerevková et al. (2013); and Butenko et al. (2017) all found total bacterivore abundance to increase following fires, likely because of increased bacterial biomass (Butenko et al. 2017) or microbial activity (Gongalsky et al. 2016). These increases were often driven by one or a few disturbance-adapted taxa, such that richness and evenness decline even as total abundance increases (Pen-Mouratov et al. 2012; Čerevková et al. 2013). Although it is likely that disturbance-adapted taxa also occur at FRA, bacterivore abundances were much more negatively impacted by the fire in this study. Studies of grasslands have generally found smaller responses to fire by bacterivores (Todd 1996; Yeates and Lee 1997; Jones et al. 2006) following prescribed burns. It is possible that the bacterial channel of the food web responds more positively to fires in forested systems, perhaps because they benefit from the suppression of the fungi, which are normally more dominant in forested systems. Alternatively, bacteria may benefit more from high intensity wildfires, from which fungi may take longer to recover. In either case, it is unclear why bacterivores at FRA were so much more negatively impacted by this light to moderate intensity wildfire than bacterivores in earlier grassland studies.

It is possible that soil food webs in more arid systems respond differently to fire than they do in wetter climates. The strong relationship between soil moisture and microbivore abundance in this study suggests that moisture is generally limiting for the soil food web, so any reduction in soil moisture following a fire is likely to have widespread impacts. Although earlier studies cover a range of latitudes and vegetation types, they are generally from regions that receive two to three times as much precipitation annually as FRA (320-mm annual precipitation), such as Biriya Forest, Northern Israel (700 mm, Pen-Mouratov et al. 2012), the High Tatras (1000–1600 mm, Čerevková et al. 2013), or Konza Prairie Biological Station, KS, USA (835 mm of precipitation annually, Soong et al. 2017). Among the five sites along a 3000-km transect studied by Butenko et al. (2017), the only site at which wildfire appeared to have reduced nematode abundances was the southernmost and driest site.

Microbivorous nematodes may also respond differently to fire in systems with different soil textures. Soil texture affects moisture retention in soils, which appeared to be an important predictor of microbivore abundance in this study. Trophic interactions are also affected by soil texture. In soils with a high clay content, nematodes may be unable to access bacteria in small soil pores (Rønn et al. 2012). Predaceous nematodes exert strong top-down effects on microbivorous nematodes (Mikola and Setälä 1998; Bastow 2011) but were virtually absent from FRA, despite being common in nearby sites with sandy soils (Bastow, *personal observation*). The relative importance of top-down, bottom-up, and moisture limitation for nematode populations recovering from fire may therefore differ in different soil types.

Impacts of the fire on herbivorous nematodes

Herbivorous nematodes were reduced in burned sites and did not appear to recover over the period of this study. Early season plant growth did not differ between burned and unburned sites the spring following the fire (April 2015), however, so it is surprising that herbivorous nematodes had not recovered in burned sites even 3 years later. It may be that aboveground biomass in April missed differences in productivity, which may have manifest later in the growing season, or there may have been differences in plant composition in burned sites that negatively impacted herbivores. Pen-Mouratov et al. (2012) and Butenko et al. (2017) also found herbivorous nematodes to be more negatively impacted than microbivores, which Butenko et al. (2017) attributed to a shift to less nutritious or younger, better defended plants at burned sites. Todd (1996) and Yeates and Lee (1997), both working in grasslands, found that herbivores increased following prescribed burns, so herbivore responses to fire may be relatively site specific, depending on the responses of individual plant species in the system.

Impacts of the fire on soil organic matter

Burned sites had less SOM than unburned sites. The difference in SOM, averaging over the entire study, suggests that burned sites had between 1254 and 1984 g less C per m^2 in the top 10 cm of the soil (assuming bulk density between 1.1 and 1.5 g per mL and that SOM is between 50 and 58% C). This would suggest that soil lost 10–18 times as much C as was lost from surface litter and vegetation at FRA, or between 52,600 and 83,200 Mg of C over the entire area of the fire. This may overestimate the C losses, however, in that it does not account for pyrogenic organic matter created by the fire. Unburned sites had higher rates of soil respiration in September 2015, 14 months after the fire. Since there was no apparent difference in plant growth between burned and unburned sites, higher soil respiration in unburned sites would be expected to decrease the difference in SOM between these sites over time. The observed difference in soil respiration in September 2015, if extrapolated over a year, would account for unburned sites respiring 757 more g of C per m^2 than burned sites. This does not account for seasonal fluctuations in soil respiration, but September is generally a low period for soil respiration in this area (Bastow, *unpublished data*). The reduction in soil respiration at burned sites, however, lasted less than 2 years following the fire and was no longer apparent in April 2016.

Applicability of the microcosm experiment

I began the microcosm experiment in September 2014, in order to assess the capacity of the soil food web to recover under favorable conditions (i.e., consistent, wet, and relatively warm). In terms of predicting the dynamics of the recovery, the microcosm experiment did a poor job quantitatively matching the field recovery but made several potentially useful qualitative predictions. Recovery of bacterivores and fungivores occurred far more rapidly in the microcosms than they did in the field, and bacterivores and fungivores reached abundances about three- and sixfold higher, respectively, than were ever observed in the field. This is likely because of both the favorable conditions and the relative scarcity of higher trophic levels. Although bacteria are generally more resilient to fire than fungi (Pressler et al. 2019) and bacterivorous nematodes often recover from fires more quickly than fungivores (Butenko et al. 2017), my microcosm experiment correctly predicted that bacterivores and fungivores at FRA would recover on a similar timescale. The microcosm experiment also predicted that surface litter would be important for this recovery. Although litter was not manipulated in the field, the recovery of these groups in the field seemed to take place over a similar timescale to the accumulation of litter.

One important factor omitted from my microcosm experiment was live plants. Plant roots provide C to soil fauna via rhizosphere bacteria and fungi, as well as direct consumption of roots (Pollierer et al. 2007). The omission of live plants could, therefore, force nematodes to rely more on litter for C than they otherwise would and overstate the importance of surface litter in recovery. This experiment was designed to simulate recovery at FRA, where fires generally occur in August and September. This is after the growing season is over, and 4 to 6 months before the next growing season begins. This microcosm therefore simulates early recovery, during which time live plants are absent or dormant and burned areas have very little surface litter. Experiments simulating longer-term recovery, or systems where there is greater overlap between the growing season and the fire season, should include live plants.

Microcosm experiments paired with manipulative field experiments, or, alternately, field microcosms experiments (Kampichler et al. 2001), would be useful for determining the role of plant and litter composition, moisture limitation, SOM, soil texture, and soil nutrients in the recovery of soil food webs after fires. Microcosm experiments have been more widely used to study soil microbes, including their recovery following experimental fire (Song et al. 2004) and their interactions with charcoal (Zackrisson et al. 1996). Gongalsky et al. (2012) used a microcosm experiment in which microcosms were burned in the lab to look at how soil depth affected soil faunal responses to fire. Such an approach would be useful for investigating the role of factors that likely affect survival during fire as well as recovery following fires.

Conclusions

Soil nematodes at Fishtrap Recreation Area were more negatively impacted by this wildfire than has been observed in earlier studies of nematode responses to fire, despite the low to moderate severity of the wildfire studied. This is likely because of the semiarid climate of this region and the increased moisture limitation at burned sites. Although previous studies of soil food web responses to fire have focused on wetter regions, arid and semiarid biomes are globally widespread and likely to experience increased fire frequency with climate change. If the low resistance and slow recovery of the soil food web seen in this study is a general feature of such systems, a decrease in fire interval may lead to long-term decreases in soil biological activity, with widespread changes to ecosystem processes, such as nutrient cycling and C storage. Additional studies, in a wider range of such dry ecosystems, would be helpful in understanding how these changes in fire regime will alter soil food webs and processes, including their feedbacks to vegetation and climate.

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Compliance with ethical standards

Conflict of interest The author declares that he/she has no conflict of interest.

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