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Effects of wild boar grubbing on the soil nematode community subject to seasonal variation in a broad-leaved Korean pine forest in Northeast China

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ABSTRACT

Soil disturbances caused by large animals impact soil biodiversity and potentially alter forest ecosystem functioning and productivity. However, most studies have focused on the effects of wild boar infestations on aboveground vegetation and soil physical and chemical properties. Little is known about the influence of wild boar grubbing on the soil faunal community within forested ecosystems. To address this knowledge gap, we conducted a long-term (10-year) exclosure experiment to investigate the responses of soil nematode communities to wild boar grubbing and seasonal variations in a broad-leaved Korean pine forest in Changbai Mountain, China. The results indicated that wild boar grubbing did not significantly impact soil nematode abundance, genus richness, diversity indices (Shannon-Wiener diversity index, Simpson index, and evenness index), and ecological indices (enrichment index, channel index, structural index, and basal index). However, we observed that grubbing reduced the relative abundance of plant parasites while increased that of bacterivores and the maturity index (MI), leading to changes in nematode community composition. Notably, the influence of grubbing was more pronounced in the spring than in the autumn. Although season itself did not significantly affect soil nematode genus richness and diversity indices, it did affect soil nematode relative abundance, bacterivores, omnivores-predators, plant parasites, *K*-strategistis, *r*-strategistis, MI, enrichment index, and channel index. Long-term wild boar grubbing appeared to mitigate seasonal effects on soil nematode communities, resulting in higher MI and increased stability in nematode community abundance. Our findings suggest that changes in soil parameters, such as soil NH_4^+, soil pH, and soil NO_3^-, likely mediate the observed impact of wild boars on the soil nematode community. In summary, our study demonstrated that wild boar grubbing altered the structure of soil nematode communities, albeit with seasonal variations, indicating that the effects of wild boar activity on forest soil ecosystems influence biogeochemical cycles through changes in nematode community composition rather than nematode genera richness.

1. Introduction

The wild boar (Sus scrofa L.), native to Eurasia, is among the most widespread large omnivorous wild animals globally (Barrios-Garcia and Ballari, 2012; Snow et al., 2017). In China, wild boar inhabits all regions except the Tibetan Plateau and the Gobi Desert (Liu et al., 2020). During the early 20th century, extensive hunting and habitat degradation nearly drove the wild boar to extirpation in China. However, their populations have rebounded over recent decades, owing to several factors. China has banned the hunting of wild animals since 1994, including wild boars, which were added to the National Land Wildlife Protection List in 2000 (Liu et al., 2020). Additionally, increased environmental awareness in China has expanded wild boar habitats. These animals have a varied diet, reproduce rapidly with a high fertility rate, and have few natural predators (O'Bryan et al., 2022), further contributing to their population growth. The estimated wild boar population is approximately 2 million individuals (National Forestry Administration, 2009), with the eastern mountainous regions of Northeast China alone

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accounting for around 80,000 individuals (Yu et al., 2009; Zhu et al., 2011). In 2008, the number of wild boars in the Changbai Mountain area of Jilin Province reached 1.15 ± 0.19 individuals/km^2 (Zhu et al., 2011). Wild boars obtain most of their food grubbing in the soil, searching for plant seeds, roots, and various animals, both vertebrates and invertebrates (Barrios-Garcia et al., 2014; Wirthner et al., 2011). This foraging behavior significantly impacts forest surface vegetation and soil structure (Sitters et al., 2020; Yu et al., 2009; Zhu et al., 2011).

Forest ecosystems, cover only 27 % of the Earth's land surface, but store more than 80 % of global carbon reserves (Zhao et al., 2021). They perform numerous ecological functions critical for maintaining global ecosystem stability and balance (De Frenne et al., 2021; Gibson et al., 2011). Wild boar grubbing can have various positive effects on forests (Kotanen, 1995), such as promoting tree growth and natural vegetation regeneration through seed dispersal (Bruinderink and Hazebroek, 1996), controlling certain invertebrate pests, and scavenging carrion (Rosell et al., 2001). These activities enhance material cycling and energy flow within the forest. However, wild boars can also negatively impact forest regeneration and understory biodiversity. They upturn extensive forest areas (Hegel and Marini, 2013; Orlowska and Nasiadka, 2022; van Doormaal et al., 2015; Wirthner et al., 2012), directly or indirectly affecting other organisms by altering habitat characteristics and resource availability (Baubet et al., 2003; Crooks, 2002; Maaroufi et al., 2022; Nagy et al., 2015). While the effects of wild boar grubbing on surface vegetation composition and function have been well-documented (Brunet et al., 2016; Dovrat et al., 2014; Orlowska and Nasiadka, 2022), less is known about their impact on soil biomes (Brunet et al., 2016; Carpio et al., 2022).

Soil food webs are composed of soil microbes and fauna, which are among the richest and most diverse groups of organisms in terrestrial ecosystems (Carrillo et al., 2011; Bardgett and Van Der Putten, 2014). Changes in soil biodiversity can alter nutrient cycling, decomposition rates, and energy flow within the soil food web (Bardgett and Van Der Putten, 2014; Wall et al., 2012). While most studies have focused on the effects of wild boar grubbing on soil microbial community composition and structure (Carpio et al., 2022; Wehr et al., 2019; Wirthner et al., 2011), reports on the effects of grubbing on the soil faunal communities are scarce (Vtorov, 1993; Barrios-Garcia et al., 2023).

Nematodes play a crucial role in the soil ecosystem (van Den Hoogen et al., 2019), representing 80 % of all multicellular animal species (Bongers and Ferris, 1999; Ferris and Bongers, 2006; Hugot et al., 2001; Martin and Sprunger, 2021). Due to their sensitivity to environmental change and diverse feeding habits, they are often used as indicators of soil environmental health (Neher, 2010; Pen-Mouratov et al., 2010; Du Preez et al., 2022). Alterations in nematode community composition can reflect changes in soil microbial community composition (Nielsen, 2019). Additionally, soil nematodes can be categorized into various trophic levels (bacterivores, fungivores, plant parasites, and omnivores-predators) within the soil food web (Bongers and Ferris, 1999). Studies have shown that nematodes, directly or indirectly, influence soil ecological processes through interactions with soil microorganisms (Wang et al., 2021; Zhang et al., 2021). Some studies have also revealed that bacterivore nematodes are more sensitive to resource changes than fungivore nematodes (Ferris and Matute, 2003). Alongside soil resource availability, the microenvironment's structure is the primary driver influencing soil nematode population density and community dynamics (Bakonyi and Nagy, 2000; Briones et al., 2009).

Wild boars modify soil physical and chemical properties (Singer et al., 1984), directly and indirectly affecting the soil nematode community. Directly, they disrupt the soil food web by altering soil physical structure and exposing the soil biota to predators and adverse abiotic conditions (Golabi et al., 2014). Indirectly, wild boar grubbing mixes organic and soil mineral layers, impacting the microenvironment and, consequently, the soil nematodes community. Moreover, wild boars feeding on plant roots can distort the composition of root-feeding nematodes (Henderson and Katznelson, 1961). The excrements and saliva secretion of wild boars can change soil microbial community composition to some extent, enhancing bacterial growth and activity by providing them with nutrients (Pan et al., 2022). As a significant portion of the forest soil nematode community feeds on soil microorganisms, changes in microbial community structure may further impact the soil nematode community (Kane et al., 2023).

The primary objective of this study was to investigate the effects of wild boar grubbing on soil nematode communities in old broad-leaved Korean pine mixed forests on Changbai Mountain, China. We hypothesized that: (1) wild boar grubbing destroys soil structure by mixing the mineral soil with surface litter which would increase the relative abundance of bacterivore nematodes relative to fungivore nematodes in the soil; (2) wild boar feeding on roots would reduce the relative abundance of plant parasitic nematode; (3) long-term boar grubbing would reduce the effects of seasonal variations on soil nematode communities, resulting in a higher Maturity Index (MI) and greater stability.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted within a natural mixed forest of Korean pine and broad-leaved species situated in Jilin province, Northeastern China (41°42′45″N–42°45′18″N, 127°33′30″E–128°16′48″E, asl: 690 m) (Fig. 1). The region experiences a typical temperate monsoon climate characterized by distinct seasonal variations. Spring is marked by strong winds and aridity, followed by a brief and rainy summer, a cool and misty autumn, and a long, cold winter. Between 2005 and 2020, the average annual precipitation amounted to 691 mm, with approximately 77 % of this rainfall occurring during the growing season (Sun et al., 2022). The average annual temperature is approximately 2.9 ℃, with January being the coldest month, registering an average minimum temperature of −16.5 °C, while August is the warmest month, with an average maximum temperature of 20.5 °C. The soil is classified as Eutric Cambisol based on the FAO classification, developed on weathered volcanic ash and basalt.

Our sampling site was in a broad-leaved Korean pine forest on the northern slope of Changbai Mountain. This forest ecosystem consists of tree species such as *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Juglans mandshurica*, and *Corylus mandshurica*, all of which are known to serve as a food source for wild boars (Zhu et al., 2011). The experimental site, known as the "Experimental Site for Long-term Positioning and Monitoring of Boars Arching Disturbance" was established within this forest in October 2011. To monitor the long-term impact of wild boar disturbance, we employed a block design approach. Ten sets of barbed wire fences, each measuring 1.2 m in height and spaced at least 30 m apart, were strategically installed to demarcate the sample sites for continuous monitoring of wild boar disturbance. These fences divided the study area into ten distinct block groups. Each block group comprised two quadrats, each spanning an area of over 900 m^2. One quadrat served as the non-grubbed plot (fenced, NG), while the other represented the grubbed plot (located outside the fence, disturbed, G) (Fig. 2). We employed a combination of artificial surveys and infrared camera monitoring to track wild boar disturbances to the forest soil. In grubbed plots, soil was overturned by wild boars at least once annually (Fig. 1a, b). Soil bulk density in the grubbed plots was 0.42 ± 0.03 g/cm^3, whereas in the non-grubbed plots was 0.52 ± 0.04 g/cm^3. Notably, wild boar grubbing activity significantly reduced soil bulk density by 20.43 % (Fig. S1).

2.2. Soil sampling and analysis

At each plot, we collected 10 soil cores, each with a diameter of 5 cm, at a depth ranging from 0 to 10 cm. This sampling took place in May (hereafter spring) and October (hereafter autumn) 2021, precisely a decade after the installation of the fence. To minimize edge effects, we

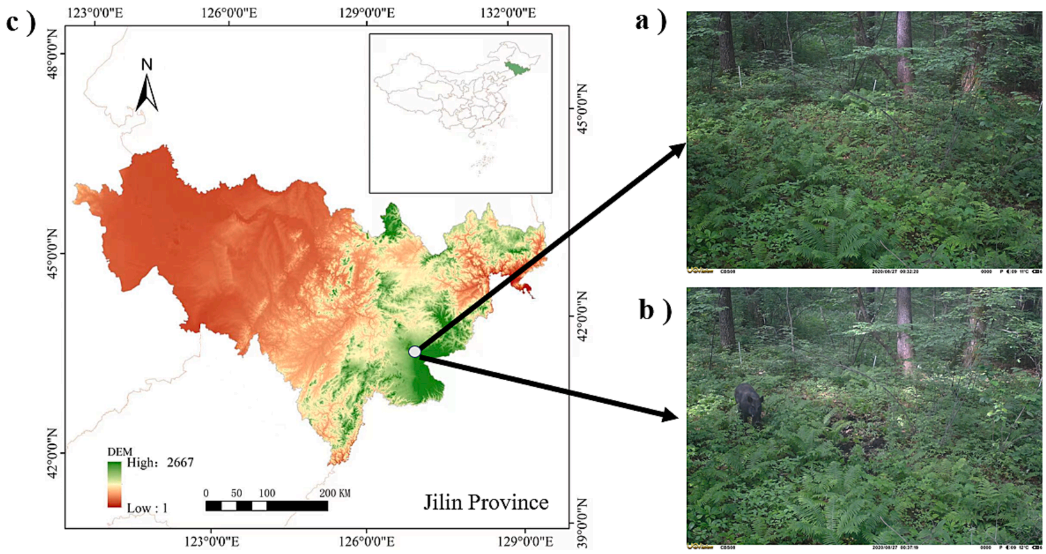

Fig. 1. Study site, including pictures of wild boar before (a) and after (b) grubbing in Jilin Province (c), China.

a. Grubbed plot b. Non-grubbed plot

Fig. 2. Soil surface condition of the grubbing plots (a) and non-grubbing plots (b). The photographs were taken on 21 July 2021.

ensured that each soil core was obtained at a minimum distance of 2 m from the fence. Prior to each sampling event, the coring equipment was meticulously cleaned using tap water and filter-sterilized water, followed by sterilization using an alcohol lamp. After collection, we manually removed stones, roots, and macro-arthropods from each of the 10 cores collected at each plot. Subsequently, these cores were thoroughly mixed by hand, yielding 20 composite soil samples for both grubbed (10 G) and non-grubbed (10 NG) plots. These composite soil samples were then placed in a cooler to maintain their integrity during transportation to the laboratory (Zheng et al., 2022).

Each composite soil sample was subdivided into two aliquots. One aliquot was used for soil chemical analyses. The suite of soil chemical parameters analyzed encompassed soil pH, soil total carbon (TC), soil total nitrogen (TN), soil total phosphorus (TP), soil available nitrogen (AN), soil available phosphorus (AP), nitrate (NO_3^--N), ammonium (NH_4^+-N), and soil water content (SWC).

Soil pH was measured using a pH meter (Precision and Scientific Corp, Shanghai, China) after shaking a suspension of soil in deionized water at a ratio of 1:2.5 (*w/v*) and allowing it to stand for 30 min. Soil TC and TN were quantified using an element analyzer (Elementar Vario EL Cube, Hanau, Germany). Soil TP content was determined employing the molybdate colorimetric method (Kuo and Sparks, 1996) following wet digestion with a mixture of H_2SO_4-$HClO_4$. Soil available phosphorus was extracted using the Mehlich-3 extractant and determined through the molybdenum blue method (Mehlich, 1984). Soil nitrate (NO_3^--N) and ammonium (NH_4^+-N) were extracted with a 2 M KCl solution and quantified using the Continuous-Flow Auto Analyzer III (Bran and Luebbe, Norderstedt, Germany). Soil water content was determined by weighing 20 g of each soil aliquot before and after drying at 105 °C overnight, with soil water content calculated as the difference between the initial and dry weights (20 g).

Soil nematodes were extracted from a second aliquot of 100 g of fresh soil sample using the Baermann funnel method (Viglierchio and Schmitt, 1983). Following a 48-hour extraction period, nematodes were fixed in a 4 % formaldehyde solution. For subsequent analysis, 100 nematodes were randomly selected from each extracted aliquot sample and identified to genus under a microscope (Olympus BX53M). Identification was based on microscopic examination of morphological features, including the lips, buccal cavity, pharynx, gonads, amphids, styles, sensilla, tail, caudal glands, and phasmids (Ahmad and Jairajpuri, 2010; Bongers, 1988; Mai, 2018). Nematodes were further categorized into four trophic groups based on morphological characteristics, bacterivores, fungivores, plant parasites, and omnivores–predators (Yeates et al., 1993). Furthermore, nematode genera were classified into five colonizer-persister (c-p) groups (c-p1 to c-p5) based on varying life cycle strategies, encompassing the transition from *r*-strategistis to *K*-strategistis (Bongers, 1990). The total abundances of nematodes and each taxonomic group were converted to the individuals per 100 g of dry soil. Nematode genus richness (GR) was expressed as the number of genera per composite sample. Shannon-Wiener diversity index [$H' = -\Sigma$ (pi (lnpi))], where pi is the proportion of *i*-th genera in a sample. Simpson index ($\lambda = \sum pi^2$), where pi is the proportion of *i*-th genera in a sample;

and evenness index [$J' = H'/\ln(GR)$] was used to characterize the diversity and stability of nematode communities, where H' is the Shannon-Wiener diversity index and GR is the nematode genus richness (Neher and Darby, 2009).

To assess nematode community characteristics, we computed several indices of community structure, including the Enrichment Index (EI), Channel Index (CI), Structural Index (SI), Basal Index (BI), Nematode Channel Ratio (NCR), and Maturity Index (MI). The EI, CI, SI, and BI were calculated following to the methods described by Ferris et al. (2001). The NCR was calculated according to the method described by Yeates (2003). The MI was calculated using the methods described by Bongers et al. (1990). These indicators can reveal the structure of the soil food web, nutrient enrichment, and decomposition pathway.

2.3. Statistical analyses

All data in this study underwent natural log transformation [ln(n + 1)] to meet the assumption of normality. To assess the normality of distribution and homogeneity of variances, we conducted Shapiro-Wilk and Bartlett's tests, respectively. Subsequently, a two-way analysis of variance (ANOVA) was conducted to investigate the influence of grubbing and seasons (spring and autumn) on various aspects, including soil nematode abundance and trophic structure, genus richness, ecological indices, as well as other abiotic factors (i.e., TC, TN, TP, AP, NO_3^--N, NH_4^+-N, AN, pH, SWC). The Tukey-Kramer test was used to test the differences between treatments. Statistical significance was considered at the $P < 0.05$ level. To visualize the variation in soil nematode community composition among different samples, we employed non-metric multidimensional scaling (NMDS) with 999 permutations, based on Bray-Curtis dissimilarity matrices. This analysis was performed using the "vegan" R package (v. 2.6.4, Oksanen et al., 2022). Furthermore, analysis of similarities (ANOSIM) with permutations = 999, also based on Bray-Curtis distances, was conducted to assess the significance of the NMDS analyses. To elucidate the impacts of soil parameters on the composition of trophic groups within soil nematodes, redundancy analysis (RDA) was carried out using the "vegan" R package. (v. 2.6.4, Oksanen et al., 2022). Additionally, Spearman's correlation was employed to investigate relationship between nematode trophic groups (bacterivores, fungivores, plant parasites, omnivores–predators), colonizer-persister (c-p) groups (c-p1 to c-p5), ecological indices (GR, H', λ, J', MI, NCR, BI, EI, SI, and CI), and nutrient parameters (TC, TN, TP, AP, AN, NO_3^--N, NH_4^+-N, pH, and SWC). The "pheatmap" R package (v. 1.0.12, Kolde, 2019) was utilized for this correlation analysis. All statistical analyses were performed using R (v. 4.1.2) Statistical Software (R Core Team, 2021).

3. Results

3.1. The impact of grubbing on soil parameters and nematode communities

Wild boar grubbing significantly increased ammonium nitrogen and nitrate nitrogen by 40.6 % and 40.7 % (relative change, $P < 0.05$), respectively, while there was no significant effect of grubbing on soil pH, AP, AN, SWC, TC, TN, and TP contents (Table 1, Table 2).

A total of 68 genera of soil nematodes were identified in this study (Table 3, Fig. 3), including 20 genera of bacterivores (Ba), 7 genera of fungivores (Fu), 19 genera of omnivores-predators (Op) and 22 genera of plant parasites (Pp). The top 10 genera in terms of relative abundance of soil nematode communities were *Filenchus*, *Teratocephalus*, *Boleodorus*, *Prismatolaimus*, *Cephalobus*, *Monhystera*, *Lelenchus*, *Aphelenchoides*, *Helicotylenchus*, and *Plectus*.

There was no significant effect of wild boar grubbing on soil nematode c-p groups and soil nematode ecological indices (all $P > 0.05$, Fig. 4, Fig. 5), while there was a significant effect on bacterivores ($P < 0.05$, Fig. 6a), increasing by 13.6 % in grubbed plots. In spring, the relative abundance of bacterivores was significantly higher by 55.8 % ($P < 0.05$, Fig. 6a), and that of plant parasites was significantly lower by 28.9 % ($P < 0.05$, Fig. 6d) in grubbed plots than in non-grubbed ones. However, there was no significant difference in the relative abundance of bacterivore and plant parasites between non-grubbed and grubbed plots in autumn (both $P > 0.05$). The relative abundance of fungivores in autumn was 34.21 % higher (relative change, $P < 0.05$) in grubbed than in non-grubbed plots (Fig. 6b). Wild boar grubbing significantly increased the proportion of *Prismatolaimus* by 28.85 % compared to non-grubbed plots (relative change, $P < 0.05$, Table S1). There was no significant effect of wild boar grubbing on any of the other top ten genera.

Table 1
Two-way ANOVA results (F-values) for the effects of grubbing (G), season (S), and their interaction on soil parameters in a broad-leaved Korean pine forest in Changbai Mountain.

Dependent variable	G	S	G × S
pH	0.951	**85.366***	0.427
SWC	0.186	0.189	0.021
TC	0.960	3.838	0.788
TN	0.535	**5.395***	1.111
TP	0.477	**8.601****	0.081
AP	1.486	**26.784*****	1.298
AN	1.486	**26.784*****	1.298
NH_4^+-N	**16.395*****	**283.664*****	**5.554***
NO_3^--N	**113.018*****	**18.377*****	**122.629*****

Notes: TC, total carbon; TN, total nitrogen; TP, total phosphorous; AP, available phosphorous; AN, available nitrogen; SWC, soil water content; NH_4^+-N, soil ammonia nitrogen; NO_3^--N, soil nitrate nitrogen. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2
Soil parameters in plots with (grubbed; G) or without (non-grubbed; NG) wild boar activity in Spring and Autumn.

Parameter	Spring_G	Spring_NG	Autumn_G	Autumn_NG
pH	5.69 ± 0.054a	5.71 ± 0.036a	5.20 ± 0.038b	5.28 ± 0.065b
TC (g/kg)	101.87 ± 5.283a	90.16 ± 3.842a	108.59 ± 7.155a	108.01 ± 7.964a
TN (g/kg)	8.51 ± 0.397a	7.68 ± 0.252a	9.10 ± 0.514a	9.25 ± 0.616a
TP (g/kg)	0.71 ± 0.060a	0.69 ± 0.039a	0.58 ± 0.029a	0.53 ± 0.057a
AP (mg/kg)	8.15 ± 1.440a	7.95 ± 2.689a	3.28 ± 0.264b	3.33 ± 0.340b
NH_4^+ (mg/kg)	12.34 ± 2.369c	7.62 ± 1.648c	65.95 ± 1.950a	48.06 ± 4.365b
NO_3^- (mg/kg)	1.48 ± 0.059b	1.50 ± 0.040b	1.78 ± 0.029a	0.82 ± 0.044c
AN (mg/kg)	13.82 ± 2.384c	9.11 ± 1.665c	67.73 ± 1.948a	48.88 ± 4.379b
SWC (%)	0.78 ± 0.088a	0.81 ± 0.053a	0.76 ± 0.038a	0.78 ± 0.049a

Notes: TC, total carbon; TN, total nitrogen; TP, total phosphorous; AP, available phosphorous; AN, available nitrogen; SWC, soil water content. Data are presented as mean ± SE. Different letters within a row indicate significant differences among treatments ($P < 0.05$).

3.2. The influence of sampling date on soil parameters and nematode communities

Season had a significant effect on soil pH, TP, AP, TN, AN, NH_4^+-N, and NO_3^--N (both $P < 0.05$, Table 1). Overall, soil pH, TP, AP, and NO_3^--N decreased by 8.06 %, 20.29 %, 50.93 %, and 12.77 %, respectively (relative change, $P < 0.05$, Table 2), while TN, AN, and NH_4^+-N increased by 13.34 %, 408.51 %, and 471.32 % (relative change, $P < 0.05$, Table 2), respectively, in autumn as compared with spring.

Season also had a significant effect on soil nematode communities.

Table 3
Taxonomic and trophic groups of the soil nematode community.

Bacterivores		Fungivores		Plant parasites		Omnivores–Predators	
Genus Name	c-p	Genus Name	c-p	Genus Name	c-p	Genus Name	c-p
Panagrolaimus	1	*Aphelenchus*	2	*Cephalenchus*	2	*Trischistoma*	3
Rhabditis	1	*Filenchus*	2	*Boleodorus*	2	*Tripyla*	3
Pelodera	1	*Aphelenchoides*	2	*Aglenchus*	2	*Eudorylaimus*	4
Plectonchus	1	*Diphtherophora*	3	*Lelenchus*	2	*Parkellus*	4
Rhuabditophanes	1	*Proleptonchus*	4	*Tenunemellus*	2	*Microdorylaimus*	4
Wilsonema	2	*Tylencholaimellus*	4	*Coslenchus*	2	*Comiconchus*	4
Cephalobus	2	*Tylencholaimus*	4	*Ditylenchus*	2	*Thonus*	4
Plectus	2			*Malenchus*	2	*Clarkus*	4
Anaplectus	2			*Tylenchus*	2	*Cobbonchus*	4
Acrobeloides	2			*Dolichorus*	3	*Labronema*	4
Acrobeles	2			*Criconemoides*	3	*Mylonchulus*	4
Monhystera	2			*Rotylenchulus*	3	*Epidorylaimus*	4
Chiloplacus	2			*Rotylenchus*	3	*Mesodorylaimus*	5
Euteratocephalus	3			*Pararotylenchus*	3	*Axonchium*	5
Prismatolaimus	3			*Nagelus*	3	*Laimydorus*	5
Teratocephalus	3			*Helicotylenchus*	3	*Aporcelaimellus*	5
Odontolaimus	3			*Ogma*	3	*Paraxonchium*	5
Bastiania	3			*Macroposthonia*	3	*Aporcelaimus*	5
Chronogaster	3			*Paratylenchus*	3	*Nygolaimus*	5
Alaimus	4			*Paratrichodorus*	4		
				Trichodorus	4		
				Longidorella	4		

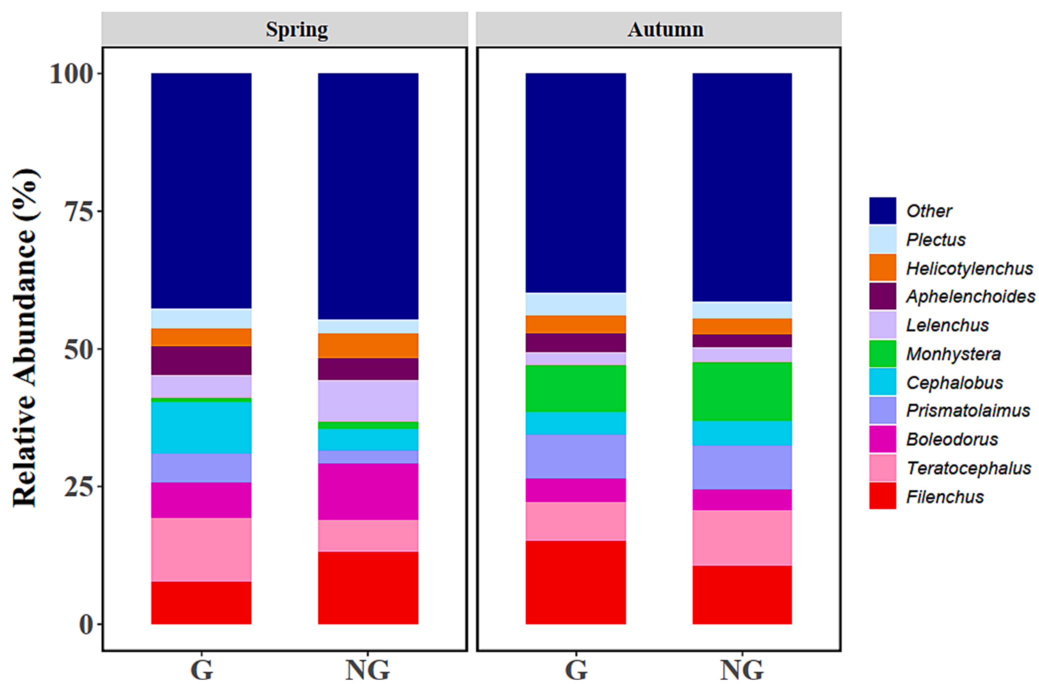

Fig. 3. Mean relative abundance of the top 10 dominant genera and other genera in the soil nematode community in non-grubbed plots (NG) and grubbed plots (G) in Spring and Autumn.

Specifically, soil nematode abundance increased by 132.1 % in autumn compared to spring (relative change, $P > 0.001$, Fig. 5a). Relative abundances of bacterivores and omnivores-predators were significantly greater (15.16 % and 127.5 %, respectively) in autumn than spring, while proportions of plant parasitic nematodes were significantly lower (47.1 %) in autumn than spring (all $P < 0.05$, Fig. 6). Season had a significant effect on soil nematode community c-p groups. Compared with spring, the relative proportions of c-p4 and c-p5 (*K*-strategists) increased by 31.2 % and 115.4 %, respectively, in autumn; whereas that of c-p1 (*r*-strategists) decreased by 71.3 % (all $P < 0.05$, Fig. 4). Other c-p classes and nematode diversity indices (GR, λ, H', J ') did not differ significantly between spring and autumn (all $P > 0.05$, Fig. 5b). Non-metric multidimensional scaling analysis (NMDS) based on Bray-Curtis dissimilarity matrices showed that soil nematode community composition clustered significantly due to grubbing in spring and autumn (ANOSIM, $P < 0.05$, Table 4, Fig. 7).

In terms of soil nematode indices, there was a significant effect of seasonal variation on MI, EI, and CI. In autumn, MI and CI increased by 37.5 % and 36.8 %, respectively; while EI decreased by 34.6 %, relative to spring (all $P < 0.05$, Fig. 5d, e, f). There were some effects of season on the relative abundance of dominant nematode genera. Proportions of *Prismatolaimus* (101.3 %) and *Monhytera* (763.6 %) were significantly greater in autumn than spring, while *Boleodorus* (50.3 %), *Lelenchus* (57.3 %) and *Aphelenchoides* (35.9 %) proportions were significantly

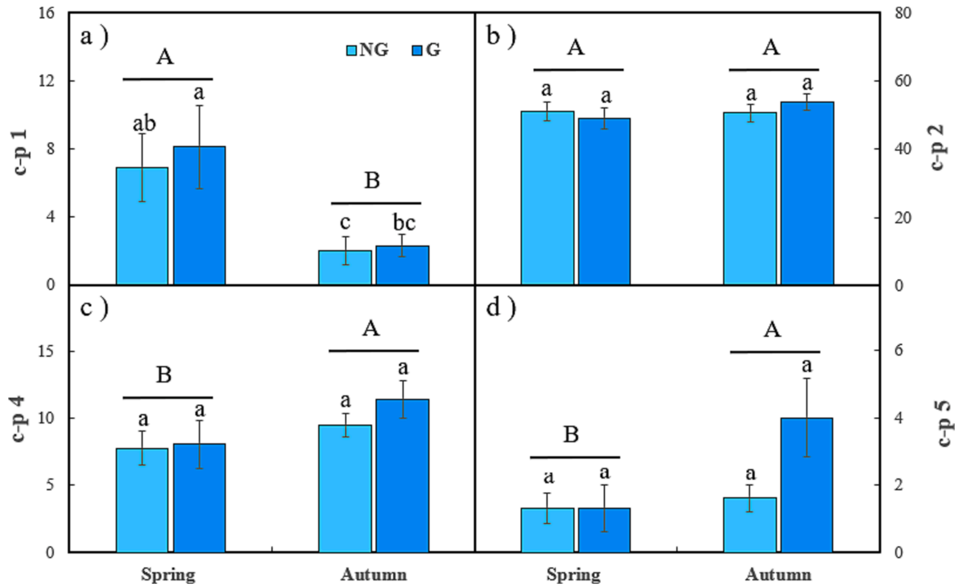

Fig. 4. Mean relative abundance of soil nematode community c-p groups in non-grubbed plots (NG) and grubbed plots (G) in Spring and Autumn. Different letters indicate significant differences at $P < 0.05$ (mean ± SE., n = 10).

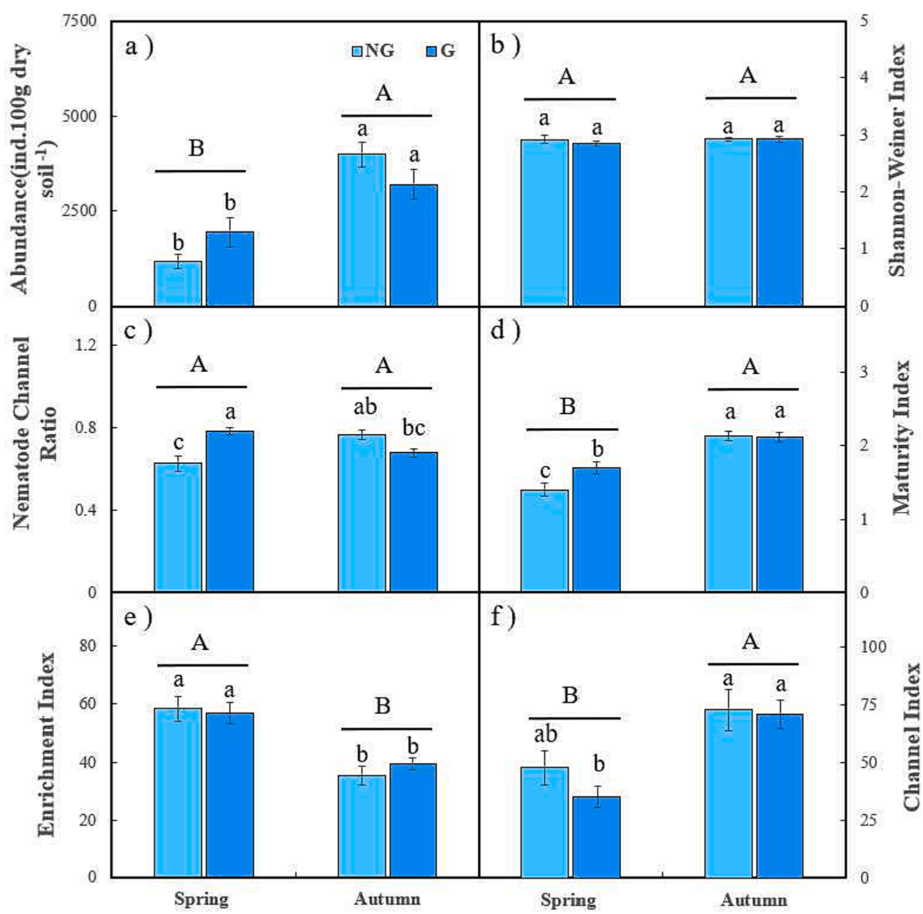

Fig. 5. Mean value of soil nematode ecological indices in non-grubbed plots (NG) and grubbed plots (G) in Spring and Autumn. Different letters indicate significant differences at $P < 0.05$ (mean ± SE., n = 10).

lower in autumn than spring (relative change, $P < 0.05$, Table S1, Fig. 3).

3.3. *The interplay between grubbing and season on soil properties and nematode communities*

There was an interaction effect between wild boar grubbing and

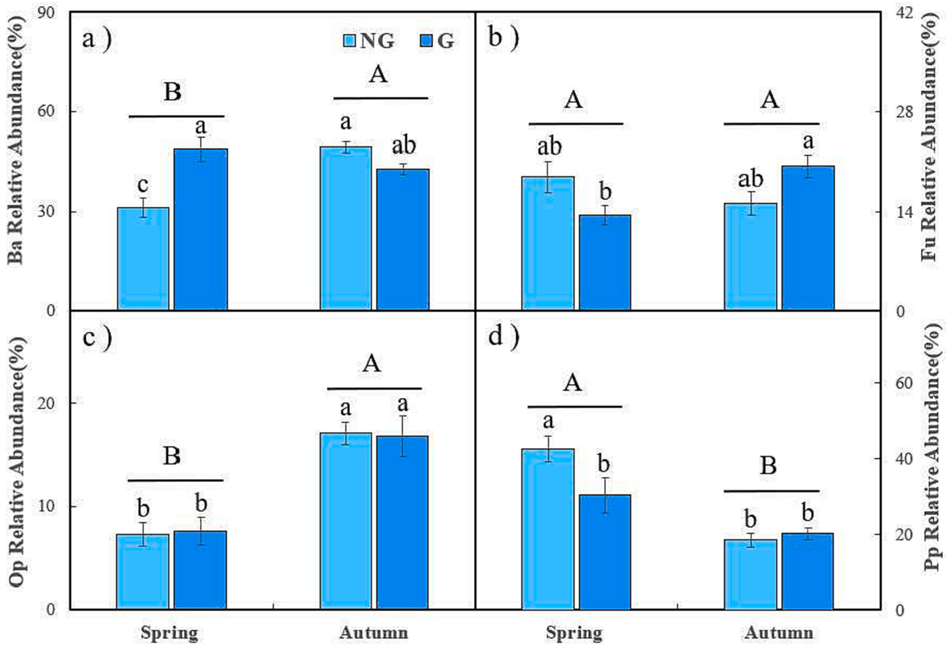

Fig. 6. Mean relative abundance of soil nematode community trophic groups in non-grubbed plots (NG) and grubbed plots (G) in Spring and Autumn. Different letters indicate significant differences at $P < 0.05$ (mean ± SE., n = 10). Ba, bacterivores; Fu, fungivores; Pp, plant parasites; Op, omnivores-predators.

Table 4
Analysis of similarities (ANOSIM), based on Bray-Curtis distances, of the soil nematode community in non-grubbed (NG) and grubbed (G) plots in May and October.

Treatment	Sums of squares	F	R^2	*P*
Spring vs Autumn	0.948	9.551	0.201	**0.001*****
NG vs G	0.139	1.156	0.029	0.273
Spring_NG vs Spring_G	0.295	2.673	0.129	**0.001*****
Spring_NG vs Autumn_NG	0.692	7.628	0.298	**0.001*****
Spring_G vs Autumn_G	0.584	6.278	0.259	**0.001*****
Autumn_NG vs Autumn_G	0.172	2.341	0.115	**0.003** **

Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

season on NH_4^+-N and NO_3^--N. In the non-grubbing plots, soil NH_4^+-N increased by 531.1 % (relative change) in autumn compared to spring, while soil NO_3^--N decreased by 45.47 % (all $P < 0.05$, relative change). Whereas, in the grubbing plots, the NH_4^+-N and NO_3^--N contents significantly increased by 434.4 % and 20.4 % ($P < 0.05$, relative change), respectively, in autumn compared to those in spring (Table 1, Table 2).

There was a significant interaction effect of grubbing and season on soil nematode abundance ($P < 0.05$, Fig. 5a). Soil nematode abundance was significantly higher in autumn than in spring for both non-grubbed (243 % higher) and grubbed plots (65 % higher) (both $P < 0.05$). However, nematode abundance did not differ significantly between grubbed and non-grubbed plots either in spring or in autumn ($P > 0.05$, Fig. 5a). No interaction between wild boar grubbing and season on soil nematode c-p groups, genus richness and nematode community diversity, as determined by the obtained Simpson index (λ), Shannon-Wiener diversity index (*H*'), and evenness index (J ') values, respectively (all $P > 0.05$, Fig. 5b). There was a significant interaction effect of wild boar grubbing and season on the relative abundance of bacterivores, fungivores, and plant parasites (all $P < 0.05$, Fig. 6). In spring, the relative abundance of bacterivores was significantly higher (relative change, $P < 0.05$) in the grubbing plots than in the non-grubbing plots (55.8 %), whereas the relative abundance of plant parasites in the non-grubbing plots was significantly higher ($P < 0.05$) than in the grubbing plots (40.6 %). The relative abundance of fungivores was 34.2 % higher (relative change, $P < 0.05$) in the wild boar grubbing plots than in the non-grubbing plots in autumn ($P < 0.05$, Fig. 6). Whereas there were no significant differences in bacterivores and plant parasites between the grubbing and non-grubbing plots in autumn.

For other nematode ecology indices, the interaction between wild boar grubbing and season was significant for both nematode channel rate ratio (NCR) and maturity index (MI) ($P < 0.05$, Fig. 5c, d). In spring, NCR was 25.1 % higher in the grubbed than in the non-grubbed plots ($P < 0.05$), while, no such difference was found in autumn ($P > 0.05$, Fig. 5c). NCR indicators for the non-grubbed plots in autumn were significantly greater (22.2 %) than those in spring. However, for the grubbed plots, NCR indicators were 13.5 % lower in autumn than in spring (all $P < 0.05$). In spring, MI was 21.7 % higher in grubbed plots than in non-grubbed ones ($P < 0.05$); however, no significant differences in MI was detected between the grubbed and non-grubbed plots in autumn ($P > 0.05$, Fig. 5d). The MI index was 53.2 % higher (relative change, $P < 0.05$) in autumn compared to spring in the non-grubbing plots, and 24.53 % higher (relative change, $P < 0.05$) in autumn in the wild boar grubbing plots compared to spring.

The interaction between season and grubbing had no significant effect on EI, BI, SI, and CI ($P > 0.05$). The interaction between wild boar grubbing and season was significant for the fungivores nematode *Filenchus* and the bacterivores nematode *Teratocephalus* ($P < 0.05$, Table S1, Fig. 3). Under the wild boar grubbing treatment, the fungivores nematode *Filenchus* increased by 94.9 % in autumn compared with spring (relative change, $P < 0.01$), whereas the bacterivores nematode *Teratocephalus* and the plant parasites nematode *Lelenchus* decreased by 39.1 % and 45.2 % (relative change, $P < 0.05$, Fig. 3), respectively.

The first and second canonical axes of redundancy analysis (RDA) collectively explained 49.5 % of the total variance. Soil NH_4^+ ($P < 0.001$), soil pH ($P < 0.001$), and soil NO_3^- ($P < 0.001$) were the primary soil parameters regulating nematode community composition (Fig. 8). Fungivores relative abundance was only significantly positively correlated with NO_3^--N. Omnivores-predators relative abundance was positively correlated with NH_4^+-N, TC, and AN and negatively with soil pH, TP, and AP. Plant parasites were positively correlated with AP, TP, and pH, and negatively with NH_4^+-N and AN (all $P < 0.05$, Table 5). At the c-p level, the relative abundance of nematodes in the c-p1 class showed a positive correlation with pH and AP, and a negative correlation with NH_4^+-N and AN. The relative abundance of c-p2 was only correlated

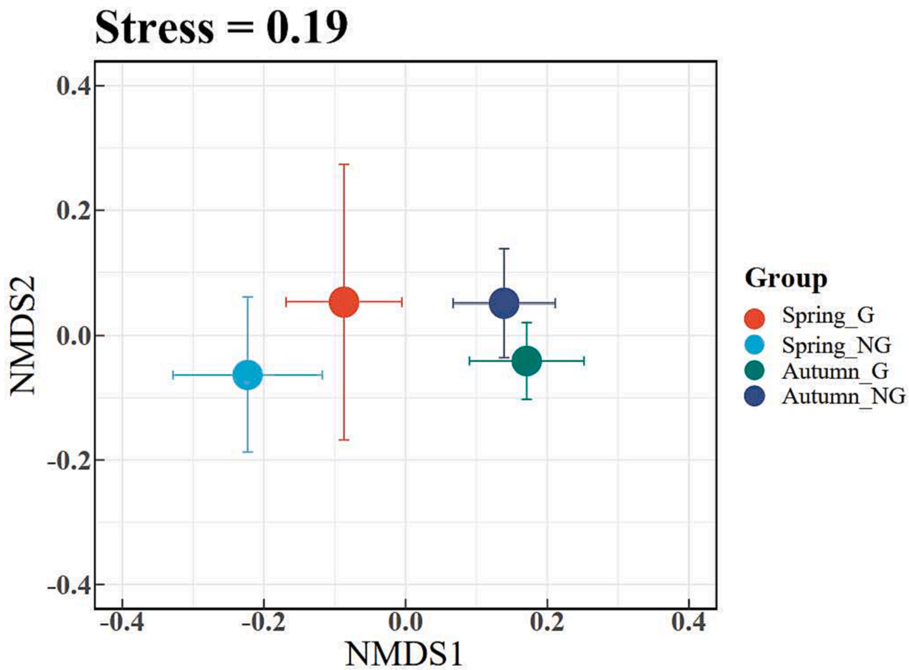

Fig. 7. Comparison of soil nematode community composition between grubbed (G) and non-grubbed plots (NG) between spring and autumn.

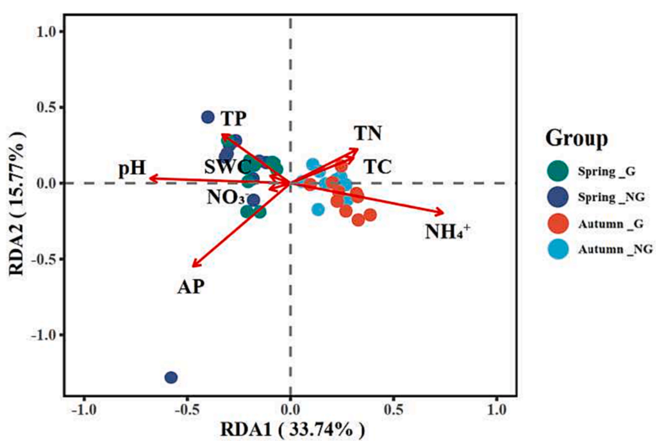

Fig. 8. Redundancy analysis (RDA) soil nematode community structure and soil parameters in grubbed plots (G) and in non-grubbed plots (NG) in spring and autumn. (TC: Soil total carbon; TN: Soil total nitrogen; TP: Soil total phosphorus; AP: Soil available phosphorus; NH_4^+: Soil ammonia nitrogen; NO_3^-: Soil nitrate nitrogen; SWC: Soil water content).

(negatively) with SWC. The relative abundance of nematodes in the c-p3 class was negatively correlated with NO_3^--N, while the relative abundance of nematodes in the c-p5 class displayed a positive correlation with NH_4^+-N and AN (all $P < 0.05$, Table 5).

Soil pH was negatively correlated with soil nematode abundance, MI, BI, and CI, and positively correlated with EI (all $P < 0.05$, Table 6). AP was negatively correlated with soil nematode abundance, MI, and CI, and positively correlated with EI (all $P < 0.05$, Table 6). TC was positively corrected to soil nematode abundance and MI (all $P < 0.05$, Table 6). NH_4^+-N showed a positive correlation with soil nematode abundance, MI, and CI, and a negative correlation with EI (all $P < 0.05$, Table 6).

4. Discussion

4.1. Grubbing effect on soil nematode community

Wild boar grubbing had no significant impact on soil nematode abundance, richness, and c-p groups, but it did exert a significant influence on soil nematode trophic groups. The result was not surprising because previous studies had shown that soil nematode trophic groups was sensitive to soil disturbance (Pothula et al., 2022). However, our research indicated that the response was not consistent among different trophic groups, and the relative abundance of bacterivores increased

Table 5
Correlation between soil nematode nutrient groups and soil parameters.

	pH	TC	TN	TP	AP	NH_4^+-N	NO_3^--N	AN	SWC
Ba	−0.26	0.21	0.27	−0.23	−0.13	0.28	−0.21	0.28	−0.06
Fu	−0.1	−0.16	−0.21	−0.2	−0.17	0.1	**0.34***	0.1	−0.17
Op	**−0.62****	**0.35***	0.28	**−0.42****	**−0.42****	**0.59****	−0.05	**0.59****	−0.14
Pp	**0.45****	−0.19	−0.15	**0.43****	**0.38***	**−0.53****	0.04	**−0.53****	0.2
c-p1	**0.58****	−0.2	−0.17	0.12	**0.33***	**−0.41****	0.15	**−0.4***	0.14
c-p2	−0.04	−0.08	−0.1	−0.24	−0.17	0.08	0.17	0.07	**−0.39***
c-p3	−0.11	0.12	0.18	0.22	0.1	−0.18	**−0.39***	−0.18	0.23
c-p4	−0.23	0.13	0.11	−0.21	−0.1	0.3	0.12	0.31	0.2
c-p5	−0.09	0.06	−0.03	−0.22	−0.22	**0.43****	0.28	**0.42****	−0.2

Note: Ba, bacterivores; Fu fungivores; Pp, plant parasites; Op, omnivores-predators; Pp, plant parasites; c-p1-5, colonizer-persister groups 1–5; TC, total carbon; TN, total nitrogen; TP, total phosphorous; AP, available phosphorous; AN, available nitrogen; SWC, soil water content. Significance level: * $P < 0.05$, ** $P < 0.01$.

Table 6
Correlation between soil nematode ecological indices and soil parameters.

	pH	TC	TN	TP	AP	NH_4^+-N	NO_3^--N	AN	SWC
Abundance	**−0.64****	**0.52****	**0.46****	−0.16	**−0.31***	**0.58****	−0.21	**0.58****	0
Richness	0.11	−0.14	−0.23	−0.31	0.06	0.08	−0.06	0.08	−0.02
H'	0.14	−0.19	−0.27	−0.32*	0.1	0.09	0.02	0.09	0.01
λ	0.13	−0.18	−0.19	−0.27	0.06	0.08	−0.02	0.08	0.06
J'	0.11	−0.06	−0.06	−0.15	0.09	0.03	0.02	0.03	0.1
NCR	−0.06	0.23	0.29	0.13	0.1	0.04	−0.28	0.04	0.08
MI	**−0.59****	**0.33***	0.29	**−0.46****	**−0.39***	**0.61****	−0.04	**0.62****	−0.14
BI	**−0.33***	−0.01	−0.02	−0.25	−0.23	0.18	−0.02	0.17	−0.25
EI	**0.67****	−0.31	−0.31	0.25	**0.39***	**−0.53****	0.15	**−0.52****	0.14
SI	−0.17	0.3	0.25	−0.06	0	0.24	−0.08	0.24	0.05
CI	**−0.59****	0.21	0.19	−0.22	**−0.35***	**0.44****	−0.07	**0.43****	−0.14

Note: Abundance, soil nematode abundance; Richness, soil nematode richness; *H'*, Shannon-Weiner index; *λ*, Simpson's diversity index; *J'*, Pielou evenness index; NCR, nematode channol ratio; MI, maturity index; BI, basal index; EI, enrichment index; SI, structure index; CI, channel index. TC, total carbon; TN, total nitrogen; TP, total phosphorous; AP, available phosphorous; AN, available nitrogen; SWC, soil water content. Significance level: * $P < 0.05$, ** $P < 0.01$.

and plant parasites decreased due to wild boar grubbing disturbances.

Specifically, wild boar grubbing significantly increased the relative abundance of bacterivores, particularly the genus *Prismatolaimus*. This phenomenon can be attributed to several factors. Bacterivores often exhibit opportunistic responses to resource enrichment than other nematode functional groups (Ferris and Matute, 2003). External applications of organic matter, such as manure and crop stubble, are known to enhance bacterivore populations (Liu et al., 2013). In the context of wild boar grubbing, the disturbance of soil structure, the mixing of litter with mineral soil, and the potential input of nutrients through wild boar excreta could collectively contribute to improved soil microbial activity, consequently influencing the relative abundance of bacterivores (Liu et al., 2020; Qi et al., 2011). This is in line with previous findings by Quist et al. (2016), who reported increased relative abundance of *Prismatolaimus* nematodes following the application of organic fertilizer.

On the other hand, the relative abundance of plant parasitic nematodes decreased significantly after grubbing. Although forest floor litter, which consists mainly of woody plant leaves, is the main source of underground soil fauna, plant parasites are host-specific, and a decrease in the abundance of plants (especially herbaceous plants) may negatively affect plant parasites (Korboulewsky et al., 2016; Poeydebat et al., 2017). This could be attributed to the fact that wild boar grubbing destroys plants and their root systems (Li et al., 2021; Bueno et al., 2013), reducing belowground plant biomass and, subsequently, less suitable habitat and food resources for plant-parasitic nematodes. Additionally, previous studies have reported that the change in physical–chemical properties is an important driving factor in affecting the activity of plant-parasitic nematodes (Jiang et al., 2015). The negative correlation observed between plant parasite abundance and soil ammonium and available nitrogen documented in this study suggests that the increase in soil ammonium levels caused by grubbing may have adverse effects on plant parasites. High ammonium concentrations in soil are known to be toxic to soil nematode communities, particularly plant parasites (Wei et al., 2012). This could be another reason for the decrease in the relative abundance of plant parasites in our study.

The Nematode Channel Ratio (NCR) is an indicator of the dominance of either bacterial or fungal decomposition pathway, with values ranging from 0 (representing fungal-dominated decomposition) to 1 (indicating bacterial-dominated decomposition) (Yeates, 2003). Notably, both decomposition pathways are dependent on each other and there is a dynamic balance between the two channels (Ruess and Ferris, 2004). In the context of wild boar grubbing, an increase in NCR was observed, signifying an elevated proportion of bacterial decomposition. The NCR values were all greater than 0.5, indicating that the soil nematode taxa in the study area were dominated by bacterivores nematodes. Wild boar grubbing promoted the decomposition of organic matter in the broad-leaved Korean pine forest ecosystem through enhancing the bacterial pathway. This may cause a "promotional effect" that supports the hypothesis of " Wild boar grubbing can promote the activation of inert organic carbon in the soil" of the study by Liu et al. (2020) and needs to be further verified in future studies.

Nematode Maturity Index (MI) serves as an indicator of soil nematode community structure stability (Bardgett and Wardle, 2010; Wei et al., 2012). In the context of wild boar grubbing, an increase in MI suggests a more mature soil food web. This phenomenon can be attributed to several factors: First, Grubbing-induced changes in soil physical structure, such as increased soil porosity and enhanced ventilation, expose previously protected soil organic matter to microbial oxidation, creating an environment conducive to rapid biota turnover within the soil food web (Long et al., 2017). Second, wild boar excreta contributes rapidly decomposable organic matter to the soil, consistent with the impact of farm manure application on MI (Dong et al., 2013; Malizia et al., 2000). Finally, wild boar grubbing can physically fragment plant litter and increase the input of organic matter into mineral soil through burial (Risch et al., 2010), thereby enhancing microbial activity and promoting the activation of inert organic carbon in the soil (Liu et al., 2020). Therefore, a complex channels of soil food web was formed by the grubbing of wild boar.

4.2. Seasonal variation of soil nematode community by grubbing effect

In this study, we observed an intriguing phenomenon where wild boar grubbing in spring had a more pronounced impact on soil nematodes compared to that in autumn. Specifically, spring grubbing significantly increased in the relative abundance of bacterivores, the Nematode Channel Ratio (NCR), and the Maturity Index (MI), coupled with a significant decrease in the relative abundance of plant parasites. These findings imply that the long-term wild boar grubbing may mitigate the effects of seasonal variation on soil nematode communities, resulting in higher MI and enhanced stability in nematode community abundance. Previous studies have reported that soil nutrients play a pivotal role in governing the seasonal dynamics of soil nematodes (De Deyn and Van Der Putten, 2005; Hu et al., 2022; Neher et al., 2005). Bacterivores and fungivores constitute the majority of soil nematode communities, with their food sources relying on the input of plant-derived organic matter through litter and roots (Neher, 1999). During spring, plants actively absorb nutrients from the soil, leading to a depletion of essential elements to microorganisms. This, in turn, results in a shortage of food resources for soil nematodes and a subsequent decline in nematode density (Song et al., 2016). Although the plant root system secretes substances and organic matter during its growth, which can serve as resources for bacterial and fungal growth, and providing prey for the both nematodes (Elfstrand et al., 2008), their food source is limited during spring (Sohlenius and Boström, 2001). As a result, the population density of bacterivore and fungivore nematodes in spring is lower. At this time, there is a scarcity of resources in the soil food web, and wild boar grubbing improves soil aeration, mixing surface litter with mineral soil and rapid growth of microbial abundance in the soil. Inputs of wild boar feces provide a fast-turnaround source of food for the scarce soil food web, which leads to changes in the soil nematode abundance. Conversely, in autumn, the input of plant litter and root materials into the soil's organic pool peaks, fostering the rapid proliferation of bacteria and fungi within the soil. This phenomenon, in conjunction with shifts in soil nematode abundance, can be attributed to the seasonality of nutrient availability (Song et al., 2016).

In underground food webs, lower trophic-level organisms are typically influenced by bottom-up forces (Bardgett and Wardle, 2010). Considering seasonal variations, we observed contrasting trends in fungivorous nematodes between grubbing plots and non-grubbing plots. Specifically, the relative abundance of fungivorous nematodes significantly increased during autumn in grubbed plots, while it decreased during autumn in non-grubbed plots. This phenomenon may be attributed to the soil and litter mixing caused by wild boar grubbing, which accelerates mineralization and promotes rapid fungal colonization (Miranda et al., 2019). It provides favorable conditions for fungal growth and colonization in autumn compared to spring. Carpio et al. (2022) discovered that wild boar grubbing substantially increased the abundance of fungal sporocarps, particularly those of saprophytic sporocarps. Free-living saprotrophic fungi play a crucial role in decomposing soil organic matter and mobilizing nutrients. An increase in the abundance of fungi can provide abundant food resources for fungivorous nematodes. The absence of this phenomenon in spring might be due to slower fungal recovery during this season and the low nutrient content in the soil, disadvantaging fungi in competition with bacteria in a nutrient-poor environment (Thakur and Geisen, 2019). Kranabetter et al. (2019) noted that saprotrophic fungal guilds exhibited higher N concentrations compared to symbiotic species, indicating a positive correlation between fungal N and soil N content. Our Spearman's correlation analysis revealed a significant positive relationship between the relative abundance of fungivorous nematodes and soil nitrate N. Our study observed a significant increase in soil nitrate concentration during the fall due to the activities of wild boar. This suggests that wild boar' disturbances alter nitrogen transformations (Bueno and Jiménez, 2014; Singer et al., 1984). Consequently, wild boar disturbances can boost the abundance of fungal, subsequently increasing the relative abundance of fungivorous nematodes.

The wild boar grubbing weakened the effect of season on plant parasites and reduced the variation range of plant parasite abundance. Plant parasites have a host-specific nature and their abundance is closely related to plant species composition. (De Deyn et al., 2004; Hu et al., 2017). Changes in plant abundance can directly affect the input of root exudates and litter to the soil food web, and thus influence the access of plant parasites to food resources (Hu et al., 2017). At the beginning of the growing season, plants begin to grow, and their root activity is high. Wild boar feed on plant roots, and reduces plant abundance (Brunet et al., 2016), which significantly decreased plant parasites in our study. Similarly, at the end of the growing season, the biomass and activity of live plant roots decrease, which result in the loss of some plant parasites owing to insufficient food or fewer hosts. Song et al. (2016) showed that some plant parasite nematodes gradually disappear in mid and late growing season, which was consistent with our findings that the proportion of some phytophagous nematodes, such as *Boleodorus* and *Lelenchus*, decreased in autumn. This result is also consistent with previous studies conducted on temperate steppe environments (Bakonyi and Nagy, 2000).

5. Conclusions

Wild boar grubbing, characterized by its disruption of above-ground vegetation and alterations to soil physical and chemical properties, especially available nitrogen levels, can influence soil nematode communities within the temperate broad-leaf Korean pine forest. Our study demonstrated that wild boar disturbance can increase the relative abundance of bacterivorous nematodes while decrease that of plant parasitic nematodes. Remarkably, the influence of grubbing was more pronounced during spring than in autumn. Over the long term, wild boar activity appears to attenuate seasonal driven variations in soil nematode communities, resulting in higher nematode MI values and greater stability in nematode community abundance. As such, our observations highlighted the response of soil nematode communities to wild boar disturbance varied with the season, an effect that should be considered when evaluating the relationship between bioturbation and soil ecosystem processes. Furthermore, this study establishes baseline data concerning the repercussions of wild boar grubbing activities on soil fauna communities, providing valuable insights into the broader field of soil ecology.

Author Contribution

JQ Zheng and FR Rong conceived the presented idea and received important feedback from all co-authors. Field management was carried out by ZJ Sun, SJ Han, and MM Cui. Sampling collections, nematode preparation and identification were carried out by ZJ Sun and JQ Zheng. Soil chemical analysis were carried by YX Cui and C Meng. The manuscript was written by ZJ Sun with help from H Setälä and JQ Zheng. All authors discussed the methods and results and contributed to the final manuscript.

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.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121549.

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