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Spruce girdling decreases abundance of fungivorous soil nematodes in a boreal forest

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ABSTRACT

The relative importance of belowground and aboveground energy inputs for the decomposer communities in soil remains largely unknown. In particular, no research has been done on the significance of root-derived resources for nematode communities in boreal forests. In two spruce stands in the taiga zone, we set up a field experiment in which girdling of spruce trees and clipping of dwarf shrubs was performed. Root-derived resources were hypothesized to be highly important; accordingly, we expected to observe a suppression of the nematode community after experimental manipulations. To obtain information on the nature of changes in the soil food web, nematode community structure indices were applied. In partial confirmation of our hypothesis, spruce girdling decreased mycorrhizal hyphae biomass as assessed via in-growth mesh bags, as well as the abundance of fungivorous nematodes, mostly of the *Aphelenchoides* and *Filenchus* genera. The enrichment index (EI) value decreased, indicating reduction of organic matter inputs into the soil food web, whereas nematode channel ratio (NCR) index value increased, indicating a shift towards domination of the bacterial energy channel. Total nematode abundance, genera richness, and abundance of herbivores, omnivores, and predators did not change in response to spruce girdling. Clipping of dwarf shrubs decreased fungal and bacterial PLFA biomarkers, but did not affect nematode communities. Thus, the resources channeled in soil by the roots of canopy trees are of different relative importance for nematodes having different trophic habits. Fungivorous nematodes are at least partly dependent on root-derived resources, suggesting feeding on ectomycorrhizal mycelium. Rhizodeposits of understory vegetation are likely of low importance for nematodes.

1. Introduction

Aboveground-belowground interactions play a fundamental role in the control of ecosystem processes and properties (Scheu, 2001; Bardgett and Wardle, 2010). Aboveground plant litter is the primary resource for soil food webs (Swift et al., 1979). However, evidence is mounting that live roots and root-derived carbon, such as rhizodeposits, may be of similar or even higher importance for some soil organisms (Högberg et al., 2001; Pollierer et al., 2007). Hence, the relative importance of belowground and aboveground energy inputs for decomposer communities remains a matter of debate (Goncharov and Tiunov, 2013; Scheunemann et al., 2015).

The potential importance of root-derived resources to various groups of soil-dwelling animals and the particular pathways by which such resources enter soil food webs remain poorly understood. Mycorrhizal fungi take up photosynthetically fixed carbon from plant roots and translocate it to the extramatrical mycelium. It has therefore been suggested that mycorrhizal fungi may be an essential link connecting living roots and soil-dwelling animals (Pollierer et al., 2012). Even though ectomycorrhizal fungi are very common in forest soils, studies using natural $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios do not support a widespread feeding of soil animals on the extramatrical mycelium of mycorrhizal fungi (Kudrin et al., 2015; Potapov and Tiunov, 2016). For instance, experimental techniques such as isotopic labeling and tree girdling have shown that most collembolan species are only weakly associated with root-derived resources (Malmström and Persson, 2011; Goncharov et al.,

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2016; Potapov et al., 2016). Apparently, not all groups of soil animals are trophically related to "root carbon".

Most research on plant-soil biota interaction in boreal forests has tended to focus on the litter and roots of canopy trees, since ecosystem processes are largely determined by the functional traits of species dominating the biomass of the community (Grime, 1998). Consequently, we know little about the significance of root-derived resources of understory vegetation for soil animals. Despite their relatively low biomass compared to canopy trees, ericoid dwarf shrubs perform important ecosystem functions, including nutrient cycling, carbon sequestration, and contributions to soil fertility in boreal forests (Nilsson and Wardle, 2005). In addition, secondary metabolites of ericoid shrubs may exert chemical allelopathic effects on other organisms (Wardle et al., 1998; Nilsson and Wardle, 2005). Indeed, experimental studies suggest that understory vegetation in boreal forests may play a role in shaping soil invertebrate communities (Mitchell et al., 2012; De Long et al., 2016). For instance, it has been shown that ericoid shrub removal could decrease the abundance of fungivorous, bacterivorous, and herbivorous nematodes (Fanin et al., 2019).

An indirect mean of measuring the significance of root-derived carbon for soil biota is to cut off the flux of root carbon into the soil system by tree girdling (Högberg et al., 2001; Remén et al., 2008). This method involves stripping the stembark and phloem to the depth of the current xylem, which leads to a cessation in the flux of carbohydrates from the canopy to the roots, associated mycorrhizal fungi, and soil (Högberg et al., 2001). Due to the fact that girdling reduces ectomycorrhizal fungi, but has no immediate effect on the supply of carbon compounds to saprotrophic fungi from organic substrates, the method has also been used to separate mycorrhizal feeders from other fungivores (Remén et al., 2008; Malmström and Persson, 2011). Besides, tree girdling may have an effect on soil properties and microbial communities (Högberg et al., 2002; Wu et al., 2011). A simple approach to assess the significance of root-derived resources of understory plants for soil biota is the removal of the above-ground green biomass, which should affect the quality and quantity of resources available for soil organisms. Experimental studies report both negative (Mikola and Kytoviita, 2002) and positive (Hamilton and Frank, 2001) effects on carbon release from roots upon defoliation. However, there is evidence that clipping of ericoids may lead to a decrease in soil respiration rates and DOC concentrations in soils (Zeh et al., 2019). Defoliation may affect soil microbial biomass (Guitian and Bardgett, 2000; Hamilton and Frank, 2001), and lead to a decrease in the abundance of nematodes (Stanton, 1983; Todd et al., 1992; Dam and Christensen, 2015).

Nematodes are one of the most abundant groups of soil inhabitants and play a key role in soil food webs through their remarkable range of feeding strategies, which include herbivory, bacterivory, fungivory, omnivory, and predation (Yeates et al., 1993; Bongers and Ferris, 1999). The dependence of nematodes on living roots has mostly been shown for herbivorous nematodes (Wallace, 1963), but some experimental data suggest a significant value of root-derived resources for nematodes belonging to other trophic groups. For instance, Keith et al. (2009) in a mesocosm experiment, showed a significant increase in the abundance of fungivorous and predatory nematodes in the presence of birch and pine roots. Kudrin (2017a), using intact forest soil microcosms, showed that the supply of readily available carbon in amounts comparable to that found in root exudates resulted in an increase in the number of microbivorous nematodes. Tree girdling in a subtropical evergreen broad-leaved forest leads to a reduction in the number of fungivorous nematodes (Li et al., 2009). However, there is still no general understanding of the importance of root-derived resources for nematodes in different ecosystems. Specifically, there is no field data on the significance of root-derived resources for soil nematode communities in boreal forests. In $^{13}CO_2$ pulse labeling field experiments (Högberg et al., 2010; Pollierer et al., 2012; Goncharov et al., 2016), soil nematodes were not taken into account, likely due to technical difficulties in collecting animals in quantities necessary for obtaining reliable isotopic measurements (Kudrin et al., 2015). Long-term field experiments using the vegetation removal approach (De Long et al., 2016; Fanin et al., 2019) did not separate the effects of litter and rhizodeposition. In tree-girdling experiments (Högberg et al., 2001; Remén et al., 2008; Malmström and Persson, 2011), soil nematode communities were not studied. Root-trenching experiments showed conflicting results; in some cases, trenching decreased the abundance of nematodes (Zhu and Ehrenfeld, 1996; Fanin et al., 2019), while in others the abundance increased (Siira-Pietikäinen et al., 2001).

Nematodes are often used as environmental and food web indicators (Bongers, 1990; Ferris et al., 2001; Yeates, 2003). Several indices have been proposed to interpret nematode community structure by relating it to ecosystem status and function. Enrichment index (EI) is an indicator of the nutrient resources available in the soil ecosystem and is evaluated by measuring the abundance of opportunistic bacterivorous and fungivorous genera that respond quickly to resource enrichment (C and N sources). EI thus suggests whether the soil environment is nutrient enriched (high EI) or depleted (low EI). The nematode channel ratio (NCR) index is used to indicate the predominance of bacterial or fungal pathways in the soil food web (Yeates, 2003). As nematodes are tightly linked to their food resources, the relative abundance of bacterivorous versus fungivorous nematodes is closely related to the ratio between bacterial and fungal biomass. An increase in the NCR index indicates a shift towards dominance of the bacterial energy channel.

In order to provide greater insight into the role of root-derived resources in the functioning of soil-dwelling animals, a field experiment was performed in the taiga zone of northwestern Russia. Spruce trees were girdled and dwarf shrubs were clipped in two spruce stands to evaluate the importance of root resources derived from canopy trees and understory vegetation for the soil nematode communities. We also evaluated soil properties, phospholipid fatty acid profile, and mycorrhizal hyphae biomass of the soil to clarify the mechanism of manipulation effects on nematodes. We hypothesized (1) that root-derived resources are important for the functioning of the nematode community in boreal forest soil. Thus, we expected that spruce girdling would lead to a reduction in nematode abundance. In particular, we expected to see a reduction in the abundance of fungivorous nematodes, as tree girdling terminates carbon flux in mycorrhizal fungi (Högberg et al., 2001). We also hypothesized (2) that the root carbon of understory vegetation is of importance for nematodes, and that the clipping of dwarf shrubs would suppress nematode communities. We applied nematode indices in order to obtain additional information on the nature of changes in soil food web structure induced by tree girdling and dwarf shrub foliage removal. We expected root-derived resources of canopy trees and understory vegetation to be an important source of easily available organic matter in the soil food web of boreal forests. Thus, experimental manipulations would be expected to lead to (3) a decrease in EI values and (4) an increase in NCR index values.

2. Material and methods

2.1. Site description

The field experiment was conducted in two natural forest stands, located at the Lalsky Nature Sanctuary in the taiga zone of northwestern Russia (Komi Republic). The mean annual air temperature is 0.5 °C, with annual precipitation of about 620 mm. The growing seasons during the experiment (2016, 2017) were characterized by above average precipitation. Temperatures were above average in 2016 and below average in 2017 (Fig. S1).

Forest stand 1 (FS1) (62.253123 N, 50.666227 E; altitude 320 m asl) is located in the southern part of the sanctuary. The soil type is Albeluvisol, with an average depth to A horizon of about 5 cm. The tree layer is dominated by Siberian spruce (*Picea obovata*), but other species, including *Abies sibirica*, *Betula pubescens* and *Populus tremula*, are interspersed. The age of spruce trees varies from 100 to 200 years. *Vaccinium*

myrtillus prevails in the ground vegetation. Less abundant species are *Vaccinium vitis-idaea*, *Oxalis acetosella*, *Maianthemum bifolium*, *Linnaea borealis*, and *Trientalis* spp. Mosses form a continuous soil cover.

Forest stand 2 (FS2) (62.280480 N, 50.739582 E; altitude 130 m asl) is located 4 km from FS1. Siberian spruce is also dominant at this stand, with aspen (*P. tremula*) interspersed. The age of spruce trees varies from 60 to 110 years. Soil properties, as well as the composition and structure of ground vegetation, are similar to those in FS1.

In both stands the relief was nearly flat and moisture content in the upper soil horizon (0–5 cm) during the experiment was similar (on average 227 ± 12 and 211 ± 7%, in FS1 and FS2, respectively).

2.2. Experimental design

We used girdling of spruce trees and clipping of ericaceous dwarf shrubs to manipulate plant rhizodeposition. In May 2016, three experimental plots (10 × 10 m) containing only spruce trees were established in each stand. The distance between the plots within each stand was at least 30 m. Each plot was divided into four sub-plots; each of the four sub-plots corresponded to one treatment. To prevent the in-growth of external roots, each sub-plot was trenched to a depth of 40 cm and isolated with buried polyethylene film (180 μm thick). Experimental manipulations were performed on June 1, 2016, and consisted of spruce girdling (G), ericaceous dwarf shrub clipping (E), spruce girdling plus clipping of ericaceous shrubs (G + E), and neither girdling or clipping (C or control). Each sub-plot contained 3–4 spruce trees, with the diameter at breast height varying from 15 to 30 cm. Girdling was performed by removing 40 cm of bark and cambium 1.2 m above the ground. Ericaceous dwarf shrubs were clipped at the soil surface using scissors. The clipping was repeated during each sampling session (see below).

2.3. Soil sampling

Soil samples were collected from the organic soil horizon. Six soil cores (5 × 5 cm, 5 cm depth) from each sub-plot were combined and mixed to form one composite sample. Each composite sample was subsequently divided into sub-samples to assess required parameters. Nematode community composition was assessed four times, on days 50, 120, 380, and 430 of the experiment. To clarify indirect pathways of spruce girdling and ericoid clipping impact on nematodes, soil properties and phospholipid fatty acid (PLFA) profiles were evaluated once, on day 380 of the experiment. Sub-samples for assessment of PLFA profile were immediately frozen and kept at −18 °C until the phospholipid fatty acid analysis.

2.4. Nematodes

Nematodes were extracted from 30 g of fresh soil from composite samples using the modified Baermann method (Ruess, 1995). Extraction lasted for 48 h. Extracted nematodes were killed at 60 °C and then preserved in 4% formaldehyde. In each soil sample, 100 individuals were identified to the genus level, using a Leica DM4000 B inverted microscope. The nematodes were identified using established taxonomic keys (Jairajpuri et al., 1992; Bongers, 1994; Brzeski, 1998). The abundance of nematodes was measured as individuals per 100 g of dry soil, and generic richness was expressed as the mean number of genera per sample. The nematodes were assigned to four trophic groups (Yeates et al., 1993): herbivores (Hrb_x), bacterivores (Ba_x), fungivores (Fu_x), and omnivores/predators (Op_x), with *x* representing the colonizer-persister (c-p) scale (Bongers, 1990). *Filenchus* was considered fungivorous, as suggested by recent studies (Christensen et al., 2007; Okada et al., 2003), whereas other genera of *Tylenchidae* were considered herbivores. C-p *x* values describe nematode life strategies and range from 1 (r-selected: colonizers with short generation times, large population fluctuations, high fecundity and tolerance to disturbance) to 5 (K-selected: persisters producing few offspring, appearing later in succession and sensitive to disturbance). Based on the trophic classification and c-p scale, we calculated the EI index as an indicator of the status of primary enrichment of the soil food web (Ferris et al., 2001):

$EI = 100 \times e/(e + b)$, with $e = (Ba_1 \times 3.2) + (Fu_2 \times 0.8)$, $b = (Ba_2 + Fu_2) \times 0.8$, where Ba_1, Ba_2, and Fu_2 are the abundances of corresponding groups of nematodes.

The nematode channel ratio (Yeates, 2003), an indicator of the relative flow of energy and nutrients through bacterial and fungal channels, was also calculated. The NCR = Ba/(Ba + Fu), where Ba and Fu are, respectively, the relative contributions of bacterivorous and fungivorous nematodes to the total nematode abundance.

2. . Soil properties

Soil moisture content (g of water per 100 g dry soil) was measured by drying fresh soil at 105 °C to a constant weight. Soil pH was determined using a 1:2.5 (w:v) ratio of soil to deionized water. The organic C and N total contents were determined using an EA-1100 analyzer (Carlo Erba); NH_4^+-N and NO_3^+-N in filtered KCl-extracts of soil sample were measured colorimetrically using the indophenol method (NH_4^+-N) and hydrazine reduction procedure (NO_3^+-N).

2.6. Fungal mycelium

Fungal mycelium was collected using the in-growth mesh bags technique (Wallander et al., 2001; Zuev et al., 2019). The fungal communities that colonize the mesh bags are usually dominated by mycorrhizal hyphae (Wallander et al., 2013). In-growth bags were made of nylon mesh (46 μm mesh size) by melting the edges together with polyurethane glue and a plastic bag sealer. The mesh size allowed the in-growth of mycorrhizal fungal hyphae but not of roots. The bags were filled with 30 ml (60 g) of acid-washed sand (0.8–1.2 mm particle size) and sealed. The mesh bags were placed horizontally at the interface between the A organic horizon and the E mineral horizon (approximate depth = 5 cm) on the day when experimental manipulations were performed. Two mesh bags were placed in each sub-plot. The bags (n = 48) were harvested after 430 days of incubation. Mycelium was extracted from the sand by shaking in sterile water (10 min, 120 rev. min^{-1}), filtering the floating mycelia through nylon mesh (Korkama et al., 2007), and weighing to an accuracy of 2 μg using Mettler Toledo MX5 electronic microscales. Fungal biomass C (C_{fun}) was determined after combusting collected samples in a Flash 1112 elemental analyzer (Thermo, USA) at the Joint Usage Center "Instrumental methods in ecology" at the A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences. To correct for the contamination of mycelium by fine mineral particles, a simple mathematical correction was used, in which average C_{mass} content in macromycete mycelium of 40% was assumed (Högberg and Högberg, 2002).

2.7. Phospholipid fatty acid profile

Soil lipids were extracted using an accelerated solvent extractor (Dionex ASE 350) (Jeannotte et al., 2008; Andersson and Mayers, 2012). Lipids were extracted from 2 g (wet weight) soil with dichloromethane/acetone (1/1, v/v) at $1.2{\cdot}10^7$ Pa and 100 °C. The phospholipid fraction was transformed into fatty acid methyl esters (FAMEs) by mild alkaline methanolysis, and then extracted with hexane-chloroform. Samples were analyzed with a Trace GC Ultra series gas chromatograph (Thermo) coupled to a DSQ mass spectrometer and equipped with a flame ionization detector. Identification and quantification of peaks was based on comparison of retention times to the internal standard 19:0 and a bacterial fatty acid methyl ester mix (Supelco, 47080-U and 47885-U). The abundance of individual fatty acids was determined as mg PLFA kg^{-1} dry soil, and standard nomenclature was used (Tunlid et al., 1989). We used the sum of 18:1ω9 and 18:2ω6,9 as fungal PLFA (Bååth and Anderson, 2003; Kaiser et al., 2010) and the sum of i15:0, a15:0, 15:0,

i16:0, 16:1ω7, a17:0, 17:0, cy17:0, and cy19:0 as bacterial PLFA (Frostegard and Baath, 1996; Bossio and Scow, 1998). It should be noted that 18:1ω9 is found not only in fungi but also in bacteria (e.g. Schoug et al., 2008), nematodes, and plant material (see Ruess and Chamberlain, 2010 for further information). However, we used 18:1ω9 since a number of studies showed that this fatty acid can be a reliable indicator of fungal biomass in coniferous forest soils (Högberg 2006; Kaiser et al., 2010; Frostegård et al., 2011). The PLFA analyses, as well as chemical analyses of the soil, were performed in the "Ekoanalit" Laboratory of the Institute of Biology (Komi Science Center, Urals Branch of the Russian Academy of Sciences).

2.8. Statistical analysis

To assess the spatial autocorrelation pattern of nematode communities, a Mantel correlation test was conducted. We used data on the nematode community structure from Control treatments at the first sampling event (dissimilarity matrix based on Bray-Curtis dissimilarity index) and physical distance between Control treatments (geographic distance matrix based on Haversine distance . Significant spatial autocorrelations were not detected (Mantel $r = -0.15$; $p = 0.73$), and thus individual experimental plots may be deemed independent variables (Kitagami et al., 2018).

To compare the community composition of nematodes between treatments, one-way Analysis of Similarity (ANOSIM) was used. Non-parametric Kruskal-Wallis test and post-hoc comparisons of mean ranks were used to estimate the significance of the treatments effect on relative abundance of nematode taxa. Differences at the $p < 0.05$ level were considered statistically significant.

Generalized mixed-effects models (GLMMs) were used to analyze the effects of spruce girdling, ericoid clipping, sampling time (day 50, 120, 380, and 430 of experiment), and their interactions on total nematode density, taxon richness, and trophic groups abundance. Due to the over-dispersion of non-zero count data, we chose a negative binomial distribution. In the case of nematode indices (EI, NCR), we used linear mixed-effects models (LMMs). LMMs were also used to assess the effects of spruce girdling and ericoid clipping on soil properties, biomass of mycorrhizal mycelium in the in-growth bag, and PLFA biomarkers. Forest stand and sum of spruce trees DBH at each sub-plots were fitted as random effects. LMMs and GLMMs were performed using the *lme4* package in R (Bates et al., 2015). We used Wald type II $\chi 2$ tests to calculate the P values from the mixed-effects models using the *car* package (Fox and Weisberg, 2019). Post-hoc Tukey tests were performed using the R package *emmeans* (Lenth, 2019).

A structural equation model was constructed to provide a mechanistic understanding of how spruce girdling and ericoid clipping affected the trophic groups of nematodes. The model was based on data on mycorrhizal hyphae biomass from in-growth mesh bags, PLFA, and soil properties from samples collected on day 380 of the experiment. Structural equation modelling (SEM) is a useful approach for disentangling complex sets of direct and indirect interactions (Grace et al., 2010), but remains relatively underutilized in soil ecology (Eisenhauer et al., 2015). The analysis was performed with the *lavaan* package in R (Rosseel, 2012). In this analysis, spruce girdling and ericoid clipping were indicated as a categorical exogenous explanatory variable, i.e. presence (1) or absence (0). Soil, microbial and nematode parameters that were significantly affected by the manipulations (as indicated by LMMs and GLMMs) were used as endogenous variables. The SEM analyses were based on an *a priori* conceptual model that contained four hierarchical pathways, as described in detail in Fig. S2. If necessary, variables were log-transformed in order to achieve normal distribution, and some of the variables were rescaled so that all variables had an approximately equal scale. Several tests were used to assess model fit, i.e., the $\chi 2$-test and its associated P-value, the comparative fit index (CFI), and the goodness-of-fit (GFI) and root square mean error of approximation (RMSEM). Based on the results of goodness-of-fit tests, we excluded less predictive measures and non-significant indicators and pathways, and retained the most informative variables. Through stepwise removal of non-significant paths from the model, the final models that best fit our data were obtained.

3. Results

3.1. Soil properties

There was no significant difference in soil properties between experimental sub-plots, except for a slightly lower content of total organic C and total organic N in girdled sub-plots (Table 1). In addition, there was a significant effect of G × E interaction on soil pH, although a posterior comparison did not reveal a difference in pH between treatments (Table 1).

3.2. Mycorrhi al mycelium

The biomass of mycorrhizal mycelium was significantly affected by girdling (Table 1). Mycelium biomass was up to 11 times lower in the girdled sub-plots. Ericoid clipping did not affect the amount of mycorrhizal mycelium.

3.3. PLFA

The abundance of bacterial and fungal PLFAs was significantly affected by the clipping of ericoids (Table 1). Ericoid clipping led to a decrease in the abundance of both bacterial and fungal PLFAs, but a posterior comparison did not show a significant difference between means. Spruce girdling did not affect microbial PLFAs.

3.4. Nematodes

In total, 39 nematode genera were recorded, with 32 genera identified in the control, 29 in the spruce girdling (G), 30 in the ericoid clipping (E) and 28 in the G + E treatment sub-plots (Table 2). Sampling time had a significant effect on all parameters of the nematode community (Table 3). Throughout the experiment, the total abundance of nematodes and of particular trophic groups varied substantially (Fig. 1). However, only G x E × T interaction was significant, indicating that the effect of experimental manipulations on nematodes depended only minimally on time (Table 3).

In general, spruce girdling decreased the abundance of fungivorous nematodes by 40%, but this effect was less pronounced in G + E treatment (significant G × E interaction, Fig. 1 and Table 3). The number of fungivorous nematodes varied substantially in both the girdled and ungirdled sub-plots. Nevertheless, a negative effect of spruce girdling on fungivorous nematodes was consistent throughout the experiment, excluding only one sampling event at day 380 (Fig. 1D). In general, the number of bacterivorous nematodes was not affected by experimental manipulations, although their abundance was higher under G and E treatment conditions than under Control conditions at day 120 (significant G x E × T interaction, Fig. 1C and Table 3).

The nematode community structure after G treatment was significantly different from that of the Control (R of ANOSIM = 0.15; $p < 0.001$) and E treatment (R of ANOSIM = 0.10; $p = 0.006$) sub-plots, and similar to that of the G + E treatment (R of ANOSIM = 0.03; $p = 0.112$) sub-plot. Girdling effect was mainly associated with a significant decrease in the relative abundance of *Aphelenchoides* and *Filenchus*, and an increase of *Plectus* (Table 2).

Ecological indices were significantly affected by spruce girdling (Table 3). EI index value decreased, indicating a reduction in the input of organic matter into the soil food web, whereas NCR index value increased, indicating a shift in the ratio of energy channels toward domination of the bacterial channel (Fig. 2). Total nematode abundance, genera richness, and the abundance of herbivores, omnivores, and

Table 1
Microbial parameters and soil properties in different treatments on day 380 of the experiment (mean ± 1 SE, n = 6). SM - soil moisture, N - total content of organic N, C - total content of organic C. Two forest stands are combined. Different letters indicate significant differences between treatments (Tukey tests; $p < 0.05$). Chi-squared values ($\chi 2$) of the linear mixed-effects models are shown. G - effect of spruce girdling, E – effect of dwarf shrubs clipping, GxE - gridling and clipping interaction effect.

	Control	Spruce girdling (G)	Ericoid clipping (E)	G + E	$\chi 2$ value		
					G	E	GxE
Microbial parameters							
Mycelium biomass (Cfun), μg g sand^{-1}	12.7 ± 2.6a	1.1 ± 0.3b	9.3 ± 2.6a	1.1 ± 0.3b	**58.67*****	0.41	1.06
Bacterial PLFAs, mg kg dry soil^{-1}	67.9 ± 9.1	77.8 ± 16.28	58.8 ± 6.3	49.8 ± 9.5	0.16	**5.47***	1.62
Fungal PLFAs, mg kg dry soil^{-1}	40.0 ± 6.9	42.9 ± 9.2	31.9 ± 4.5	28.2 ± 5.7	0.25	**6.08***	0.71
Soil properties							
SM, %	221.3 ± 39.3	206.5 ± 18.9	244.3 ± 23.1	249.8 ± 22.6	0.11	3.44	0.34
pH	4.2 ± 0.2	4.3 ± 0.1	4.3 ± 0.2	3.9 ± 0.2	0.03	2.06	**5.96***
N–NH4^{+}, mg kg^{-1}	171.5 ± 22.6	184.8 ± 30.8	178.0 ± 15.1	166.0 ± 25.9	0.08	0.04	0.43
N–NO3^{-}, mg kg^{-1}	25.5 ± 2.7	27.1 ± 4.8	22.5 ± 2.5	26.6 ± 4.9	0.24	0.27	0.45
N, %	1.58 ± 0.04 ab	1.41 ± 0.05b	1.59 ± 0.05a	1.41 ± 0.03b	**17.98*****	0.01	0.01
C, %	40.2 ± 0.3 ab	38.1 ± 1.8b	43.1 ± 0.9a	40.1 ± 1.6 ab	**7.11****	3.07	0.03
C:N ratio	30.8 ± 1.7	31.0 ± 0.6	31.7 ± 0.8	33.3 ± 1.4	0.01	3.33	1.19

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

predators did not change in response to spruce girdling (Table 3).

The effect of clipping of ericaceous dwarf shrubs was recorded only through its interaction with other factors (Table 3). For fungivorous nematodes, ericoid clipping mitigated the effect of girdling (see above) (Fig. 1D). The nematode community structure after E treatment did not differ from that of the Control (R of ANOSIM = 0.01; p = 0.832) and G + E (R of ANOSIM = 0.01; p = 0.252) sub-plots. On average, ericoid clipping reduced the effect of girdling on the NCR index value (Fig. 2, Table 3). Genera richness, abundance of herbivores, omnivores/predators, and EI index value did not change in response to clipping of ericaceous dwarf shrubs (Table 3).

3. . irect and indirect effects of girdling and clipping on nematode trophic groups

Structural equation modeling was used to assess the direct and indirect effects of girdling and clipping on nematode trophic groups. The final models adequately fit the data ($\chi 2 = 16.28$; df = 12; $P = 0.18$; CFI = 0.94; GFI = 0.99; RMSEA = 0.12, Fig. 3). The SEM analysis indicated that a decrease in the abundance of fungivorous nematodes was induced by a decrease in mycorrhizal biomass in the soil, while changes in the abundance of bacterivorous nematodes were associated with chemical soil properties. Clipping of ericaceous dwarf shrubs had no direct or indirect effect on nematodes.

4. Discussion

4.1. Are root-derived resources of canopy trees important for nematodes

It is still poorly understood how strongly soil nematodes depend on “root carbon” in boreal forests. Study of the impact of forest clear-cutting on nematodes can provide some insight into this question. Clear-cutting terminates the flux of root-derived resources (Striegl and Wickland, 1998), but is also associated with significant change in hydrothermal conditions and soil disturbance (Johnson et al., 1991). A meta-analysis conducted by Kudrin (2017b) showed a significant reduction in the total abundance of nematodes in coniferous forests after clear-cutting. Such changes can mainly be explained by a sharp decrease in the abundance of fungivorous nematodes (e.g. Forge and Simard, 2000). Meanwhile, root-trenching experiments have given controversial results (Zhu and Ehrenfeld, 1996; Siira-Pietikäinen et al., 2001; Fanin et al., 2019).

We applied a girdling technique in boreal forest, hypothesizing that a reduction in the flux of photosynthates from spruce canopy to the roots and soil would lead to a significant reduction in the number of nematodes. However, we found a significant reduction in the abundance of fungivorous nematodes only, while the total abundance, genera richness, and abundance of other trophic groups did not change, with the number of bacterivorous nematodes actually increasing by day 120 of the experiment (Table 3; Fig. 1). Thus, our first hypothesis was partially confirmed. The root-derived resources of canopy trees are of different importance to nematodes having different trophic habits.

Using the in-growth mesh bags, we found significantly smaller biomass of ectomycorrhizal mycelium after spruce girdling treatments (Table 1). PLFA analysis did not show a reduction of the fungal biomarkers one year after girdling (Table 1), which is not surprising, since the PLFA profile does not distinguish mycorrhizal and saprotrophic fungi. Saprotrophic fungi could increase their abundance after girdling via feeding on dead roots and ectomycorrhizal mycelium necromass (Esperschütz et al., 2009; Drigo et al., 2012). Thus, the observed reduction in the abundance of fungivores was likely associated with the decrease in the biomass of ectomycorrhizal mycelium, which was confirmed by the SEM analysis (Fig. 3).

Laboratory experiments (Ruess and Dighton, 1996; Ruess et al., 2000) have indicated that fungivorous nematodes may be associated with mycorrhizal fungi. In our study, genera of fungivorous nematodes such as *Aphelenchoides* and *Filenchus* respond most clearly to the girdling of spruce (Table 2). Despite the ability of *Aphelenchoides* to feed on a wide range of different fungi (Okada and Kadota, 2003), mycorrhizal fungi may still be more palatable than saprotrophic ones (Shafer et al., 1981; Giannakis and Sanders, 1989) and sustain the culture of *Aphelenchoides* in the laboratory (Ruess et al., 2000). *Filenchus* spp. can also feed on a wide range of fungi (Okada and Kadota, 2003), but Hanel (1996, 1998) has suggested that in spruce forests, this genus is associated mainly with mycorrhizal fungi. These data corroborate our findings, and indicate that fungivorous nematodes in boreal forest soil may feed preferentially on ectomycorrhizal mycelium. We therefore suggest that fungivorous nematodes, and genera *Aphelenchoides* and *Filenchus* in particular, may be among the relatively few consumers of ectomycorrhizal fungi, which includes the proturans (Bluhm et al., 2019) and some species of oribatid mites (Remen et al., 2008).

During the experiment, we also observed a transient increase in the abundance of bacterivorous nematodes after girdling. Apparently, this reaction can be associated with the appearance of a large amount of dead organic matter in the soil after tree girdling. A similar reaction has been observed after clear-cutting (Forge and Simard, 2000). However, SEM showed that the increase in the number of bacterivores after spruce girdling was associated with a decrease in total nitrogen in the soil, reflecting interactions not identified in this study.

4.2. Is the understory vegetation important for nematodes

Dwarf shrubs can produce high quantities of litter and affect belowground processes such as decomposition and nutrient availability

Table 2
Relative abundance of nematode genera (%) in different treatments (mean ± 1 SE, n = 24). C – control, E – clipping of ericaceous dwarf shrubs, G – spruce girdling, G + E – girdling and clipping simultaneously. Two forest stands and all sampling events are combined. Different letters indicate significant differences between treatments (Kruskal-Wallis test and post-hoc multiple comparisons of mean ranks, $p < 0.05$).

Nematode genera	c-p value[a]	C	G	E	G + E	Kruskal-Wallis test, p-values[c]
Fungivores[b]						
Aphelenchus	2	0.1 ± 0.1	0.0	0.0	0.0	0.391
Aphelenchoides	2	7.7 ± 1.4^{ab}	3.9 ± 0.7^{b}	8.7 ± 1.5^{a}	4.6 ± 0.9^{ab}	**0.011**
itylenchus	2	0.6 ± 0.2	0.4 ± 0.2	0.6 ± 0.2	0.4 ± 0.1	0.708
Filenchus	2	17.9 ± 2.5^{a}	9.2 ± 1.8^{b}	13.3 ± 1.9^{ab}	12.7 ± 2.5^{ab}	**0.011**
Tylencholaimus	4	7.5 ± 1.2	5.3 ± 0.6	7.7 ± 1.1	6.9 ± 1.2	0.751
Bacterivores						
Achromadora	3	0.1 ± 0.1	0.0	0.0	0.0	0.391
Acrobeles	2	0.0	0.3 ± 0.2	0.1 ± 0.1	0.0	0.499
Acrobeloides	2	8.6 ± 1.7	7.6 ± 1.6	11.0 ± 1.8	7.8 ± 1.5	0.204
Alaimus	4	2.6 ± 0.6	3.5 ± 0.7	2.1 ± 0.5	3.2 ± 0.5	0.284
Anaplectus	2	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.795
Bunonema	1	0.1 ± 0.1	0.0	0.1 ± 0.0	0.1 ± 0.1	0.548
Ceratoplectus	2	0.5 ± 0.2	1.0 ± 0.3	0.6 ± 0.3	0.2 ± 0.1	0.216
Eucephalobus	2	0.1 ± 0.1	0.1 ± 0.1	0.0	0.1 ± 0.1	0.549
Eumonhystera	2	0.1 ± 0.1	0.0	0.0	0.0	0.568
eterocephalobus	2	0.1 ± 0.1	0.0	0.0	0.0	0.568
Metateratocephalus	3	1.1 ± 0.3	1.0 ± 0.4	1.3 ± 0.3	2.4 ± 0.5	0.086
Monhystera	2	1.4 ± 0.4	1.5 ± 0.6	1.4 ± 0.4	1.9 ± 0.6	0.872
Panagrolaimus	1	0.1 ± 0.1	0.0	0.2 ± 0.1	0.0	0.283
Plectus	2	12.6 ± 1.4^{b}	22.4 ± 2.7^{a}	15.7 ± 1.9^{ab}	16.1 ± 2.3^{ab}	**0.013**
Prismatolaimus	2	1.5 ± 0.4	1.0 ± 0.3	0.8 ± 0.2	1.0 ± 0.3	0.647
Prodesmodora	3	0.6 ± 0.3	0.5 ± 0.2	0.5 ± 0.3	1.0 ± 0.4	0.837
Rhabditidae	1	2.3 ± 1.0	1.0 ± 0.5	1.3 ± 0.8	1.1 ± 0.3	0.456
Teratocephalus	3	1.7 ± 0.6	2.2 ± 0.4	1.8 ± 0.4	2.4 ± 0.5	0.324
Tylocephalus	2	0.0	0.0	0.0	0.1 ± 0.1	0.391
ilsonema	2	0.1 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.817
Omnivores						
Aporcelaimellus	5	0.4 ± 0.1	0.8 ± 0.3	0.6 ± 0.2	0.4 ± 0.2	0.431
Eudorylaimus	4	15.6 ± 1.4	18.1 ± 1.5	15.8 ± 1.7	20.3 ± 1.8	0.144
Mesodorylaimus	4	0.1 ± 0.1	0.3 ± 0.2	0.7 ± 0.4	0.1 ± 0.1	0.260
Predators						
Anatonchus	4	0.1 ± 0.1	0.0	0.0	0.0	0.391
Clarkus	4	3.4 ± 0.5	5.6 ± 1.3	4.0 ± 0.6	4.5 ± 0.8	0.702
Diplogasteridae	1	0.1 ± 0.1	0.0	0.0	0.7 ± 0.4	0.292
Iotonchus	4	1.9 ± 0.7	1.5 ± 0.4	0.1 ± 0.1	1.0 ± 0.2	0.073
Mylonchulus	4	0.0	0.1 ± 0.1	0.0	0.0	0.568
Prionchulus	4	5.0 ± 1.4	6.1 ± 1.0	3.8 ± 0.7	3.8 ± 0.6	0.066
Tripyla	3	0.0	0.1 ± 0.1	0.0	0.0	0.391
Herbivores						
Aglenchus	2	0.0	0.0	0.1 ± 0.1	0.0	0.391
Malenchus	2	1.6 ± 0.4	0.8 ± 0.3	1.6 ± 0.6	1.7 ± 0.5	0.402
eterodera	3	0.0	0.1 ± 0.1	0.1 ± 0.1	0.0	0.567
Paratylenchus	3	0.7 ± 0.5	0.4 ± 0.2	0.7 ± 0.5	0.3 ± 0.2	0.856
Tylenchus	2	0.0	0.0	0.2 ± 0.1	0.2 ± 0.1	0.152
Tylenchorhynchus	3	0.4 ± 0.4	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.257
Unidentified		3.2 ± 0.4	3.2 ± 0.4	4.4 ± 0.4	4.6 ± 0.4	

[a] c-p values according to Bongers (1990).
[b] Trophic groups according to Yeates et al. (1993).
[c] Significant effects are given in bold ($p < 0.05$).

(Wardle et al., 2003; Wardle and Zackrisson, 2005). Long-term dwarf shrub removal experiments have shown a significant reduction in the abundance of bacterivorous and fungivorous nematodes, by up to 30% and 50%, respectively (De Long et al., 2016; Fanin et al., 2019).

In contrast, the effect of ericoid clipping in our experiment was weak, and only revealed in interaction with other factors (Table 3). The nematode community structure did not change after clipping, suggesting the relatively low importance of root-derived resources from understory vegetation for nematodes in boreal forests. Thus, our second hypothesis was not confirmed.

Discrepancies with the results of earlier studies may be related to differences in the relative importance of litter and rhizodeposits for soil nematodes. In long-term experiments, the removal of dwarf shrubs led to a reduction in the organic matter quality that strongly affected soil microbiota, and consequently soil nematodes (Fanin et al., 2019). In our experiment, the effects of dwarf shrub clipping were monitored for just over one year. Clipping likely reduced rhizodeposits and affected ericoid mycorrhiza (see below), but did not decrease (or even increased) the amount of root litter. This is most likely the reason that soil properties were unaffected by the clipping of ericoids (see section 3.1) and the reaction of soil microbiota was weakly pronounced (Table 1).

However, we did find a significant G × E interaction (Table 3), which was expressed in the less pronounced effect of spruce girdling on fungivorous nematodes in G + E treated sub-plots (Fig. 1). Ericoid shrubs produce phenolic compounds, which may reduce germination and growth of seedlings (Nilsson et al., 2000; Wallstedt et al., 2005) and impair the activities of ectomycorrhizal fungi (Nilsson et al., 1993) and other soil microorganisms (Wardle et al., 1998). Moreover, most plants belonging to Ericales form a distinctive type of mycorrhiza, termed ericoid mycorrhiza, which can interact with ectomycorrhiza (Perotto et al., 2002). For instance, ericoid mycorrhizal fungi may co-colonize ectomycorrhizal root tips (Tedersoo et al., 2009; Kernaghan and Patriquin, 2015). The presence of ericaceous host plants has been found to inhibit the ectomycorrhizal colonization of coniferous seedlings (Walker et al., 1999) and reduce the number of species or change community

Table 3
Chi-squared values ($\chi 2$) of the mixed-effects models for the effects of spruce girdling, ericoid clipping and sampling time and their interaction on soil nematode variables.

	Spruce girdling (G) d.f. = 1	Ericoid clipping (E) d.f. = 1	Sampling time (T) d.f. = 3	GxE	GxT	ExT	GxExT
Total abundance	1.67	0.07	**397.59*****	1.07	2.02	1.18	2.40
Genera richness	0.01	0.36	**25.87*****	0.10	3.17	0.55	0.15
Trophic groups							
Fungivores	**21.78*****	0.15	**275.04*****	**4.57***	2.15	1.56	3.92
Bacterivores	0.08	0.01	**383.98*****	0.65	2.76	1.66	**9.32***
Pr + Om	3.24	0.56	**206.22*****	0.37	0.73	5.62	1.74
Herbivores	1.29	0.03	**418.38*****	1.11	1.52	1.29	2.06
Nematode indices							
EI	**9.04****	0.01	**22.65*****	2.93	2.83	0.35	0.39
NCR	**13.66*****	0.02	**59.04*****	**4.34***	1.39	6.15	**8.80***

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

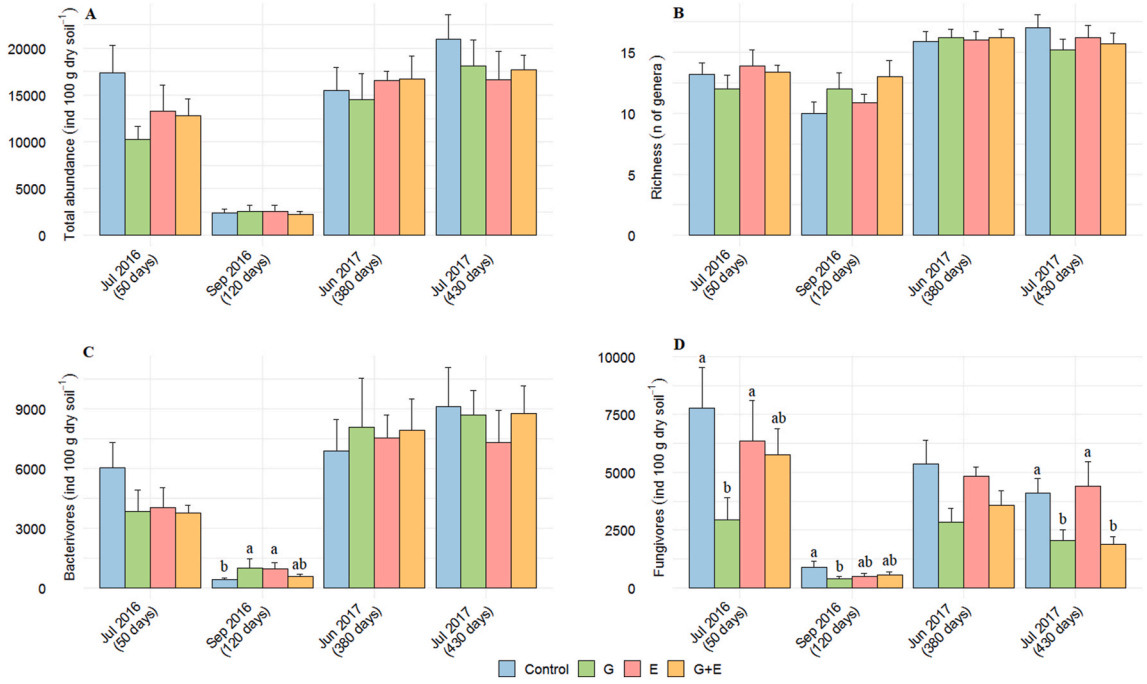

Fig. 1. Total nematode abundance (A), genera richness (B), fungivorous (C) and bacterivorous (D) trophic groups in different treatments in each sampling event. C – control, G – spruce girdling, E – clipping of ericaceous dwarf shrubs, G + E – girdling and clipping simultaneously. Data are averaged across two forest stands. Whiskers show 1SE (n = 6). Contrasting letters in each sampling event indicate significant differences among treatments (Tukey tests; $p < 0.05$, see Table 3 for GLMM results) in other cases the difference was not significant.

composition of ectomycorrhizal fungi (Collier and Bidartondo, 2009; Kohout et al., 2011). Because of the short range of the extramatrical mycelium of ericoid mycorrhiza, its production or biomass cannot be estimated using in-growth bags (Finlay and Clemmensen, 2017). Our data on the fungal biomass (Table 1) do not, therefore, reflect changes in the abundance of ericoid mycorrhizal fungi. The inhibition of ericoid roots and/or ericoid mycorrhiza in the G + E treatment could have led to a less dramatic effect on ectomycorrhiza after spruce girdling, and therefore, on fungivorous nematodes. The observed effect suggests specific interactions between ericoides and/or ericoid mycorrhiza and ectomycorrhizal fungi that affect higher trophic levels, and nematodes in particular. Mechanisms of such interactions deserve further study.

It should be noted that clipping is not a perfect analog of girdling, and likely is not the best approach for assessing the importance of root-derived resources of understory vegetation for soil fauna, as the removal of green biomass may lead to both decreases and increases in resources available for soil organisms (Hamilton and Frank, 2001; Mikola and Kytoviita, 2002). However, we found a weak but significant decrease in fungal and bacterial PLFA biomarkers in response to clipping of dwarf shrubs, which may indicate a decrease in the availability of root-derived resources for soil biota.

4.3. Are root-derived resources an important energy channel

Readily available organic matter is of high importance for the functioning of soil ecosystems. Besides fueling soil food webs, it is involved in the regulation of microbial pools, plant litter decomposition, and stability of soil organic carbon (Fontaine et al., 2007; Pollierer et al., 2012). The amount and turnover rates of readily available resources in soil can be estimated using the enrichment (EI) index (Ferris et al., 2001). In support of our third hypothesis, we observed a decrease in EI value after spruce girdling (Table 3; Fig. 2), which confirms that root-derived resources form a functionally important flux of nutrients in the soil food web of boreal forests. The change in EI value after spruce girdling but not after ericoid dwarf shrub clipping indicates that this flux is controlled more by canopy trees than by ground vegetation. A significant reduction in root exudation, soil DOC concentration, and soil respiration after tree girdling (Högberg et al., 2001; Scott-Denton et al., 2006) corroborates this assertion.

Decomposition processes in soil, although ultimately dependent on

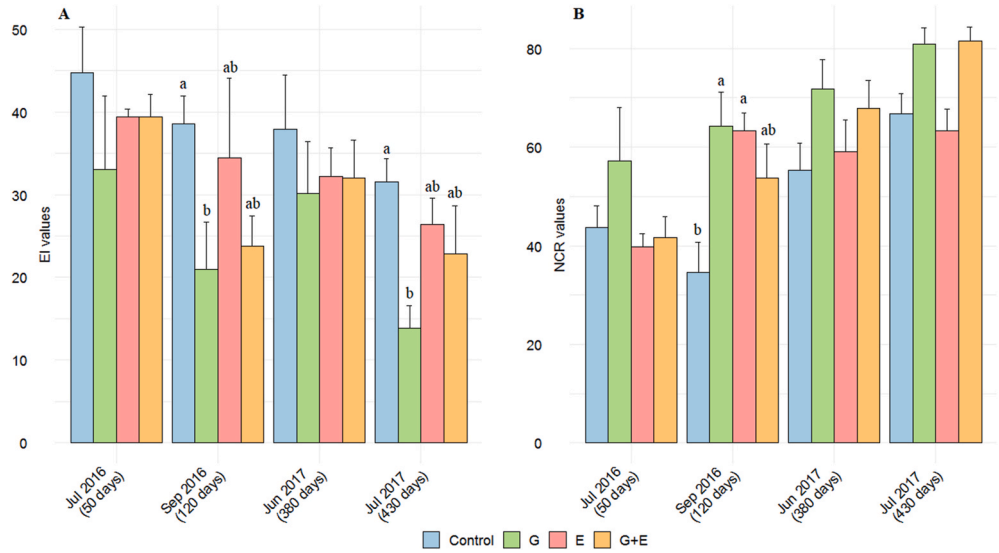

Fig. 2. Values of EI (A) and NCR (B) indices in different treatments in each sampling event. C – control, G – spruce girdling, E – clipping of ericaceous dwarf shrubs, G + E – girdling and clipping simultaneously. Data are averaged across two forest stands. Whiskers show 1SE (n = 6). Contrasting letters in each sampling event indicate significant differences among treatments (Tukey tests; $p < 0.05$, see Table 3 for LMM results) in other cases the difference was not significant.

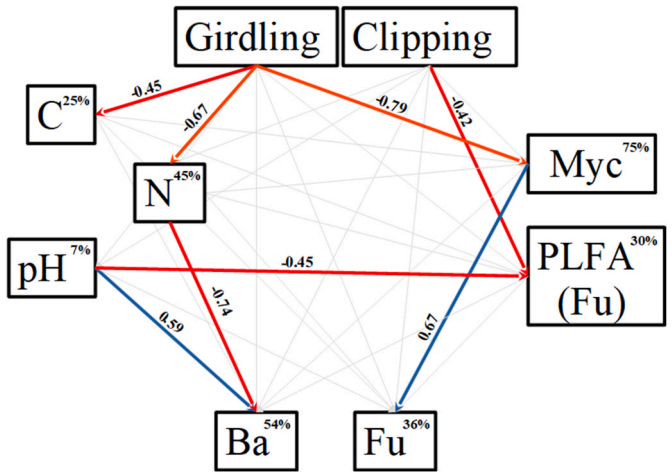

Fig. 3. Structural equation model of the effects of spruce girdling and clipping of ericoid dwarf shrubs on nematode trophic groups ($\chi 2 = 16.28$; df = 12; $P = 0.18$; CFI = 0.94; GFI = 0.99; RMSEA = 0.12). Numbers next to the arrows are the standardized path coefficients. Red arrows indicate negative and blue arrows indicate positive relationships ($P < 0.05$). Grey thin arrows indicate non-significant relationships or paths removed to improve model fits. Percentages within boxes show the variance of each endogenous variable explained by the model. N, total soil organic nitrogen; C, total soil organic carbon; pH, soil acidity; Myc, (ectomycorrhizal) fungal mycelium biomass in in-growth mesh bags; PLFA (Fu) - amount of fungal PLFAs; Ba, abundance of bacterivorous nematodes; Fu, abundance of fungivorous nematodes. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

plant residues, are often allocated to either the bacterial-based fast energy channel (pathway) or the slower fungal-based channel (Moore and Hunt, 1988). The nematode-based NCR index was introduced for estimating the ratio between bacterial and fungal channels in soil food webs (Yeates, 2003). In support of our fourth hypothesis, we observed NCR index values to increase after spruce girdling (Table 3; Fig. 2), which indicates a shift towards the dominance of the bacterial energy channel. On the one hand, this is in good agreement with the observed decrease in ectomycorrhizal mycelium biomass. On the other hand, it seems to disagree with the absence of a decrease in fungal biomarkers after spruce girdling. This finding suggests that the interpretation of the NCR index for forest ecosystems should be reconsidered. Traditionally, nematode indices have been regarded as indicators of predominant detritus decomposition pathways (Ruess and Ferris, 2004). Based on such indices, coniferous forests are usually regarded as systems in which fungal pathways dominate. This is ascribed to the presence of high amounts of recalcitrant substrates, such as lignin, available mainly to saprotrophic fungi (Matveeva and Sushchuk, 2016; Ruess and Ferris, 2004). However, our results indicate that a significant proportion of the energy in the fungal channel, as assessed based on nematode community structure, is provided by freshly-fixed carbon from trees, rather than by dead organic matter. Thus, the dominance of the fungal pathway in boreal forests previously detected using nematode indices may more accurately be attributed to the joining of brown (based on detritus) and green (based on roots and mycorrhizal fungi) trophic chains in the belowground food web.

4.4. Conclusion

Spruce girdling and clipping of dwarf shrubs were used to gain a better understanding of the importance of root-derived resources for nematodes at two boreal forest stands. Tree girdling induced a significant decrease in the abundance of fungivorous nematodes. Based on the abundance of mycorrhizal mycelium in in-growth mesh bags and the results of structural equation modeling, we suggest that this effect was mainly associated with the reduction in the abundance of ectomycorrhizal fungi. These results indicate that fungivorous nematodes are at least partly dependent on root-derived resources. Members of the *Aphelenchoides* and *Filenchus* genera, in particular, may be specialized consumers of ectomycorrhizal fungi. Clipping of dwarf shrubs did not affect nematode communities, reflecting the minimal importance of ground vegetation rhizodeposits for soil food webs. Clipping of ericoids did mitigate the negative effect of girdling on fungivorous nematodes, suggesting that interactions between ericoid plants and/or ericoid mycorrhiza and ectomycorrhiza can affect higher trophic levels in soil food webs. EI and NCR nematode indices confirmed that the roots of canopy trees provide readily available organic matter for the soil food web.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108184.

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