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Post-Fire Recovery of Soil Nematode Communities Depends on Fire Severity

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Abstract: Following the creation of a new organic layer after a forest fire, there is an initial build-up phase of overall biota. We studied soil nematode community development in a chronosequence of post-fire coniferous forest sites in relation to different fire severity. The taxonomic and functional composition of the soil nematode community was analyzed to detect immediate changes and levels of post-fire recovery in soil food web structures, i.e., 0, 1, 4, 8, 14, 20, 45, and 110 years after the event. Unburned forest sites served as controls. With small exceptions recorded immediately after the burn (mean nematode abundance, total biomass), the low severe wildfires had no impacts on the structures of nematode communities. The structures of nematode communities were found to be stable on sites affected by low severe wildfires, without considerable fluctuations in comparison to the unburned sites during chronosequence. On the contrary, nematode communities responded considerably to fires of high severity. The significant changes, i.e., a decrease of mean nematode abundance, plant parasites, omnivores and predators, species number, and nematode diversity, the values of CI, SI, MI, but an increase in the number of bacterivores and EI were recorded immediately after the fire. Such status, one year after a fire of high severity, has been observed. Full recovery of nematode communities 14 years after the disruption was found. Overall, our results showed that fire severity was a considerable element affecting soil nematode communities immediately after events, as well as the time needed to recover communities' structure during post-fire chronosequence.

Keywords: ecosystem recovery; fire severity; nematoda; soil; diversity; coniferous forest; wildfire

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1. Introduction

Terrestrial nematodes, i.e., species that inhabit exclusively the soil environment, are by far the most abundant edaphic animals [1]. As estimated [2], approximately 4.4×10^{20} nematode individuals inhabit the upper layer of soils across the globe. They interact with many other organisms, consuming and being consumed by other components of the soil fauna [3]. High diversity is the basis for their multiple functions and roles; for example, by eating bacteria and fungi, they regulate their populations [4], feeding on plant roots damages the hosts, many times at economically important levels [5]. Acting as top-down regulators of lower trophic levels, e.g., predator and omnivore nematodes, as components of the higher trophic levels of the soil food web, may play an important role in regulating plant-feeding nematode populations, particularly where bottom-up resources are restricted [3]. Therefore, their contribution to nutrient dynamics, energy flow, global carbon (C) cycle, organic matter decomposition or mineralization is decided [6–8]. Inhabitting the soil, nematodes are thus essentially dependent on soil characteristics and are sensitive to any modifications [9–11], e.g., after a disturbance.

Disturbances, both human-induced and natural, shape forest systems by influencing their composition, structure, and functional processes [12]. Natural disturbances with the greatest effects on forests include droughts, introduced species, insect and pathogen outbreaks, windstorms, and wildfires. Wildfires are usually unexpected events, which occur irrespectively of whether ecologists are prepared to explore them or not [13]. Nevertheless, fires present a wide range of opportunities for ecologists as a model of natural disturbances to study secondary successions, spatial patterns of recovery, the resilience of soil communities and ecosystems, processes structuring soil animal communities, and other generally relevant questions.

In certain forests, fires are considered part of the natural life cycle that most often help to renew itself when they occur in normal intervals [14]. However, in fire-non-adapted forests, burning can have a large impact on biota [15,16]. Exploring how such hardly predictable, yet rather destructive processes affect soil biota seems to be a challenging, risky (both physically and scientifically), and complex task [13]. One important factor of the ecological impact of fire on ecosystems and their post-fire regeneration is its intensity and/or severity [17]. At low severe fires, the soil organic layers are largely intact, and charring is limited to a few mm of depth. On the opposite, high severe fires largely consume soil's organic layer and sometimes burn down the soil with all its inhabiting organisms [17].

Specifically, micro and meso-organisms that are similar to plants, cannot move away from the fire and are particularly sensitive [18–20]. Among them, just omnipresent nematodes with high diversity and abundance, especially in natural forest soils [21–23], can provide interesting insights into the fire effect on the soil environment. Diverse nematode taxa, particularly trophic and functional groups, are sensitive to specific disturbances at different levels [24–26], thus nematode communities pose as valuable bioindicators of environmental monitoring [27]. Several previous studies investigated the impacts of burn after forest-fire events on the communities of soil nematodes, but the reported results are contradictory [28–32]. According to the study by [18,33] on invertebrates and microarthropods, fire severity is a decisive factor influencing the long-term recovery of soil fauna. To the best of our knowledge, the status of post-fire recovery of soil nematode communities in relation to different fire severity has never been examined.

In the present study, soil nematode communities and soil properties were examined in the coniferous forest sites after fires. The aim of the present study was to evaluate the immediate impact of burn, as well as the level of recovery of forest soil nematode communities in long-term chronosequence (1 up to 110 years) after fires of different severity, high vs. low. We hypothesized that total nematode abundance would decrease, the species number, diversity, and trophic composition would change as an immediate response to fire, and that these variables would be more affected by high severe fires. We also hypothesized that the soil nematode community would recover more slowly in high severe burned plots.

2. Materials and Methods

2.1. Site Description

For the purpose of the present study, we selected coniferous forests in the Bohemian Switzerland National Park in the northern tip of the Czech Republic. Although the park's area is small (79 km^2), it has one of the highest frequencies of forest fires in the Czech Republic [34]. According to [35], at least 72 forest fire events were experienced between the years 1976 and 2008 in the area of the park, as well as several fires since 2008, the last one in 2020. The long-term mean annual temperature is about 7 °C and the mean annual precipitation is 800 mm. The soils at the park were described as Albic Podzols and Podzols (WRB classification) and vegetation was composed of coniferous forests with prevailing Norway spruce (*Picea abies*) and Scots Pine (*Pinus sylvestris*). The most common understory species are *Avenella flexuosa, Calamagrostis epigejos, Pteridium aquilinum,* and *Vaccinium myrtillus.*

2.2. Soil Sampling and Processing

Eight sites in an unburned (control, CON) and eight sites in a burned area (FIR) by high severe fires with similar vegetation and geological substrate were selected in a chronosequence 0, 1, 4, 8, 14, 20, 45, and 110 years after the fire events (Table 1). The same pattern for eight sites affected by low severe fires and eight related unburned controls has been used. Fire severity was estimated according to the degree of combustion of surface litter and organic soil layer as high or low. On each site, three soil samples with a cylinder to a depth of 4 cm including the humus layer were randomly collected. The sites were sampled twice, in September 2020 and April 2021. A total of 192 representative soil samples were thus collected; six from each site (three in September and three in April). The soil samples were transferred to the laboratory in sealed plastic bags. The bags were stored at 5 °C until processing, max for two weeks.

The weight of each sample was measured, and soil was homogenized by gentle hand mixing, and soaked in 1 L of tap water for 30–60 min. A combination of Cobb sieving and decanting [36] and a modified Baermann technique [37] has been used for nematode extraction. Firstly, an aqueous soil suspension was sieved by 1 mm (16 mesh) and 0.05 mm (300 mesh) sieves. The obtained suspension with nematodes without coarse soil was then placed on a funnel containing a sieve 0.5 mm (30 mesh) and a set of two cotton–propylene filters. Aqueous suspensions were removed after 48 h of extraction at room temperature and nematode abundance was counted under a stereomicroscope (40 and 60_magnification). Later, excessive water was removed, and the nematodes were fixed with a hot 99:1 solution of 4% formaldehyde: pure glycerol [38]. At least 100 nematodes were identified to species level (several taxa and juveniles to genus level) based on the original species descriptions and accessible taxonomic keys of nematode genera and groups, by using an Eclipse 90i Nikon light microscope (Tokyo, Japan) at standard magnifications.

Soil water content (SWC) was calculated as a difference between the weight of fresh soil and oven-dried soil, divided by the weight of fresh soil (expressed in g g^{-1}). To determine pH, dissolved organic C (DOC), dissolved nitrogen (DN), and dissolved phosphorus (DP), fresh soil (10 g) was placed in 50 mL of deionized water (dH_2O) and shaken at 80 oscillations per min for 45 min. Then the suspension was centrifuged at $1370\times g$ for 30 min and passed through a 0.45-μm membrane filter. Soil pH was measured using a glass electrode. Filtrates were then frozen and stored at −20 °C until the analysis of DOC, DN, and DP. Contents of DOC and DN were measured using a TOC analyzer (model TOC-LCPH/CPN, Shimadzu) and content of DP was determined using spectrophotometry according to [39] (expressed in mg g^{-1}).

Table 1. Description of fire affected (FIR) and control (CON) plots of study forests.

Plot	Coordinates	Year of Fire	Time from Fire in 2020 (y)	Fire Severity	Dominant Tree	Tree Layer %	Shrub Layer %	Herb Layer %	Moss Layer %
FIR	N50.8751 E14.3314	2020	0	High	-	1		3	
CON	N50.8752 E14.3311				Pine, Spruce, Birch	25	10	80	10
FIR	N50.8745 E14.3313	2020	0	Low	Pine	20		30	1
CON	N50.8752 E14.3311				Pine, Spruce, Birch	25	20	80	10
FIR	N50.8937 E14.3612	2019	1	High	Pine	17		15	10
CON	N50.8886 E14.3467				-	23	1	12	50
FIR	N50.8631 E14.4223	2019	1	Low	Spruce	1	2	40	25
CON	N50.8886 E14.3467				-	5	2	40	25
FIR	N50.8804 E14.3574	2016	4	High	Pine	10	1	70	15
CON	N50.8804 E14.3570				Spruce, Pine	10	20	65	70
FIR	N50.8494 E14.3487	2016	4	Low	Pine, Spruce	45		50	15
CON	N50.8499 E14.3484				Spruce, Beech	40	5	70	70
FIR	N50.8607 E14.4061	2012	8	High	Birch, Spruce	10	75	20	2
CON	N50.8608 E14.4063				Birch	40	3	80	5
FIR	N50.8816 E14.3390	2012	8	Low	Pine	40		25	25
CON	N50.8813 E14.3392				Spruce, Pine	25	20	50	20
FIR	N50.8565 E14.4050	2006	14	High	Birch	60	20	20	10
CON	N50.8608 E14.4063				Birch	40	3	80	5
FIR	N50.8804 E14.3147	2006	14	Low	Pine, Beech	15		10	5
CON	N50.8819 E14.3120				Beech, Pine, Spruce	60	15	30	10
FIR	N50.8817 E14.2987	2000	20	High	Birch, Pine	50	25	40	2
CON	N50.8817 E14.2961				Pine	40	3	70	1
FIR	N50.9278 E14.4336	2000	20	Low	Spruce, Pine	30	2	55	20
CON	N50.9282 E14.4348				Spruce, Pine	70		6	10
FIR	N50.9041 E14.3528	1975	45	High	Birch, Larch	30	3	60	60
CON	N50.9025 E14.3537				Spruce, Beech	40	3	1	20
FIR	N50.9232 E14.4042	1975	45	Low	Spruce, Pine, Birch	40	5	10	25
CON	N50.9239 E14.4045				Spruce, Pine	50	18	15	50

Table 1. *Cont.*

Plot	Coordinates	Year of Fire	Time from Fire in 2020 (y)	Fire Severity	Dominant Tree	Tree Layer %	Shrub Layer %	Herb Layer %	Moss Layer %
FIR	N50.8947 E14.3507	1910	110	High		30	10	65	70
CON	N50.8886 E14.3467					60	10	50	5
FIR	N50.9084 E14.2218	1910	110	Low	Pine, Birch	3	2	15	15
CON	N50.9057 E14.2196				Beech, Spruce, Oak			10	15

2.3. Nematode Community Analysis

Nematode abundance in each sample was expressed as the number of individuals per 1 g of dry soil. Nematode species were assigned to the trophic groups, i.e., bacterivores, fungivores, plant feeders, carnivores, and omnivores as recommended by [40], and adjusted and supplemented following [41]. Several community indices were calculated. The Shannon-Weaver diversity index (H'spp) was calculated using species data to estimate the diversities of the nematode communities [42]. Ecological indices were calculated to assess the maturity of the nematode communities within chronoseqence after fire events: Maturity index (MI) for free-living nematodes; and plant parasitic index (PPI) for plant-feeding nematodes. Both maturity indices are weighted means calculated as $\sum(v_i) \times (f_i)$ where (v*i*) is the c-*p* value of taxon *i* according to their r and K characteristics, and(f_i) is the frequency of taxon *i* in a sample [43,44]. Species with c–*p* values of 1 or 2 are r-selected; that is, colonizers. These species are very tolerant to disturbance due to their short generation times, large population fluctuations, and high fecundities. Species with a c–*p* value of 5 are k-selected, or persisters, with long life cycles, low reproductive rates, low metabolic activities, and slow movement; they are thus very sensitive to disturbance. Lower c–*p* values are indicative of more disturbed environments, and higher values are characteristic of less disturbed environments [43].

Ferris [45] expanded the concept of the maturity index to a weighted faunal analysis to allow an extended assessment of soil food webs through the analysis of nematode communities. Nematode taxa are assigned to functional guilds, where all nematodes in a functional guild have the same feeding habit [40] and the same c–*p* values (e.g., the functional guild Ba_3 includes all bacterivores with a c–*p* value of 3). These functional guilds are indicators of basal (*b*), structured (*s*), and enriched (*e*) soil food webs. An enrichment index (EI) and structure index (SI) were calculated using an indicator weighting system based on the importance of the functional guilds along hypothesized trajectories of enrichment and structure [45]. The EI provides the location of the food web along the enrichment trajectory and is calculated as $10 \times (e/(e + b))$. Similarly, the SI provides the location of the food web along the structure trajectory and is calculated as $100 \times (s/(s + b))$. For example, the *b* component is calculated as $\sum k_b n_b$, where k_b is the weighting assigned to guilds that indicate basal characteristics of the food web (Ba_2, Fu_2) and n_b are the abundances of nematodes in the sample. The *e* and *s* components are calculated similarly, using those guilds indicating, respectively, enrichment (Ba_1, Fu_2) and structure (Ba_3–Ba_5, Fu_3–Fu_5, Om_3–Om_5, Ca_2–Ca_5) (for more details see original work; [45]).

Additionally, the channel index (CI) indicates the predominant decomposition channel in the soil food web, calculated as $CI = (0.8\ Fu_2/(3.2\ Ba_1 + 0.8\ Fu_2))$, where Ba_1 abundance in the sample of nematodes in the family Rhabditidae, Panagrolaimidae or Diplogasteridae, and Fu2L'abundance of nematodes in the family Aphelenchidae, Aphelenchoididae or Anguinidae. A high CI (>50%) indicates a higher proportion of fungal decomposition. A low CI (<50%) suggests bacterial decomposition channels [45].

All indices (except H'spp) and total biomass were calculated using the NINJA online program [41]; http://spark.rstudio.com/bsierieb/ninja; accessed on 14 July 2021), including graphic depictions of the conditions of the soil food webs, and the "faunal profile", which was modeled separately for each sample.

2.4. Statistical Analysis

All response variables, except those for nematode functional guilds, were subjected to one-way analysis of variance (ANOVA) to determine the overall effect of fire severity on nematode communities and development within post-fire chronosequence using Statistica 9.0 (StatSoft Inc., Tulsa, Oklahoma, USA). Significant differences between fire and control means for individual sites were evaluated by Tukey's honestly significant difference (HSD) at $p < 0.05$ and $p < 0.01$.

A redundancy analysis (RDA) was used on the nematode functional guilds of particular trophic groups for the fire severity, with explanatory variables soil pH, soil-moisture content, dry matter, DOC, DN, and DP to identify the relationships between the functional guilds and soil properties. Additionally, RDA was used on the bacterivorous, fungivores, and plant parasitic nematode functional guilds and vegetation characteristics to identify the relationships between those guilds and dominant plant species (trees, herbs, and mosses layers) on study plots. All data were log-transformed before use. The effects of the explanatory variables were quantified by automatic forward selection. These ordination analyses were performed in Canoco 5 for Windows [46].

3. Results

3.1. Variation in Physico-Chemical Properties of Soil

Some physicochemical properties measured were found to be significantly affected by burnt, fire severity, and chronosequence age (Table 2). However, a clear pattern cannot be deducted from the data obtained. The soils in all sites were strongly acidic or acidic (pH/KCl 3.60–6.00). The pH varied little between unburned and burned sites of two different severities of fire within followed chronosequence years. Similar answers at soil moisture and DP were observed, nonetheless DP content was significantly higher immediately after high severe burn ($p < 0.05$).

Dry matter content, DOC and DN amount in the soil responded significantly to burnt ($p < 0.05$). In general, the values of dry matter increased with increasing chronosequence age in sites affected by both, high and low-severe wildfires, but their values irregularly varied between FIR and CON sites within the post-fire succession. The values of DOC increase with increasing chronosequence age after fires of both severities, with the highest contents generally 110 years post-fire. On the contrary, values of DN decreased with increasing chronoseqence age, but an increase 110 years after event was observed.

Table 2. Mean values (±S.D, *n* = 3) of physicochemical soil properties in high and low severe fires (FIR) and related control (CON) sites in September 2020 and April 2021.

Year of Fire	Time from Fire in 2020 (Years)	Fire of High Severity				Fire of Low Severity			
		XI/2020		IV/2021		XI/2020		IV/2021	
		FIR	CON	FIR	CON	FIR	CON	FIR	CON
pH									
2020	0	4.83 ± 0.21	4.83 ± 0.41	5.11 ± 0.18	5.15 ± 0.22	4.89 ± 0.25	5.19 ± 0.08	5.13 ± 0.38	5.27 ± 0.36
2019	1	4.63 ± 0.51	4.61 ± 0.15	4.85 ± 0.18 *	5.21 ± 0.06	4.54 ± 0.31	4.01 ± 0.24	5.00 ± 0.35	4.71 ± 0.23
2016	4	4.37 ± 0.33	3.98 ± 0.13	4.96 ± 0.36	4.47 ± 0.19	4.22 ± 0.19	3.96 ± 0.13	4.12 ± 0.33	4.37 ± 0.15
2012	8	4.10 ± 0.40	3.87 ± 0.09	5.14 ± 0.28 *	4.79 ± 0.12	4.21 ± 0.13 *	3.82 ± 0.14	4.56 ± 0.31	4.79 ± 0.12
2006	14	4.92 ± 0.21	4.83 ± 0.24	6.06 ± 0.05	6.07 ± 0.43	4.14 ± 0.09 *	3.81 ± 0.16	5.25 ± 0.80	4.50 ± 0.39
2000	20	4.31 ± 0.03	4.03 ± 0.19	4.60 ± 0.53	4.88 ± 0.37	3.78 ± 0.41	3.66 ± 0.06	4.54 ± 0.51	4.73 ± 0.06
1975	45	4.09 ± 0.14	3.89 ± 0.18	5.12 ± 0.32 *	4.65 ± 0.12	3.59 ± 0.18	3.75 ± 0.17	4.54 ± 0.14	4.59 ± 0.03
1910	110	3.69 ± 0.32	3.74 ± 0.06	4.13 ± 0.15	4.43 ± 0.29	4.80 ± 0.18	4.78 ± 0.22	5.18 ± 0.11	5.38 ± 0.29
DM									
2020	0	0.45 ± 0.07 *	0.61 ± 0.05	0.40 ± 0.03 *	0.29 ± 0.02	0.54 ± 0.15	0.47 ± 0.16	0.29 ± 0.02 *	0.45 ± 0.16
2019	1	0.44 ± 0.05	0.52 ± 0.19	0.36 ± 0.04	0.36 ± 0.01	0.47 ± 0.12 *	0.61 ± 0.03	0.39 ± 0.21	0.38 ± 0.08
2016	4	0.62 ± 0.24	0.58 ± 0.06	0.74 ± 0.15 *	0.43 ± 0.12	0.86 ± 0.17 *	0.58 ± 0.06	0.58 ± 0.08	0.47 ± 00.9
2012	8	0.67 ± 0.05	0.66 ± 0.04	0.42 ± 0.09	0.32 ± 0.03	0.92 ± 0.04 *	0.59 ± 0.03	0.56 ± 0.14 *	0.29 ± 0.01
2006	14	0.91 ± 0.09	0.92 ± 0.04	0.78 ± 0.06	0.80 ± 0.07	0.50 ± 0.09	0.66 ± 0.02	0.38 ± 0.09	0.49 ± 0.03
2000	20	0.84 ± 0.05 *	0.66 ± 0.02	0.54 ± 0.06 *	0.34 ± 0.07	0.81 ± 0.12 *	0.64 ± 0.03	0.56 ± 0.11 *	0.35 ± 0.06
1975	45	0.73 ± 0.12	0.67 ± 0.04	0.60 ± 0.12 *	0.39 ± 0.03	0.67 ± 0.06	0.59 ± 0.03	0.40 ± 0.06	0.34 ± 0.02
1910	110	0.66 ± 0.07	0.73 ± 0.08	0.48 ± 0.01	0.51 ± 0.12	0.32 ± 0.03	0.38 ± 0.08	0.29 ± 0.01	0.36 ± 0.06
DOC									
2020	0	592.3 ± 185.2	781.3 ± 139.9	315.1 ± 112.5 *	930.5 ± 271.1	503.3 ± 17.4	507.4 ± 17.2	481.5 ± 104.9	469.4 ± 45.8
2019	1	650..8 ± 234.7	644.1 ± 458.2	397.7 ± 160.2	667.3 ± 93.7	335.1 ± 81.0	478.1 ± 193.2	607.2 ± 474.0	338.2 ± 150.9
2016	4	319.6 ± 217.3 *	747.1 ± 154.1	103.6 ± 77.4 *	507.8 ± 144.5	264.0 ± 173.7	579.1 ± 107.9	564.2 ± 393.6	420.8 ± 146.2
2012	8	838.3 ± 78.5	735.1 ± 196.1	323.7 ± 100.9 *	509.4 ± 55.6	177.3 ± 64.6 *	669.1 ± 103.3	272.3 ± 179.6 *	632.9 ± 105.4
2006	14	382.7 ± 185.0	416.8 ± 199.4	103.5 ± 60.5	170.3 ± 14.5	544.7 ± 89.7	882.9 ± 206.7	423.9 ± 146.9	635.3 ± 41.8
2000	20	326.7 ± 26.5 *	670.1 ± 102.8	140.9 ± 25.5	381.9 ± 130.6	724.7 ± 795.4	830.2 ± 177.9	487.1 ± 466.0	674.3 ± 207.8
1975	45	434.0 ± 189.6	612.9 ± 286.9	243.2 ± 94.8 *	497.8 ± 130.2	1042.6 ± 551.8	825.4 ± 355.9	345.6 ± 81.7 *	670.1 ± 58.1
1910	110	1406.5 ± 1502.7	476.2 ± 130.9	509.6 ± 88.2	605.0 ± 222.3	1246.5 ± 269.3	2318.9 ± 1561.2	877.4 ± 232.6	705.3 ± 176.6

Table 2. *Cont.*

Year of Fire	Time from Fire in 2020 (Years)	Fire of High Severity				Fire of Low Severity			
		XI/2020		IV/2021		XI/2020		IV/2021	
		FIR	CON	FIR	CON	FIR	CON	FIR	CON
DN									
2020	0	116.4 ± 37.3 *	72.7 ± 7.8	32.1 ± 11.0 *	126.7 ± 74.6	125.1 ± 27.8 *	74.9 ± 19.2	56.4 ± 10.6	64.1 ± 7.5
2019	1	148.1 ± 63.9	102.4 ± 70.9	55.9 ± 29.4 *	96.6 ± 17.8	51.8 ± 42.7	28.4 ± 13.2	72.1 ± 57.9	30.1 ± 30.6
2016	4	20.2 ± 8.1 *	41.6 ± 9.8	10.2 ± 11.7	33.6 ± 7.4	14.8 ± 6.3	31.2 ± 2.6	30.4 ± 22.9	16.5 ± 6.6
2012	8	35.6 ± 3.2	29.6 ± 9.1	26.5 ± 10.9	43.4 ± 15.1	9.5 ± 5.4 *	36.1 ± 17.2	13.4 ± 4.7 *	84.4 ± 10.1
2006	14	22.3 ± 9.9	20.6 ± 5.0	13.9 ± 5.7	16.4 ± 5.7	30.6 ± 2.3	56.1 ± 9.5	26.9 ± 6.5	46.6 ± 7.2
2000	20	12.3 ± 0.9 *	32.1 ± 5.8	13.3 ± 6.2	38.5 ± 22.2	24.5 ± 27.8	28.9 ± 9.0	35.5 ± 41.2	66.3 ± 25.5
1975	45	25.2 ± 10.7	26.8 ± 6.6	29.4 ± 7.5	47.1 ± 16.7	39.9 ± 22.5	34.2 ± 14.1	26.6 ± 1.6 *	50.9 ± 3.0
1910	110	54.2 ± 46.6	16.4 ± 4.2	57.5 ± 12.3	50.9 ± 20.9	138.9 ± 19.5 *	291.0 ± 159.5	101.4 ± 33.1	101.2 ± 13.1
DP									
2020	0	71.5 ± 53.9 *	10.4 ± 13.5	42.7 ± 23.8	16.6 ± 6.8	84.1 ± 30.1	82.0 ± 10.5	63.0 ± 26.8	68.1 ± 14.6
2019	1	23.9 ± 9.6	10.7 ± 9.2	23.7 ± 8.4	26.1 ± 9.9	14.1 ± 7.1 *	1.3 ± 1.7	26.2 ± 19.5	5.5 ± 6.9
2016	4	0.8 ± 0.1	3.5 ± 2.4	6.8 ± 1.5	2.7 ± 2.0	0.9 ± 0.2	0.6 ± 0.1	3.5 ± 1.9	3.2 ± 4.9
2012	8	0.7 ± 0.9	1.6 ± 1.1	41.9 ± 60.4	1.3 ± 0.5	2.7 ± 1.6	0.5 ± 0.5	4.8 ± 3.2 *	18.7 ± 7.6
2006	14	19.2 ± 11.4	22.6 ± 5.3	15.8 ± 12.3	18.1 ± 11.1	-	3.8 ± 1.3	15.2 ± 5.1	17.3 ± 13.8
2000	20	9.7 ± 6.3 *	0.5 ± 0.9	12.9 ± 4.1	10.8 ± 7.3	2.2 ± 3.5	2.5 ± 2.0	8.8 ± 3.2	17.2 ± 16.7
1975	45	0.5 ± 0.4	0.4 ± 0.2	3.4 ± 2.6	5.2 ± 9.1	4.1 ± 4.9	0.06 ± 0.11	14.6 ± 6.2	5.7 ± 9.8
1910	110	0.6 ± 0.8	0.9 ± 0.5	9.6 ± 12.1	6.7 ± 5.2	26.8 ± 4.8	46.0 ± 12.8	31.6 ± 5.8	43.4 ± 14.0
SM									
2020	0	45.5 ± 15.4 *	26.2 ± 3.8	60.4 ± 13.2	66.6 ± 1.1	60.1 ± 8.1	61.3 ± 9.2	68.9 ± 3.7	65.4 ± 7.5
2019	1	38.8 ± 2.2	52.9 ± 15.8	60.7 ± 2.7	59.7 ± 3.1	54.3 ± 8.0	39.4 ± 13.2	63.6 ± 7.5	61.3 ± 5.3
2016	4	14.7 ± 5.5	22.6 ± 2.5	36.5 ± 16.6	54.8 ± 5.7	6.9 ± 4.5 *	31.1 ± 1.4	37.6 ± 13.0	54.8 ± 7.4
2012	8	26.6 ± 2.7	19.7 ± 7.3	61.1 ± 6.2	65.5 ± 2.1	19.7 ± 13.3	40.0 ± 14.9	38.5 ± 15.7	65.6 ± 1.6
2006	14	2.7 ± 2.0	10.3 ± 2.1	30.3 ± 2.4	30.5 ± 6.1	32.0 ± 10.4 *	14.7 ± 7.2	60.6 ± 4.5	50.1 ± 7.8
2000	20	12.3 ± 6.2	17.4 ± 8.4	47.2 ± 5.5 *	59.6 ± 4.8	14.0 ± 7.0	21.5 ± 2.7	44.8 ± 10.5	54.1 ± 6.4
1975	45	25.7 ± 6.4	28.1 ± 2.3	46.6 ± 15.2	55.5 ± 5.7	25.8 ± 4.2	20.4 ± 2.4	54.3 ± 8.6	62.5 ± 1.0
1910	110	25.7 ± 17.5	15.1 ± 5.2	50.2 ± 3.4	42.9 ± 12.0	58.9 ± 4.8	50.2 ± 10.0	67.1 ± 1.3	58.5 ± 4.1

Soil pH, soil moisture (SM), dissolved phosphorous (DP), dissolved nitrogen (DN), dissolved organic carbon (DOC) and dry matter (DM) on forest sites affected by high and low severe fires. * means significantly different to unburned sites according Tukey's honestly significant difference (HSD) at $p < 0.05$ and $p < 0.01$ ($n = 3$).

3.2. Status and Nematode Communities' Development after High and Low Fire Severity

Immediately after the fire, mean nematode abundance per g of soil was significantly reduced ($p < 0.01$) in comparison to the related unburned investigated site (Table 3). The value of nematode abundance increased gradually in the next year, however, remained significantly lower up to four years after the fire ($p < 0.01$, 0.05). Almost 10 times higher mean nematode abundance than the value immediately after the fire, 8 years post-fire was recorded (maximum value in followed chronosequence), without significant difference in comparison to unburned forest site. Then, nematode abundance decreased and values on burned sites were similar to those observed on all unburned sites in general. In contrast, the impact of fires of low severity on nematode abundance was observed only immediately after the event, when the value was significantly lower than that on the unburned site ($p < 0.05$). No significant differences in nematode abundance between FIR and CON sites were found 1 year after low severe burnt (Table 4).

A total of 115 nematode species were recorded in the sites affected by high severe fires. Altogether, 46, 34, 64, 64, 63, 69, 53, and 56 species were found at 0, 1, 4, 8, 14, 20, 45, and 110 years, respectively (Table S1). The mean number of species was significantly different in unburned sites ($p < 0.05$) immediately and 1 year after fire (Table 3). Among them, *Acrobeloides nanus, Plectus acuminatus, Wilsonema schuurmanstekhoveni, Microdorylaimus parvus,* and *Rhabditis* spp. belongs to the dominant (>10%) or subdominant (5–10%) for all chronosequence years (Table S1). Severe fire strongly affected the abundance of higher c-p groups of bacterivores, all carnivores, and several omnivores e.g., from genera *Prismatolaimus, Alaimus, Teratocephalus, Anatonchus, Clarkus* or *Aporcelaimellus* which disappeared or were rare in the soil immediately and 1 year after the event. Similarly, many species of the genus *Eudorylaimus* had low abundance (or miss) after burn, while relatively high number of juveniles of this genus since 1 year after the disaster has been found. Plant parasitic species *Malenchus bryophilus* (Pp_2) was found to be dominant (>10%) 8 and 45 years after the fire.

A total of 110 nematode species were identified in the sites affected by low severe fires. Altogether, 42, 46, 66, 70, 64, 69, 54, and 63 species were found within followed post-fire chronoseqence on burned sites (Table S2), however without considerable differences between FIR and CON sites for all chronosequence years (Table 4). Species *Acrobeloides nanus, Plectus acuminatus,* and *Wilsonema schuurmanstekhoveni* belong to the dominant (>10%) or subdominant (5–10%) for all chronosequence years on burned sites (Table S2). *Aphelenchoides minimus* was subdominant to 8 years post-fire than decreased.

Considering the nematode trophic groups, we recorded that bacterivores dominated the nematode communities with 46 identified species, followed by fungivores, plant parasites, omnivores, and carnivores at fire-affected sites (Table S1). The proportion of Ba nematodes significantly increased ($p < 0.05$) immediately after the fire (0, 1 year) comprising over 70% of the nematode community. With increasing chronosequence age, there was a considerable decrease of Ba abundance in soil, and no significant difference between FIR and CON sites was found since 4 years post-fire (Table 2). Reverse patterns at plant parasitic, omnivores, and carnivores have been observed. High severe fire did not considerably affect the abundance of fungivores, but within post-fire chronoseqence numbers of individuals of species belong to higher functional guilds (Fu_3-Fu_4) e.g., *Tylolaimophorus typicus, Diptheropthora communis* or *Tylencholaimellus mirabilis* increased. Bacterial-feeding nematodes with 42 identified species, dominated the nematode communities also in sites affected by low sever fires, followed by plant parasites, fungivores, omnivores, and carnivores (Table S2). With exception of plant parasites which were significantly less abundant 1 year after fire, mainly from genera *Helicotylenchus, Geocenamus, Criconema* and *Pratylenchus* (c-p3), no differences in proportion of trophic groups between FIR and CON sites were recorded during followed post-fire chronosequence (Table 4).

Table 3. Mean value (±S.D, $n = 6$) of nematode community indices taken from forest plots affected by high severe fires.

	Years from Fire															
	0		1		4		8		14		20		45		110	
	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON
Abundance (g^{-1})	5.00 ± 3.2 **	33.1 ± 13.1	10.1 ± 5.2 **	45.9 ± 15.7	33.5 ± 11.7 *	49.0 ± 5.6	95.5 ± 29.1	91.7 ± 21.3	42.8 ± 14.9	51.3 ± 15.2	44.2 ± 26.1	55.9 ± 24.9	58.2 ± 23.5	59.9 ± 20.4	36.6 ± 13.8	38.4 ± 7.3
H spp	2.98 ± 0.16 *	3.24 ± 0.15	2.40 ± 0.20 **	3.23 ± 0.12	3.19 ± 0.13	3.27 ± 0.17	3.25 ± 0.07	3.27 ± 0.19	3.38 ± 0.20	3.47 ± 0.08	3.20 ± 0.18	3.13 ± 0.17	3.14 ± 0.12	3.12 ± 0.32	3.20 ± 0.25	3.40 ± 0.04
Species number	26.8 ± 2.5 *	35.1 ± 5.1	19.8 ± 3.2 **	35.3 ± 3.6	37.8 ± 6.4	36.7 ± 5.2	38.0 ± 4.9	38.8 ± 6.1	38.8 ± 7.5	41.7 ± 2.4	35.8 ± 6.3	33.0 ± 6.0	33.7 ± 2.6	37.7 ± 4.6	35.7 ± 6.9	41.3 ± 3.7
Plant parasites (%)	1.4 ± 1.9 **	9.9 ± 1.7	0.6 ± 0.7 *	4.2 ± 0.7	6.2 ± 2.6	7.9 ± 4.5	17.4 ± 7.9	15.3 ± 6.9	6.7 ± 1.0	7.1 ± 0.3	4.6 ± 3.6	5.8 ± 3.0	20.6 ± 1.6	13.3 ± 5.5	10.8 ± 1.4	9.1 ± 1.0
Bacterivores (%)	74.9 ± 10.7 *	48.1 ± 5.9	70.5 ± 5.5 *	56.8 ± 4.9	57.4 ± 4.5	48.9 ± 9.9	51.4 ± 8.0	42.4 ± 8.2	51.5 ± 5.0	46.4 ± 7.4	56.3 ± 10.1	53.2 ± 8.1	44.5 ± 12.6	57.7 ± 8.4	50.1 ± 4.0	53.4 ± 4.1
Fungivores (%)	18.9 ± 11.7	22.6 ± 7.5	14.4 ± 5.2	22.2 ± 2.4	20.7 ± 6.8	21.2 ± 6.3	17.5 ± 4.9	25.8 ± 6.7	20.8 ± 3.3	27.5 ± 4.7	19.1 ± 6.6	23.4 ± 5.5	18.4 ± 8.6	16.1 ± 5.2	29.7 ± 3.6	23.2 ± 1.7
Omnivores (%)	4.8 ± 0.9 *	14.4 ± 3.8	14.3 ± 7.2	14.1 ± 4.1	13.4 ± 4.4	18.9 ± 6.8	10.2 ± 3.6	13.1 ± 4.0	15.2 ± 31	16.8 ± 1.9	15.7 ± 6.5	16.3 ± 6.2	11.6 ± 6.0	10.9 ± 3.1	8.3 ± 2.5	12.4 ± 3.7
Carnivores (%)	-	5.0 ± 2.5	-	2.6 ± 1.1	2.3 ± 1.2	3.4 ± 3.1	3.5 ± 1.9	3.4 ± 2.2	5.8 ± 2.4	4.1 ± 2.6	4.4 ± 1.5	1.4 ± 1.0	4.9 ± 1.6	2.1 ± 1.2	1.0 ± 1.0	1.8 ± 1.5
MI	2.13 ± 0.11 *	2.51 ± 0.18	2.27 ± 0.16 *	2.45 ± 0.18	2.29 ± 0.16 *	2.69 ± 0.18	2.39 ± 0.08	2.55 ± 0.13	2.61 ± 0.16	2.64 ± 0.11	2.63 ± 0.24	2.69 ± 0.19	2.69 ± 0.17	2.61 ± 0.11	2.36 ± 0.11	2.47 ± 0.14
PPI	2.44 ± 0.51	2.12 ± 0.09	2.54 ± 0.51	2.13 ± 0.24	2.28 ± 0.06	2.28 ± 0.27	2.14 ± 0.13	2.17 ± 0.16	2.15 ± 0.13	2.04 ± 0.06	2.33 ± 0.37	2.39 ± 0.22	2.07 ± 0.06	2.07 ± 0.08	2.25 ± 0.07	2.27 ± 0.21
CI	16.2 ± 11.3 *	54.7 ± 22.2	31.5 ± 14.4 *	52.8 ± 9.8	43.9 ± 15.5 *	71.8 ± 22.4	28.9 ± 11.1 *	67.4 ± 23.0	43.5 ± 21.3	53.6 ± 19.3	60.8 ± 28.9	73.1 ± 18.9	48.5 ± 25.6	49.5 ± 20.7	65.1 ± 7.8	56.1 ± 12.6
EI	60.5 ± 6.6 *	47.6 ± 6.9	39.9 ± 11.8	46.0 ± 16.2	39.7 ± 10.6	42.1 ± 10.3	55.0 ± 8.4	41.8 ± 10.3	45.5 ± 15.5	47.6 ± 6.0	31.7 ± 14.8	44.2 ± 11.9	39.9 ± 13.9	32.5 ± 6.5	40.7 ± 6.1	54.5 ± 9.1
SI	54.2 ± 5.3 *	68.5 ± 6.3	48.8 ± 15.8 *	66.3 ± 4.1	65.1 ± 7.7	71.9 ± 8.7	65.9 ± 1.9	66.6 ± 7.5	73.1 ± 7.9	73.4 ± 4.2	70.1 ± 7,1	76.9 ± 5.6	74.6 ± 8.25	69.5 ± 6.1	63.6 ± 8.1	68.4 ± 5.2
Total biomass	0.3 ± 0.2	1.7 ± 1.1	0.6 ± 0.4	2.9 ± 2.2	2.3 ± 1.4	1.5 ± 1.0	4.1 ± 1.3	2.9 ± 2.0	4.3 ± 2.1	4.1 ± 1.7	1.3 ± 0.6	1.7 ± 0.8	3.3 ± 1.5	2.0 ± 0.5	1.1 ± 1.0	2.2 ± 0.9

* means significantly different to unburned sites according Tukey's honestly significant difference (HSD) at $p < 0.05$ * and $p < 0.01$ ** ($n = 6$).

Table 4. Mean value (±S.D, $n = 6$) of nematode community indices taken from forest plots affected by low severe fires.

	Years from Fire															
	0		1		4		8		14		20		45		110	
	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON	FIR	CON
Abundance (g^{-1})	14.9 ± 2.9 **	36.8 ± 6.9	30.9 ± 11.5	45.9 ± 11.8	40.2 ± 7.8	44.7 ± 15.7	41.5 ± 18.4	80.6 ± 35.3	20.2 ± 10.6	18.8 ± 5.6	19.3 ± 6.4	22.3 ± 20.2	60.1 ± 17.6	66.8 ± 23.1	73.2 ± 19.0	82.8 ± 18.9
H spp	2.61 ± 0.4	3.18 ± 0.22	2.96 ± 0.20	3.10 ± 0.2	3.22 ± 0.33	3.33 ± 0.21	3.13 ± 0.40	3.86 ± 0.11	3.31 ± 0.22	3.30 ± 0.22	3.15 ± 0.24	3.14 ± 0.32	2.92 ± 0.25	3.16 ± 0.22	3.31 ± 0.07	3.35 ± 0.18
Species number	25.2 ± 4.1	33.0 ± 7.8	28.5 ± 3.6	33.0 ± 6.0	35.8 ± 7.6	43.5 ± 5.2	35.8 ± 9.5	42.0 ± 3.5	37.0 ± 6.8	37.5 ± 8.01	33.0 ± 6.8	35.2 ± 11.4	27.0 ± 6.3	34.3 ± 6.8	38.5 ± 2.0	42.2 ± 2.4
Plant parasites (%)	2.6 ± 2.0	5.4 ± 2.8	2.6 ± 1.7 *	14.7 ± 6.6	6.9 ± 2.1	11.4 ± 5.5	11.6 ± 5.3	6.2 ± 1.2	12.2 ± 5.2	12.0 ± 4.9	11.4 ± 2.9	13.6 ± 6.5	13.4 ± 7.3	9.2 ± 6.0	6.1 ± 3.0	4.9 ± 2.5
Bacterivores (%)	70.6 ± 10.6	53.0 ± 12.6	59.0 ± 5.4	45.9 ± 4.6	52.3 ± 5.8	42.5 ± 11.0	50.1 ± 5.1	45.2 ± 6.5	52.6 ± 8.1	52.1 ± 8.6	50.1 ± 13.7	48.6 ± 8.2	52.0 ± 6.3	55.1 ± 8.4	61.2 ± 4.1	60.2 ± 2.7
Fungivores (%)	16.4 ± 6.1	29.9 ± 6.9	20.3 ± 3.8	22.8 ± 4.2	25.6 ± 3.4	28.0 ± 9.2	22.4 ± 4.3	28.3 ± 6.7	18.8 ± 3.9	15.7 ± 2.9	22.2 ± 8.7	20.8 ± 4.7	23.6 ± 9.2	25.0 ± 4.1	18.1 ± 2.4	23.1 ± 3.2
Omnivores (%)	7.2 ± 4.1	8.7 ± 5.0	17.0 ± 5.8	12.3 ± 4.5	14.6 ± 5.3	13.9 ± 1.8	12.9 ± 4.8	17.4 ± 5.8	13.0 ± 3.8	16.7 ± 5.3	14.6 ± 5.7	14.5 ± 5.7	9.5 ± 1.7	9.2 ± 2.1	12.1 ± 2.1	12.2 ± 5.1
Carnivores (%)	3.3 ± 3.2	3.1 ± 0.6	1.1 ± 1.0	4.2 ± 1.6	2.4 ± 2.3	4.3 ± 1.2	3.0 ± 1.9	3.0 ± 1.5	3.4 ± 1.7	3.5 ± 2.2	1.6 ± 1.8	2.6 ± 2.4	1.7 ± 1.5	1.5 ± 1.3	2.5 ± 1.5	2.6 ± 2.4
MI	2.41 ± 0.13	2.27 ± 0.16	2.40 ± 0.20	2.48 ± 0.10	2.55 ± 0.18	2.60 ± 0.14	2.42 ± 0.15	2.62 ± 014	2.64 ± 0.14	2.59 ± 0.10	2.46 ± 0.25	2.54 ± 0.15	2.39 ± 0.12	2.47 ± 0.09	2.54 ± 0.03	2.44 ± 0.10
PPI	2.0 ± 0.0	2.0 ± 0.0	2.50 ± 0.35	2.10 ± 0.12	2.25 ± 0.14	2.16 ± 0.13	2.16 ± 0.13	2.25 ± 0.19	2.24 ± 0.25	2.23 ± 0.18	2.20 ± 0.12	2.27 ± 0.16	2.10 ± 0.14	2.18 ± 0.13	2.40 ± 0.31	2.39 ± 0.06
CI	38.6 ± 12.1	36.9 ± 17.7	27.7 ± 8.4	43.2 ± 18.9	57.5 ± 14.3	39.9 ± 19.6	42.4 ± 13.0	58.7 ± 19.8	63.1 ± 23.4	43.2 ± 21.6	39.7 ± 23.2	61.8 ± 32.0	59.2 ± 22.3	64.9 ± 26.7	51.9 ± 26.6	51.5 ± 25.2
EI	40.1 ± 13.1	57.9 ± 7.1	55.5 ± 9.8	48.8 ± 10.9	39.7 ± 4.5	52.9 ± 11.1	44.0 ± 4.7	45.2 ± 8.5	33.7 ± 8.8	42.6 ± 11.5	48.9 ± 9.9	38.1 ± 16.8	38.5 ± 8.5	40.9 ± 16.7	42.1 ± 11.9	42.1 ± 7.6
SI	62.9 ± 10.7	57.2 ± 9.8	65.9 ± 8.6	67.5 ± 3.3	66.2 ± 13.0	74.2 ± 8.5	61.2 ± 9.9	73.4 ± 7.6	70.4 ± 7.9	70.6 ± 4.9	64.0 ± 14.7	66.7 ± 8.8	55.9 ± 12.2	63.8 ± 9.2	69.5 ± 3.2	60.8 ± 8.5
Total biomass	0.7 ± 0.5 *	2.5 ± 0.7	2.3 ± 1.2	2.5 ± 1.4	2.1 ± 0.7	1.6 ± 0.8	2.1 ± 1.1	4.4 ± 3.4	0.6 ± 0.2	1.3 ± 1.1	0.9 ± 0.6	0.8 ± 0.8	1.2 ± 0.7	1.2 ± 0.7	3.6 ± 1.3	5.1 ± 2.5

* means significantly different to unburned sites according Tukey's honestly significant difference (HSD) at $p < 0.05$ * and $p < 0.01$ ** ($n = 6$).

3.3. *Nematode Community Indices and Faunal Analysis*

In sites affected by high severe fires, the values of H´spp, MI, CI, and SI were significantly lower than on unburned sites during the first four years post-fire ($p < 0.01$, 0.05) (Table 3). No significant differences in values of those indices between FIR and CON sites since 8 years were found. Values of EI showed the opposite pattern: they increased immediately after the fire, however, quickly decreased to be similar to unburned sites 1 year after burning. The fires of low severity did not cause considerable changes in the values of all nematode community indices = immediately after the event (Table 4).

The FIR sites affected by high severe fires had 50% of samples collected immediately and 1 year after the event in quadrat A and D, following the weighted faunal analysis by Ferris et al. (2001), and the food web was characterized as stressed or highly disturbed (Figure 1A), consistent with the mean EI and SI values (Table 3). In contrast, all samples from the control plots are depicted in quadrats B and C, which represent a maturing or structured food web, low to moderate disturbance, and balanced/fungal decomposition of organic matter (Figure 1C). The majority of samples collected from sites affected by fires of low severity, as well as their controls are depicted in quadrats B and C, suggesting few impacts of slight burn on nematode communities (Figure 1B,D).

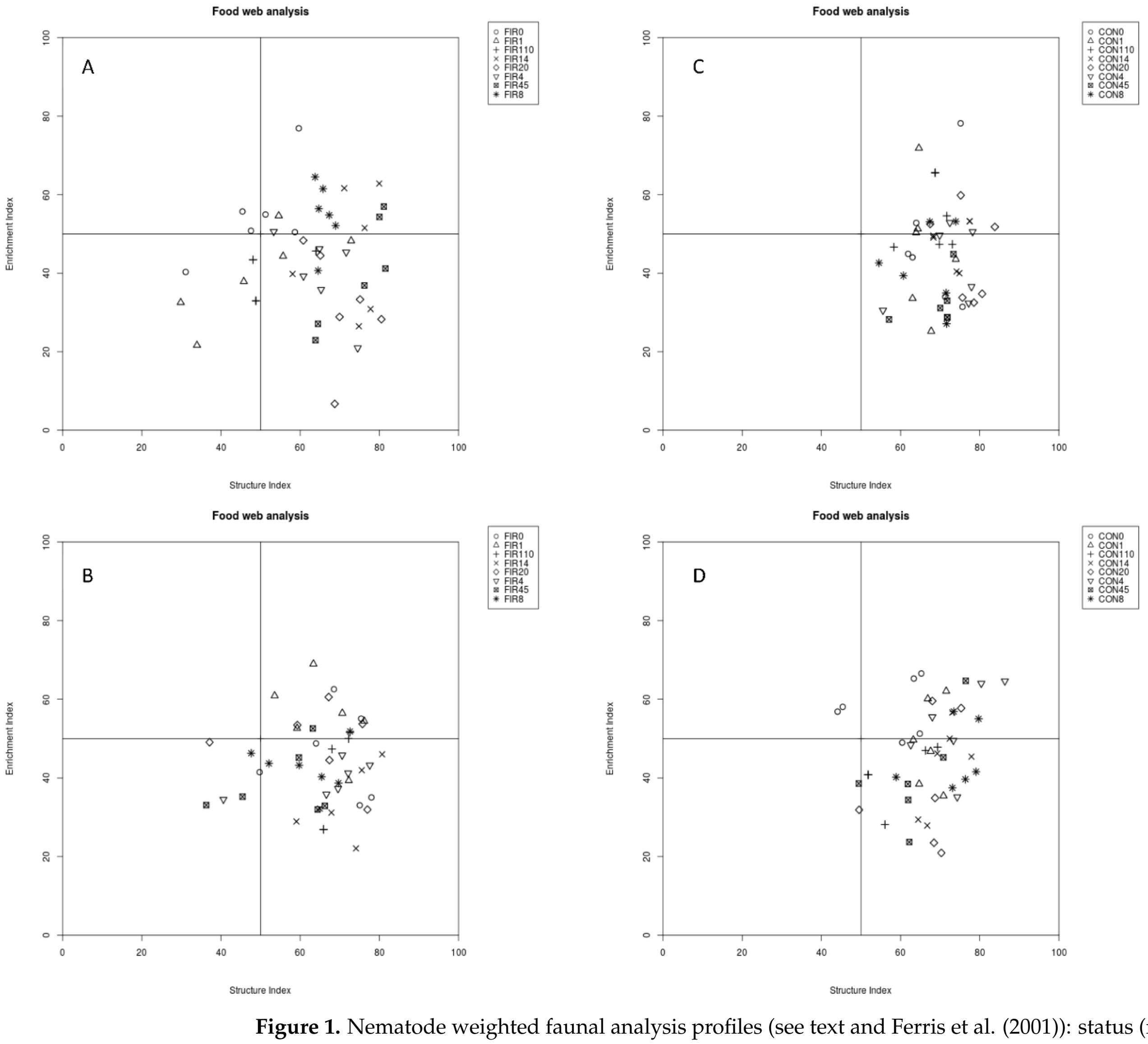

Figure 1. Nematode weighted faunal analysis profiles (see text and Ferris et al. (2001)): status (recovery) of soil nematode communities in chronosequence 0–110 y post-fire depending on fire severity ((**A**), high; (**B**), low; (**C**,**D**) related control plots) along axes of structure (SI) and enrichment (EI).

3.4. Interaction between Soil Properties, Vegetation Composition, and Nematode Functional Guilds

Regarding soil properties, an RDA identified a positive correlation between the abundance of Ba_1, $Ba_{2,}$ and Ba_3 nematodes and values of soil pH, soil moisture, and content of DP, while negatively correlated with dry matter content (Figure 2A). Ba_4 nematodes negatively correlated with the content of DOC but tend to have a higher abundance on control and sites affected by low-severe wildfires. Fungivores of cp2 positively correlated with soil acidity, while negative interaction between Fu_3 and Fu_4 and DN, DOC, and DP content was recorded (Figure 2B). Nematode functional guild of higher trophic groups ($Ca_{2–5}$ and $Om_{4–5}$) was found in positive correlation with soil pH and moisture content and tend to have a higher abundance on control sites and sites affected by low severe fires (Figure 3A). Plant parasitic nematode of Pp_2 negatively correlated with DOC and DN, while Pp_3 with DP (Figure 3B).

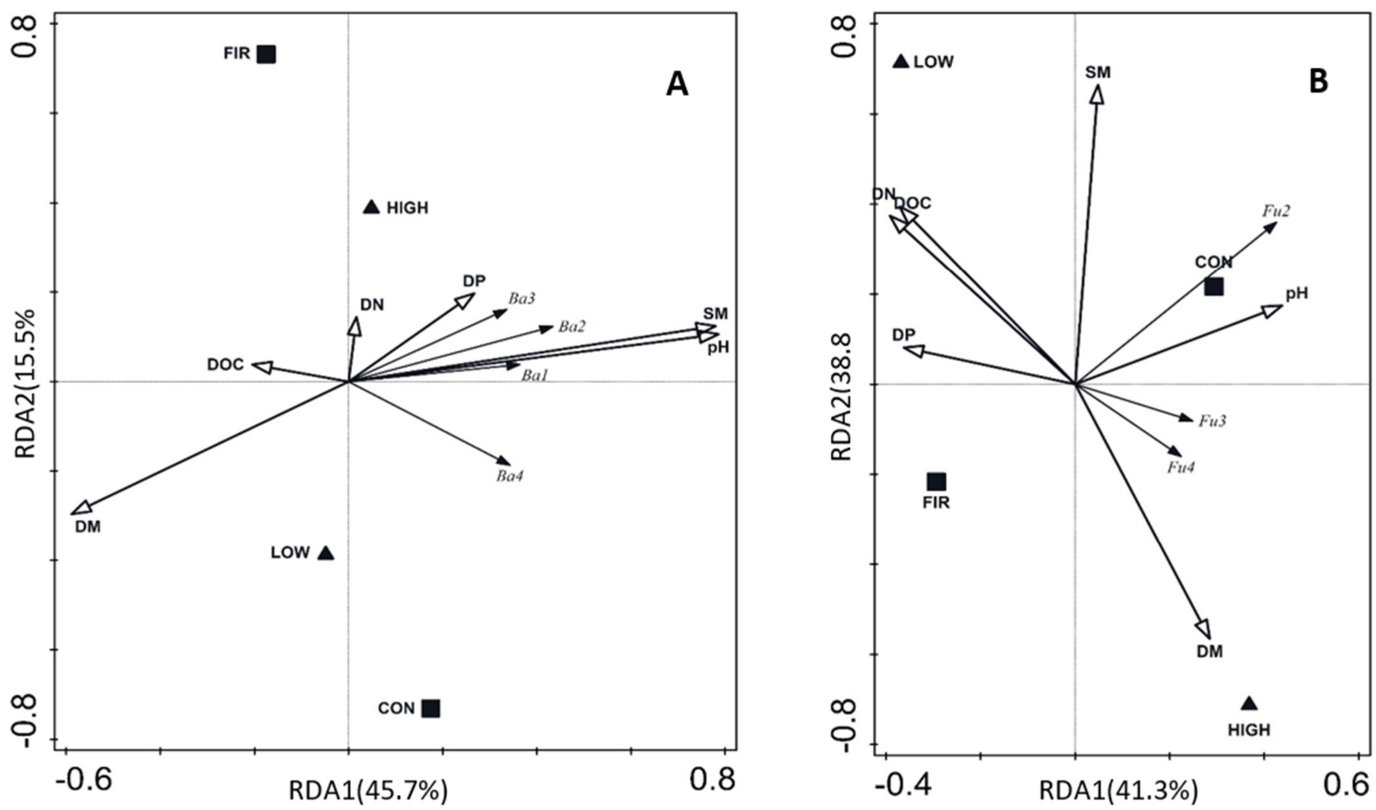

Figure 2. Ordination diagram based on RDA of the data for the total abundance of bacterivorous (**A**) and fungivorous (**B**) nematode feeding guild constituting c−p1, c−p2, c−p3, c−p4, and the environmental variables: soil pH, soil moisture (SM), dissolved phosphorous (DP), dissolved nitrogen (DN), dissolved organic carbon (DOC), and dry matter (DM) on forest sites affected by high and low severity fires.

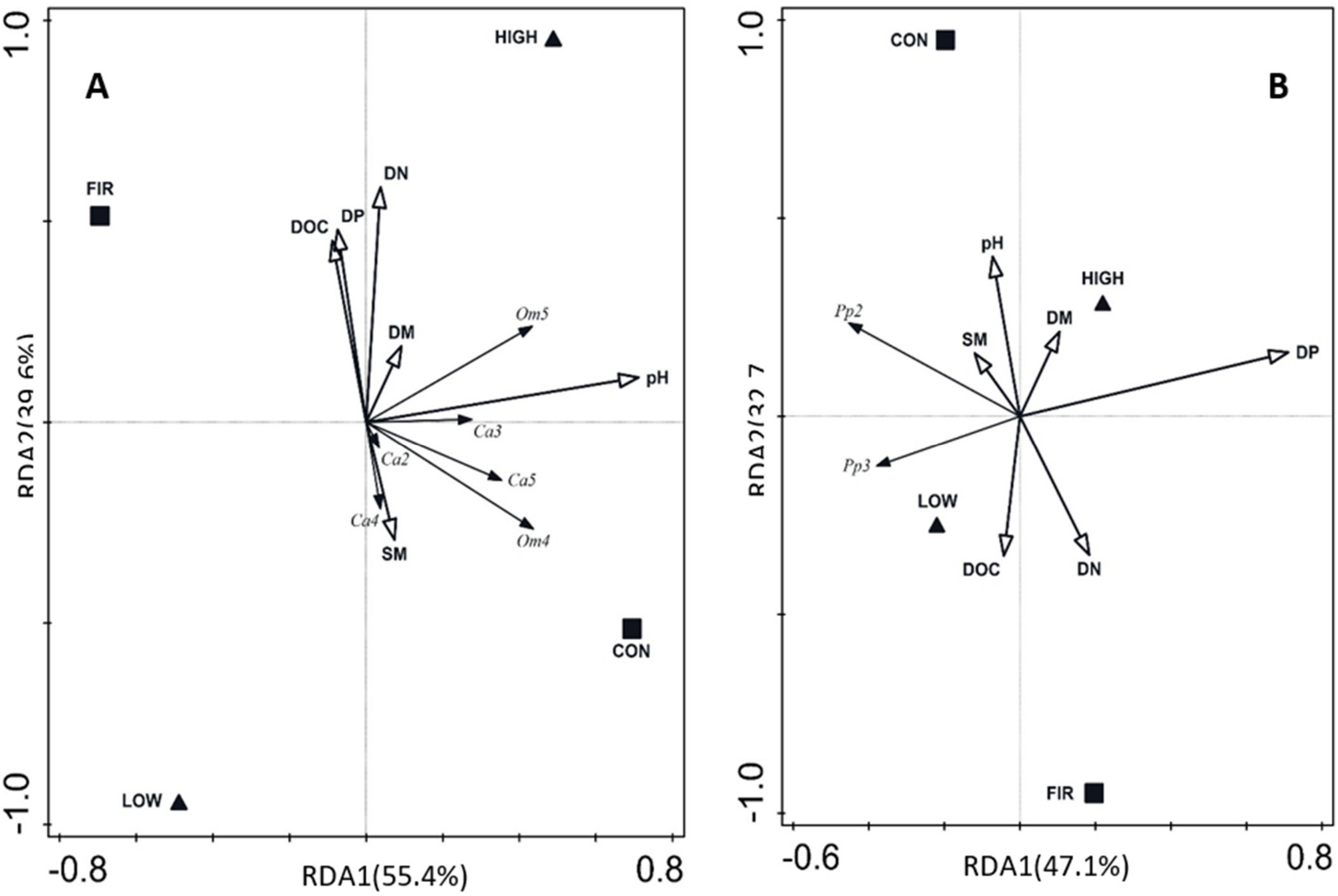

Figure 3. Ordination diagram based on RDA of the data for the total abundance of omnivorous and carnivorous (**A**) and (**B**) plant parasitic nematodes feeding guilds, constituting c−p2, c−p3, c−p4, c−p5, and the environmental variables: soil pH, soil moisture (SM), dissolved phosphorous (DP), dissolved nitrogen (DN), dissolved organic carbon (DOC), and dry matter (DM) on forest sites affected by high and low severe fires.

Regarding vegetation, an RDA analysis revealed a positive interaction between abundances of bacterivore and fungivore nematode functional guilds ($Ba_{1–4}$, $Fu_{2–4}$) and various species of mosses mainly on unburned sites (Figure 4). Plant parasites of Pp_2 (represented mainly by facultative parasites of Tylenchida) and obligate plant parasites (Pp_3) positively correlated with the presence of moss *Campylopus flexuosus* and tend to have higher numbers under a dense layer of *Vaccinum myrtillus.* A negative correlation between populations of plant parasites and herbs, e.g., grasses *Calamagrostis villosa* and *Avenella flexuosa* was recorded on burned sites. The species of tree layer were found to be not an important factor influencing Ba, Fu, and Pp nematode functional guilds, except *Betula pendula* which seems to positively affect the abundance of Ba_3, Ba_4, $Pp_{3,}$ and Fu_2 nematodes.

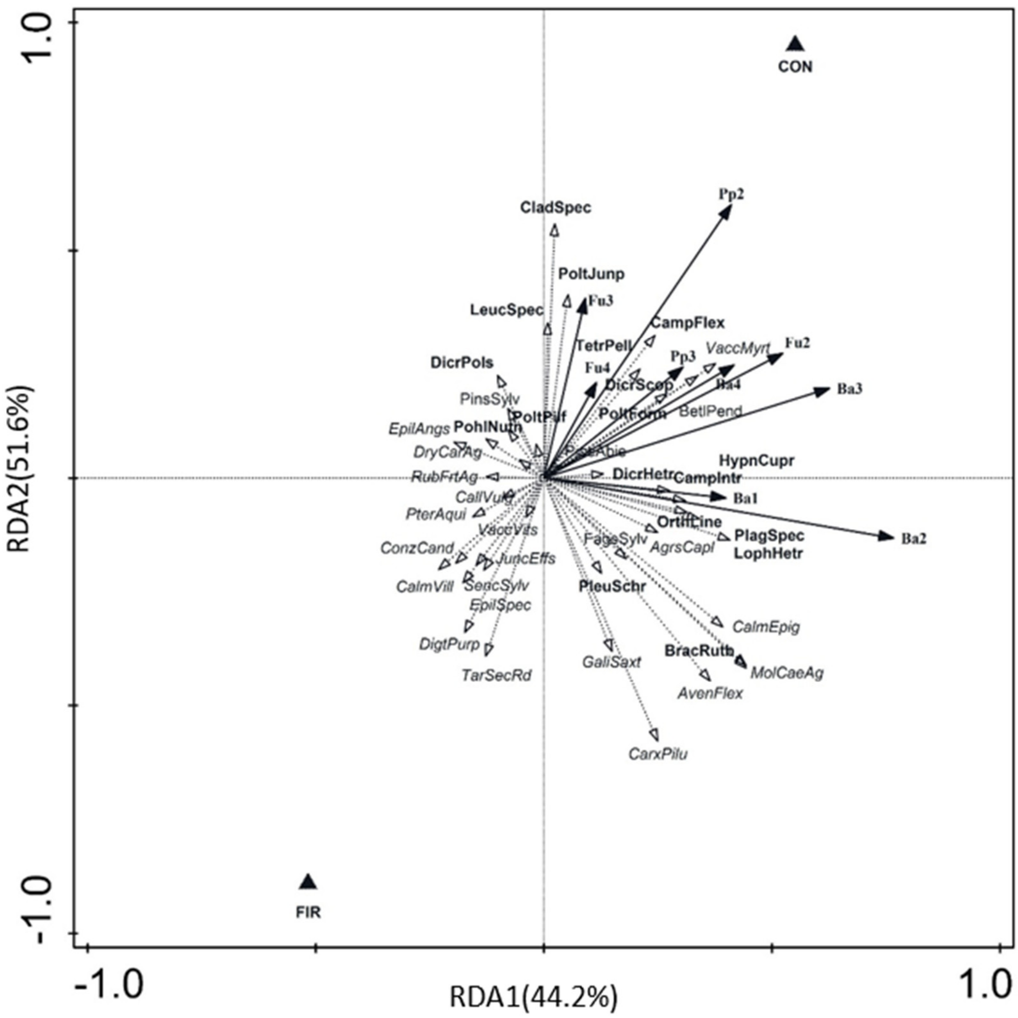

Figure 4. Ordination diagram based on RDA illustrating plant species (trees—normal, herbs—italics, mosses—bold) and nematode functional guilds composition of Ba, Fu, and Pp nematodes on forest sites affected by high (HIGH) and low (LOW) severe fires. Plants abbreviations used: **trees**—*BetlPend—Betula pendula, FagsSylv—Fagus sylvatica, PiceAbie—Picea abies, PinsSylva—Pinus sylvestris;* **herbs**—*AgrsCapl—Agrostis capillaris, AvenFlex—Avenella flexuosa, CalmEpig—Calamagrostis epigejos, CalmVill—Calamagrostis villosa, CallVulg—Calluna vulgaris, CarxPilu—Carex pilulifera, ConzCand—Conyza canadesis, DigtPurp—Digitatis purpurea, DryCarAg—Dryopteris carthusiana agg., EpilAngs—Epilobium angustifolium, EpilSpec—Epilobium species, GaliSaxt—Galium saxatile, JuncEffs—Juncus effusus, MolCaeAg—Molinia caerulea agg., PterAqui—Pteridium aquilinum, RubFrtSp—Rubus fruticosus agg., SencSylv—Senecio sylvaticus, TarSecRd—Taraxacum sect. Ruderalia, VaccMyrt—Vaccinium myrtillus, VaccVits—Vaccinium vitis-idaea;* **mosses**—*BracRutb—Brachythecium rutabulum, CampFlex—Campylopus flexuosus, CampIntr—Campylopus introflexus, CladSpec—Cladonia species, DicrHetr—Dicranella heteromalla, DicrPols—Dicranum polysetum, DicrScop—Dicranum scoparium, HypnCupr—Hypnum cupressiforme, LeucSpec—Leucobryum species, LophHetr—Lophocolea heterophylla, OrthLine—Orthodontium lineare, PlagSpec—Plagiothecium species, PleuSchr—Pleurozium schreberi, PohlNutn—Pohlia nutans, PoltForm—Polytrichum formosum, PoltJunp—Polytrichum juniperinum, PoltPilf—Polytrichum piliferum, TetrPell—Tetraphis pellucida.* Ba = bacterivores; Fu = fungivores; Pp = plant parasites; 2−4 colonizers-persisters value.

4. Discussion

Forest fires may have serious impacts on the aboveground biodiversity and soil abiotic and biological properties [16]. The extent of these impacts depends mainly on fire severity which, in turn, is controlled by several environmental factors that affect the combustion process, such as amount, nature, and moisture of live and dead fuel, air temperature and humidity, wind speed, and topography of the site. Essentially, two types of forest fires exist: prescribed (controlled) and wildfires. Prescribed burning is a standard forestry practice to reduce fuel levels from the naturally accumulated forest floor or slash following tree harvest with the intention of minimizing the extent and severity of potential wildfires. In contrast, wildfires generally occur in the presence of an abundant and dry fuel load and thus are often very severe [47].

Numerous findings on the effects of fire on physicochemical soil properties, nutrient cycling, and transformation are available in the literature [48–51]. However, organisms, especially edaphic are much more sensitive to burnt than abiotic parameters and are typically used to measure the magnitude of fire events. Overall, responses of soil or litter-dwelling organisms e.g., macroinvertebrates, arthropods mesofauna or microbes to fires differing in their severity levels have been previously studied [16,52,53]. However, the level or rate of community restoration after fires of different severity with increasing time post-fire in a comprehensive study is rarely documented [18,33].

We assessed the immediate effect of a wildfire of two different severities (low vs. high) on the structure of soil nematode communities in coniferous forests of Bohemian Switzerland National Park. We also evaluated and compared the level as well as the rate of nematode communities' recovery in post-fire chronosequence regarding the different fire severity. With small exceptions recorded immediately after burn (mean nematode abundance, total biomass), the low severe fires had no impacts on the structures of nematode communities. Moreover, the structures of nematode communities were found to be stable on sites affected by low severe wildfires, without considerable fluctuations in comparison to unburned sites during followed chronosequence. On the contrary, nematode communities responded considerably to fires of high severity. The significant changes i.e., a decrease of mean nematode abundance, plant parasites, omnivores and predators, species number, and nematode diversity, the values of CI, SI, MI, but an increase in the number of bacterivores and EI were recorded immediately after the fire. Such status, one year after a fire of high severity has been also observed. Partial recovery of soil nematode communities four years after a fire was visible, nevertheless, nematode abundance, MI, and CI values remained significantly lower on burned than unburned sites. Full recovery of nematode communities when similar on both, burned and unburned sites, 14 years after disruption, were found.

Our results partially agree with those of previous investigations of the immediate impacts of fire on soil nematode communities but are in contradiction at several points. For example, ref. [28] in pine forests found that fire increased the abundance of bacterial-feeding nematodes, but nematode trophic diversity, generic diversity, generic richness, and values of maturity indices decreased, while total nematode abundance was not changed which supports the findings after fires in oak forests [54], arid juniper savanna [30] or Mediterranean and broadleaves forest [32]. Considerable higher abundance of bacterivorous nematodes 12, 24, and 36 months after the fire in the spruce forest of High Tatra National Park was recorded [29], while eight years after this fire, bacterivores abundance returned to the level of those on reference control site [31]. Similarly, [32] reported an increase in the abundance of bacterial-feeding nematodes, which may reflect an increasing availability of bacterial prey after burnt Mediterranean and broadleaves forests, contradicting the findings by [55] immediately after the fire on semiarid grasslands. On the other hand, a reduction of several fungal feeding and plant parasitic nematodes was found after fire in forests as well as grassland [32,55], in agreement with our results from coniferous forests but only for plant parasites. Little data is available about the nematodes of the higher trophic groups, i.e., omnivores and predators, and their responses to fire impact. A negative effect of burning resulting in a decrease of the omnivore-predator abundance in burned compared to unburned forests was reported [28], consistent with our current observations immediately after a severe fire. Similarly, wildfires in a spruce forest of High Tatra National Park have had dramatic negative impacts on the abundance of predaceous nematodes [29], which did not regenerate eight years post-fire [31]. In contrast, omnivorous nematodes were found not to be affected by fire in the above-mentioned spruce forest, inconsistent with our current results.

The reported contradictory answers of nematode communities and particular trophic groups to fires among previous studies as well as our current data are probably due to differences in fire severities and the direct effect of the heat by fire on the soil organisms [47]. A study by [56] revealed, that fires with light severity had a slight impact on soil microarthropods and their total abundance was recovered within one year after the events. After fires with strong severity, all mesofauna groups, i.e., Collembola, Oribatida, Protura, Mesostigmata needed more than five years to recover as regards abundance and species number. Moreover, individual soil fauna species had different response patterns to fire. Surface-living species were more subjected to fire, than species living deeper in the soil, and although surface-living species have generally better dispersal ability, their recovery was probably delayed by the destruction of the topsoil resources and habitats [56]. This suggests that the spatial (vertical) distribution of soil nematode taxa and trophic groups within studied wildfire-affected ecosystems could be an important factor in the impact of fire-produced heat on given nematode communities [57,58].

Additionally, wildfire-disturbed forests are highly different among and within forests mainly in terms of forest type, soil type and profile depth, tree and tree species composition as well as ground vegetation composition which affect the quality and quantity of organic matter inputs to the soil food web, etc. Such different forests thus have specific compositions of aboveground, as well as edaphic biota including nematodes [11,59]. However, how various nematode taxa (genera and/or species), not trophic groups answer to a specific type of disturbance is little known. For example, ref. [26] found that cultivation reduced abundances of *Diphtherophora, Prismatolaimus,* and *Tylenchorhynchus.* Application of synthetic fertilizers reduced numbers of *Eurorylaimus* [60] or *Plectus* [26] *while* application of organic fertilizers resulted in an increased number of *Eudorylaimus* [61], *Cruznema, Mesorhabditus, Mesodorylaimus,* and *Nygolaimus* nematodes [26]. Heavy metals soil contamination decreased abundance of *Plectus, Alaimus, Eumonhystera, Tylencholaimus, Aporcelaimellus, Eudorylaimus, Microdorylaimus, Mesodorylaimus, Clarkus, Mylonchulus,* and many others nematode taxa in the study by [62]. Invasion by *Fallopia japonica* into ruderal forests reduced a number of primary consumers, i.e., plant parasites of the *Helicotylenchus, Rotylenchus, Geocenamus,* or *Paratylenchus*, but bacterivorous nematodes *Acrobeloides, Plectus, Cephalobus* or *Wilsonema* were not affected by invasion [63].

In our study, the nematodes of the genera *Acrobeloides*, *Plectus,* and *Wilsonema* belonged to the dominant nematode taxa among bacterivores in sites affected by both, low and high severity fires since time immediately after burn as well as during followed chronosequence. Similar, ref. [28] recorded a high abundance of bacterivorous nematodes of the genus *Acrobeloides* or *Cephalobus* in soils shortly after fire. *Acrobeloides, Cephalobus, Wilsonema* and *Plectus* nematodes were considerably more abundant in burned compared to unburned sites immediately after the fire also in the study by [29]. This suggests that above-mentioned bacterivore taxa are able survive fire or even are not so sensitive to heat. In contrast, nematode taxa of higher c-*p* values (3–5) as bacterivores *Prismatolaimus, Alaimus, Teratocephalus*, predators *Anatonchus* and *Clarkus* or omnivores *Aporcelaimellus* and *Eudorylaimus* were decreased immediately after high severe fire in our study. This contradict the findings by [64] where *Eudorylaimus* and *Mesodorylaimus* were not adversely affected by controlled burning of pine forest sites in Florida. Instead, each of them increased within six weeks of the burning possibly due to increases in potentially prey, such as *Acrobeloides,* in accordance with our findings, where relative high number of *Eudorylaimus* juveniles in the soil one year after fire suggest its ability to quickly regenerate after burnt. Similar, only *Eudorylaimus* survived in the soils after solarization in the study by [65], nevertheless that belong to c-p4 groups as typical k-strategist [66]. This suggests relative resilience of this nematode genus to higher soil heat and fast recovery after disturbance by heat produced by fire when available food sources, while sensitivity to other types of disruption [26,61].

In our study, the negative impact of both, low and high severe wildfires on the population of obligate plant parasitic genera such as *Helicotylenchus, Geocenamus, Criconema* and *Pratylenchus* (c-p3) has been observed, which were considerably less abundant or disappeared immediately after the event but increase with increasing chronoseqence age. Moreover, a negative correlation between populations of Pp_3 and Pp_2 and herbs, e.g., grasses *Calamagrostis villosa* and *Avenella flexuosa* were recorded on burned sites. Similar [55] reported a clear impact of the fire on the population of plant parasitic nematodes in grasslands, which were less abundant in burned sites two months after the fire and over the entire study of four years after the event.

Refs. [28,32] also recorded fewer plant parasitic nematodes in burned forest soils shortly after the fire. This may be explained by the shift in vegetation cover after fires, as stated [32]. Co-called pyrophytic plants which prevail in the burnt areas e.g., (*Calamagrostis arundinacea* and *Chamerion angustifolium*) offer food resources of lower quality for these nematodes, or these resources are simply not used. This disagrees with previous findings by [29] from spruce forests affected by the fire with *Calamagrostis villosa*, *Avenella flexuosa*, and *Chamerion angustifolium* dominant post-fire herbs. On burned plots, a similar population of plant parasites in terms of abundance and species as at unburned plots was found two years, even eight years after fire [31]. However, Pp2 nematodes (represented mainly by facultative parasites of Tylenchida) and obligate plant parasites (Pp3) positively correlated with the presence of *Vaccinum myrtillus* with a dense layer of moss *Campylopus flexuosus* on unburned sites. Similar, undisturbed spruce forest sites, as well as sites where tree layers, but not *V. myrtillus* disturbed by heavy windstorm, had considerably more abundant populations of plant parasites than sites disturbed by wildfire in the study by [29,31].

It seems that plant parasitic nematode responses to fire may be relatively site, as well as nematode species-specific, depending on the responses of individual plant species in the various forests.

5. Conclusions

Wildfires are unexpected events of various duration, intensity, or severity. Given this fact, ecologists can evaluate the impact of wildfires on ecosystems by collecting the data from burned sites merely after events. Mostly, such data are compared to those from unburned stands of affected ecosystem hoping, that on both sites were relatively similar before fire. The impact of forest wildfires in coniferous forest in the Bohemian Switzerland National Park on communities of soil nematodes as well as recovery time considerable depended upon fire severity. On forest sites affected by the low severe wildfires, the nematode communities showed no significant changes in comparison to unburned sites since time immediately after event, as well as any fluctuation during following 110 years chronosequence. In contrast, high severe wildfire reduced mean nematode abundance, number of plant parasites, omnivores and predators, species number and nematode diversity, values of CI, SI, MI for a period of at least one year as compared to unburned forests. Total nematode abundances, the values of MI and CI remained considerably reduced for a period of at least four years after high severe wildfire, while nematode communities needed fourteen years after wildfire to full recovery. Several bacterivore taxa as *Acrobeloides, Plectus* or *Wilsonema* were able survive fire or even are not so sensitive to heat, cause considerably increase of bacterial feeding nematodes abundance. Plant parasitic nematode taxa, e.g., *Helicotylenchus, Geocenamus, Criconema,* and *Pratylenchus* were found to be in negative correlation to post-fire dominant grasses on burned sites. Together our results suggest that fire severity is a decisive factor explaining direct impact and recovery rate of soil nematode communities. This factor should always be considered when fire effects on soil organisms would be evaluated in forthcoming studies.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14121116/s1, Table S1: Check list of nematode species in sites affected by high severe fires (abundance, n = 6); Table S2: Check list of nematode species in sites affected by low severe fires (abundance, n = 6).

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References

1. Bardgett, R.D.; Van Der Putten, W.H. Belowground biodiversity and ecosystem functioning. *Nature* **2014**, *515*, 505–511. [CrossRef] [PubMed]
2. Hoogen, J.; Geisen, S.; Routh, D.; Ferris, H.; Traunspurger, W.; Wardle, D.A.; Crowther, T.W. Soil nematode abundance and functional group composition at a global scale. *Nature* **2019**, *572*, 194–198. [CrossRef] [PubMed]
3. Sánchez-Moreno, S.; Ferris, H. Suppressive service of the soil food web: Effects of environmental management. *Agric. Ecosyst. Environ.* **2007**, *119*, 75–87. [CrossRef]
4. Xiaoyun, C.; Huixin, L.; Feng, H.; Manqiang, L. Effect of bacterivorous nematode on soil microbial biomass and microbiocoenosis. *Acta Ecol. Sin.* **2004**, *24*, 2825–2831.
5. Perry, R.N.; Moens, M. *Plant Nematology*; CAB International: Wallingford, UK, 2013.
6. Chen, J.; Ferris, H. The effects of nematode grazing on nitrogen mineralization during fungal decomposition of organic matter. *Soil Biol. Biochem.* **1999**, *31*, 1265–1279. [CrossRef]
7. Carrascosa, M.; Sánchez-Moreno, S.; Alonso-Prados, J.L. Relationships between nematode diversity, plant biomass, nutrient cycling and soil suppressiveness in fumigated soils. *Eur. J. Soil Biol.* **2014**, *62*, 49–59. [CrossRef]
8. Jiang, Y.; Qian, H.; Wang, X.; Chen, L.; Liu, M.; Li, H.; Sun, B. Nematodes and microbial community affect the sizes and turnover rates of organic carbon pools in soil aggregates. *Soil Biol. Biochem.* **2018**, *119*, 22–31. [CrossRef]
9. Ferris, H. Contribution of nematodes to the structure and function of the soil food web. *J. Nematol.* **2010**, *42*, 63.
10. Melakeberhan, H.; Maung, Z.; Lartey, I.; Yildiz, S.; Gronseth, J.; Qi, J.; Adjei-Gyapong, T. Nematode community-based soil food web analysis of Ferralsol, Lithosol and Nitosol soil groups in Ghana, Kenya and Malawi reveals distinct soil health degradations. *Diversity* **2021**, *13*, 101. [CrossRef]
11. Renčo, M.; Gömöryová, E.; Čerevková, A. The effect of soil type and ecosystems on the soil nematode and microbial communities. *Helminthologia* **2020**, *57*, 129. [CrossRef]
12. Dale, V.H.; Joyce, L.A.; McNulty, S.; Neilson, R.P.; Ayres, M.P.; Flannigan, M.D.; Wotton, B.M. Climate change and forest disturbances. *BioScience* **2001**, *51*, 723–734. [CrossRef]
13. Zaitsev, A.S.; Gongalsky, K.B.; Malmström, A.; Persson, T.; Bengtsson, J. Why are forest fires generally neglected in soil fauna research? A mini-review. *Appl. Soil Ecol.* **2016**, *98*, 261–271. [CrossRef]
14. Pausas, J.G.; Keeley, J.E. A burning story: The role of fire in the history of life. *BioScience* **2009**, *59*, 593–601. [CrossRef]
15. Mantoni, C.; Di Musciano, M.; Fattorini, S. Use of microarthropods to evaluate the impact of fire on soil biological quality. *J. Environ. Manag.* **2020**, *266*, 110624. [CrossRef]
16. Castro-Huerta, R.; Morales, C.; Gajardo, J.; Mundaca, E.A.; Yáñez, M. Soil mesofauna responses to fire severity in a Sclerophyllous Forest in central Chile. *Forests* **2021**, *12*, 1444. [CrossRef]
17. Keeley, J.E. *Ecological Foundations for Fire Management in North American Forest and Shrubland Ecosystems*; US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2009; Volume 779.
18. Wikars, L.O.; Schimmel, J. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *For. Ecol. Manag.* **2001**, *141*, 189–200. [CrossRef]
19. García-Carmona, M.; García-Orenes, F.; Mataix-Solera, J.; Roldán, A.; Pereg, L.; Caravaca, F. Salvage logging alters microbial community structure and functioning after a wildfire in a Mediterranean forest. *Appl. Soil Ecol.* **2021**, *168*, 104130. [CrossRef]
20. Vourlitis, G.; Steinecke, D.; Martinez, T.; Konda, K.; Rendon, R.; Hall, V.; Sethuraman, A. Fire and post-fire management alters soil microbial abundance and activity: A case study in semi-arid shrubland soils. *Appl. Soil Ecol.* **2022**, *171*, 104319. [CrossRef]
21. Háněl, L.; Čerevková, A. Species and genera of soil nematodes in forest ecosystems of the Vihorlat Protected Landscape Area, Slovakia. *Helminthologia* **2010**, *47*, 123–135. [CrossRef]
22. Renčo, M.; Čerevková, A.; Gömöryová, E. Soil nematode fauna and microbial characteristics in an early-successional forest ecosystem. *Forests* **2019**, *10*, 888. [CrossRef]

23. Čerevková, A.; Renčo, M.; Miklisová, D.; Gömöryová, E. Soil Nematode Communities in Managed and Natural Temperate Forest. *Diversity* **2021**, *13*, 327. [CrossRef]
24. Bloemers, G.F.; Hodda, M.; Lambshead, P.J.D.; Lawton, J.H.; Wanless, F.R. The effects of forest disturbance on diversity of tropical soil nematodes. *Oecologia* **1997**, *111*, 575–582. [CrossRef]
25. Renčo, M.; Čerevková, A. Windstorms as mediator of soil nematode community changes: Evidence from European spruce forest. *Helminthologia* **2017**, *54*, 36–47. [CrossRef]
26. Zhao, J.; Neher, D.A. Soil nematode genera that predict specific types of disturbance. *Appl. Soil Ecol.* **2013**, *64*, 135–141. [CrossRef]
27. Bongers, T.; Ferris, H. Nematode community structure as a bioindicator in environmental monitoring. *Trends Ecol. Evol.* **1999**, *14*, 224–228. [CrossRef] [PubMed]
28. Pen-Mouratov, S.; Ginzburg, O.; Whitford, W.G.; Steinberger, Y. Forest fire modifies soil free-living nematode communities in the Biriya Woodland of Northern Israel. *Zool. Stud.* **2012**, *51*, 1018–1026.
29. Čerevková, A.; Renčo, M.; Cagáň, L. Short-term effects of forest disturbances on soil nematode communities in European mountain spruce forests. *J. Helminthol.* **2013**, *87*, 376–385. [CrossRef]
30. Whitford, W.G.; Pen-Mouratov, S.; Steinberger, Y. The effects of prescribed fire on soil nematodes in an arid juniper savanna. *Open J. Ecol.* **2014**, *4*, 66–75. [CrossRef]
31. Renčo, M.; Čerevková, A. Long-term effects of a wildfire on the soil nematode communities in the spruce forest ecosystem of High Tatra National Park. *Int. J. Wild. Fire* **2015**, *24*, 702–711. [CrossRef]
32. Butenko, K.O.; Gongalsky, K.B.; Korobushkin, D.I.; Ekschmitt, K.; Zaitsev, A.S. Forest fires alter the trophic structure of soil nematode communities. *Soil Biol. Biochem.* **2017**, *109*, 107–117. [CrossRef]
33. Malmström, A.; Persson, T.; Ahlström, K. Effects of fire intensity on survival and recovery of soil microarthropods after a clearcut burning. *Can. J. For. Res.* **2008**, *38*, 2465–2475. [CrossRef]
34. Seller, U.; Ebner, K.; Wild, J. *Informační List K Projektu Cíl 3 "Historický Vývoj Lesa"*; Technische Universität Dresden: Dresden, Germany, 2011.
35. Bogusch, P.; Blažej, L.; Trýzna, M.; Heneberg, P. Forgotten role of fires in Central European forests: Critical importance of early post-fire successional stages for bees and wasps (Hymenoptera: Aculeata). *Eur. J. For. Res.* **2015**, *134*, 153–166. [CrossRef]
36. Cobb, N.A. Nematodes of the slow sand filter-beds of American cities. *Contrib. Sci. Nematol.* **1918**, *7*, 189–212.
37. Baermann, G. Eine einfache methode zur auffindung von Ancylostomum (Nematoden) larven in erdproben. *Geneeskd Tijdschr Ned Indie* **1917**, *57*, 131–137.
38. Seinhorst, J.W. On the killing, fixation and transferring to glycerin of nematodes. *Nematologica* **1962**, *8*, 29–32. [CrossRef]
39. Murphy, J.; Riley, J.P. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* **1962**, *27*, 31–36. [CrossRef]
40. Yeates, G.W.; Bongers, T.; De Goede, R.G.; Freckman, D.W.; Georgieva, S. Feeding habits in soil nematode families and genera—An outline for soil ecologists. *J. Nematol.* **1993**, *25*, 315.
41. Sieriebriennikov, B.; Ferris, H.; de Goede, R.G. NINJA: An automated calculation system for nematode-based biological monitoring. *Eur. J. Soil Biol.* **2014**, *61*, 90–93. [CrossRef]
42. Shannon, C.E.; Weaver, W. *The Mathematical Theory of Communication*; University of Illinois Press: Urbana, IL, USA, 1949.
43. Bongers, T. The maturity index: An ecological measure of environmental disturbance based on nematode species composition. *Oecologia* **1990**, *83*, 14–19. [CrossRef]
44. Yeates, G.W. Modification and qualification of the nematode maturity index. *Pedobiologia* **1994**, *38*, 97–101.
45. Ferris, H.; Bongers, T.; de Goede, R.G. A framework for soil food web diagnostics: Extension of the nematode faunal analysis concept. *Appl. Soil Ecol.* **2001**, *18*, 13–29. [CrossRef]
46. ter Braak, C.J.; Šmilauer, P. *Canoco Reference Manual and User's Guide: Software for Ordination, Version 5.0*; Microcomputer Power: Ithaca, NY, USA, 2012.
47. Certini, G. Effects of fire on properties of forest soils: A review. *Oecologia* **2005**, *143*, 1–10. [CrossRef] [PubMed]
48. Ulery, A.L.; Graham, R.C.; Amrhein, C. Wood-ash composition and soil pH following intense burning. *Soil Sci.* **1993**, *156*, 358–364. [CrossRef]
49. Arocena, J.M.; Opio, C. Prescribed fire-induced changes in properties of sub-boreal forest soils. *Geoderma* **2003**, *113*, 1–16. [CrossRef]
50. González-Pérez, J.A.; González-Vila, F.J.; Almendros, G.; Knicker, H. The effect of fire on soil organic matter—A review. *Environ. Int.* **2004**, *30*, 855–870. [CrossRef]
51. Inbar, A.; Lado, M.; Sternberg, M.; Tenau, H.; Ben-Hur, M. Forest fire effects on soil chemical and physicochemical properties, infiltration, runoff, and erosion in a semiarid Mediterranean region. *Geoderma* **2014**, *221*, 131–138. [CrossRef]
52. Ammitzboll, H.; Jordan, G.J.; Baker, S.C.; Freeman, J.; Bissett, A. Diversity and abundance of soil microbial communities decline, and community compositions change with severity of post-logging fire. *Mol. Ecol.* **2021**, *30*, 2434–2448. [CrossRef] [PubMed]
53. Buckingham, S.; Murphy, N.; Gibb, H. Effects of fire severity on the composition and functional traits of litter-dwelling macroinvertebrates in a temperate forest. *For. Ecol. Manag.* **2019**, *434*, 279–288. [CrossRef]
54. Fenster, M.; Ferrick, C.; Scott, M. Fall burning does not affect nematode density or carbon and nitrogen levels in Iowa oak forest soils. *Tillers* **2004**, *5*, 9–12.

55. Bastow, J. The impacts of a wildfire in a semiarid grassland on soil nematode abundances over 4 years. *Biol. Fertil. Soils* **2020**, *56*, 675–685. [CrossRef]
56. Malmström, A. Effects of wildfire and prescribed burning on soil fauna in boreal coniferous forests. Ph.D. Thesis, Faculty of Natural Resources and Agricultural Sciences, Acta Universitatis Agriculturae Sueciae, Uppsala, Sweden, 2006.
57. Hu, C.; Pen-Mouratov, S.; Steinberger, Y. Vertical distribution of soil free-living nematode in a playa habitat in the North-Western Negev desert, Israel. *Helminthologia* **2020**, *57*, 361–375. [CrossRef] [PubMed]
58. Liang, W.; Zhang, X.; Li, Q.; Jiang, Y.; Ou, W.; Neher, D.A. Vertical distribution of bacterivorous nematodes under different land uses. *J. Nematol.* **2005**, *37*, 254–262. [PubMed]
59. Neher, D.A.; Wu, J.; Barbercheck, M.E.; Anas, O. Ecosystem type affects interpretation of soil nematode community measures. *Appl. Soil Ecol.* **2005**, *30*, 47–64. [CrossRef]
60. Ruess, L.; Schmidt, I.K.; Michelsen, A.; Jonasson, S. Manipulations of a microbial based soil food web at two arctic sites—Evidence of species redundancy among the nematode fauna? *Appl. Soil Ecol.* **2001**, *17*, 19–30. [CrossRef]
61. Wang, K.H.; McSorley, R.; Gallaher, R.N. Effect of *Crotalaria juncea* amendment on nematode communities in soil with different agricultural histories. *J. Nematol.* **2003**, *35*, 294.
62. Šalamún, P.; Renčo, M.; Kucanová, E.; Brázová, T.; Papajová, I.; Miklisová, D.; Hanzelová, V. Nematodes as bioindicators of soil degradation due to heavy metals. *Ecotoxicology* **2012**, *21*, 2319–2330. [CrossRef]
63. Renčo, M.; Čerevková, A.; Homolová, Z. Nematode communities indicate the negative impact of Reynoutria japonica invasion on soil fauna in ruderal habitats of Tatra National park in Slovakia. *Glob. Ecol. Conserv.* **2021**, *26*, e01470. [CrossRef]
64. McSorley, R. Short-term effects of fire on the nematode community in a pine forest. *Pedobiologia* **1993**, *37*, 39–48.
65. McSorley, R. Effect of disturbances on trophic groups in soil nematode assemblages. *Nematology* **2001**, *13*, 553–559. [CrossRef]
66. Bongers, T.; Bongers, M. Functional diversity of nematodes. *Appl. Soil Ecol.* **1998**, *10*, 239–251. [CrossRef]