RESEARCH ARTICLE

Effects of tree species identity and soil origin on soil nematode communities and trophic composition in coniferous and broad-leaved forests

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Abstract

Purpose The effects of trees on soil nematode communities are related to nutrient cycles in forest ecosystems. We conducted greenhouse pot experiments to determine the effects of a single tree species for each of coniferous and broad-leaved tree on soil nematodes.

Methods Soils were collected from a coniferous plantation and broad-leaved forests. Seedlings of a coniferous tree (*Cryptomeria japonica*) and a broad-leaved tree (*Quercus serrata*) were planted in soils derived from each species. After 11 months, seedling biomass, soil properties, and ectomycorrhizal fungal colonization of *Q. serrata* were measured. Soil nematodes were morphologically identified to the genus/family level and differentiated by community and trophic composition.

Results *C. japonica* root biomass was significantly higher than that of *Q. serrata* regardless of the soil and nematode community structures were significantly different between the species. The fungal: bacterial ratio and density of fungivorous nematodes were significantly higher in broad-leaved soils. Herbivorous nematodes increased significantly in *C. japonica* seedlings grown in broad-leaved soils. Structural equation modeling indicated that soil origin and tree species directly regulated nematode trophic compositions.

Conclusion Our findings suggest that tree species modify soil micro-food webs by affecting microbial abundance and nematode trophic composition. Specifically, *C. japonica*, with a larger root biomass, increased the number of herbivorous nematodes, whereas *Q. serrata*, with ectomycorrhizal fungal symbiosis, increased the number of fungivorous nematodes. Thus, tree species are tightly involved in shaping nematode communities in forest ecosystems through root traits and mycorrhizal types.

Keywords *Cryptomeria japonica* · Morphological identification · *Quercus serrata* · Root trait · Structural equation modeling

Responsible Editor: Sven Marhan.

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Introduction

In the rhizosphere, root exudates and sloughing root cells provide resources that support hotspots of microbes and soil fauna (Bonkowski et al. 2009). Lower trophic level animals such as herbivores and bacterivores are more responsive to changes in plant

species diversity and composition than organisms at higher trophic levels (De Deyn et al. 2004). Consumers at higher trophic levels may have access to a larger variety of prey than those at lower trophic levels (Scherber et al. 2010). Extramatrical fungal hyphae are vulnerable to grazing by soil fauna (Klironomos and Hart 2001). Thus, the bottom-up control of plant diversity may be weaker at higher trophic levels. Bacteria and fungi, together with the soil fauna that feed on them, are organized into micro-food webs, and their diverse interactions significantly affect plant growth (Berg et al. 2014; Fierer 2017).

Nematodes are a major group of soil microfauna and the most abundant animals on Earth (van den Hoogen et al. 2019). They play crucial roles in ecosystem processes, such as improving soil physical properties, participating in carbon and nitrogen cycling by feeding on bacteria and fungi (Ingham et al. 1985), and maintaining ecosystem health by occupying key positions in the soil food cycle (Bongers and Bongers 1998; Ferris 2010; Zhang et al. 2017; Thakur and Geisen 2019). In contrast, soil nematode communities are affected by subtle changes in both abiotic and biotic factors (Neher et al. 2005). For example, soil pH and organic carbon (C) are factors that determine the spatial distribution of soil nematodes in forest soils (Kitagami et al. 2020; Liu et al. 2019). In terms of biotic factors, root traits influence soil nematode abundance and community structure (De Deyn et al. 2008; Wilschut et al. 2019; Zhang et al. 2020, 2022). However, most observations have been based on herbaceous plants in agricultural soils, and there is a lack of knowledge regarding how abiotic and biotic factors affect the nematode community structure in woody plants in forest soils. Tree species influence soil biological, physical, and chemical properties through different root qualities (De Schrijver et al. 2012; Keith et al. 2009); yet our understanding of root-mediated effects on the composition and diversity of soil biota is still limited. In this study, we identified the factors that determine the structure of soil nematode communities by comparing the community patterns of these organisms in coniferous and broad-leaved forest soils.

Coniferous and broad-leaved trees exhibit significantly different effects on nematode trophic groups (Kondratow et al. 2019; Liu et al. 2023). Differences in litter quality among tree species have different effects on soil chemical properties (such as pH) and microbial communities (Sawada et al. 2021; Tanikawa et al. 2023), which, in turn, alter the trophic composition of nematodes (Cesarz et al. 2013). Moreover, root-associated mycorrhizal types, either arbuscular or ectomycorrhizal, are related to nematode communities in forest soils (Kudrin et al. 2021; Liu et al. 2023). Mycorrhizal associations shape activity and biomass of soil bacterial and fungal communities which are food resources for nematodes, i.e., arbuscular mycorrhizal trees showed higher bacterial growth whereas ectomycorrhizal trees showed higher fungal growth (Heděnec et al. 2020). Thus, tree species identities, through root traits and mycorrhizal types, can shape specific nematode communities; therefore, they are tightly involved in shaping nematode communities in forest ecosystems.

Japanese cedar, *Cryptomeria japonica* (Cupressaceae), is afforested in a large area as much as 18% of Japan (Forest Agency of Japan 2022). Recently, monocultural forests have been converted to coniferous-broadleaf mixed forests to maintain ecosystem functioning and services (Cavard et al. 2011). Alternatively, *Quercus serrata* (Fagaceae) is one of the candidate representative broadleaf trees for planting, especially in warm temperate climatic zones (Forest Agency of Japan 2022). In ecological relevance, the fine roots of *C. japonica* and *Q serrata* are associated with arbuscular mycorrhizal and ectomycorrhizal fungi, respectively (Matsuda et al. 2013, 2021). Such a different mycorrhizal type affects soil ecological processes and functions (Tedersoo et al. 2020).

This study aimed to determine the effects of a single tree species for each of conifer and broad-leaved tree on micro-food webs of soil nematodes communities by a pot experiment in a greenhouse. Seedlings of coniferous (*C. japonica*) and broad-leaved (*Q. serrata*) trees, both of which are the predominant species in Japan (Forest Agency of Japan 2022), were grown in monospecific pots with soils derived from either tree species. This monoculture of the pot experiment in a greenhouse could be useful for focusing on the effects of tree species and avoiding interference from other factors such as microclimate, topography, tree age, or the admixture of other plant species that generally exist in field experiments (Stefanowicz et al. 2021). We hypothesized that the abundance, community, and trophic composition of nematodes would be synergistically affected by the root traits and soil origin of tree species. Moreover, we hypothesized that nematodes were affected by soil biotic (i.e., microbes and root traits) and abiotic factors (i.e., pH and C/N), which are characterized by each tree species.

Materials and methods

Experimental set-up

In November 2019, we collected approximately 150 L each of soil layer from 0 to 20 cm in depth from a 50-year-old coniferous *C. japonica* plantation and broad-leaved *Q. serrata* forest in Mie Prefectural Forest Institute, Japan (34°65′N, 136°37′E). Soil from each site was classified as Brown Forest Soil (Forest Soil Division 1976) or Inceptisol (Soil Survey Staff 2014). Soil pH at the collecting points was slightly acidic, 5.62 and 4.17, at the coniferous plantation and broad-leaved forest, respectively. Annual precipitation and annual mean temperature in 2018, recorded at the nearest weather station (Tsu, 20 km from the forest), were 1630 mm and 16.9 °C.

Coarse roots, litter, and stones in the soil samples were discarded using a 2-cm mesh sieve. The sieved soil was gently homogenized before filling up Wagner pots (NF-5, top φ17 cm × bottom φ16 cm × height 19 cm) with 2 L of soils. After immersion in running water for 24 h, three seeds of either *C. japonica* or *Q. serrata* were sown in individual pots. The pots were placed in a greenhouse at 25 °C under a natural light condition and were supplied with distilled water for the first 3 months every day. For the next 8 months, 450 ml of distilled water was added to the pots every 3 days to maintain the water content at more than 10%. In total, 96 pots were established by combining two soil origins (*C. japonica* and *Q. serrata*) × two tree species (*C. japonica* and *Q. serrata*) × 24 replicates. Thus, four soil and tree species treatment combinations were established (Fig. S1): *C. japonica* soil with *C. japonica* seedlings (CC), *Q. serrata* soil with *C. japonica* seedlings (QC), *C. japonica* soil with *Q. serrata* seedlings (CQ), *Q. serrata* soil with *Q. serrata* seedlings (QQ).

Plant biomass, root traits, and mycorrhizal colonization

After 11 months, we carefully harvested the *C. japonica* and *Q. serrata* seedlings from each pot. The seedlings were used to observe root morphology and to measure shoot and root biomass. The soil remaining in the pots was used to measure environmental conditions and nematode extraction. The harvested seedlings were divided into shoot and root systems using pruning shears. Root systems in the soil blocks were washed in a 2-mm-mesh sieve under running tap water to remove adhering soil particles. The root systems were divided into two categories based on diameter: coarse roots ≥2 mm and fine roots ≤2 mm. The shoots and coarse and fine roots were dried at 70 °C for 2 weeks and then weighed. Images of all individual fine roots were acquired using a scanner (500 dpi; GT-9800, EPSON, Nagano, Japan). The average diameter and length of all individual fine roots were obtained using the image analysis software IJ Rhizo (Pierret et al. 2013). From these data, the specific root length (SRL), that is, the root length per unit dry weight (expressed as m g^{-1}), was calculated. The SRL represents the cost-benefit relationship of fine root production (Eissenstat and Yanai 1997). A higher SRL corresponds to thinner roots and a more frequent branching pattern, indicating efficient nutrient uptake (Ostonen et al. 2007).

Quercus serrata seedlings per pot were transferred onto 9-cm Petri dishes to count the number of root tips under a stereomicroscope (SZX16, Olympus, Tokyo, Japan). Root tips were defined as ectomycorrhizal (ECM) roots when fungal sheaths covered them entirely, with no cracks or shrinkage (Matsuda et al. 2013). We defined root tips with root hairs without ECM fungal colonization as non-mycorrhizal (non-ECM).

Soil environmental conditions

Soil pH (H$_2$O) was determined using air-dried fine soil (soil-to-distilled water ratio, 1:2.5) using a pH meter (MP220; Mettler-Toledo, Greifensee, Switzerland). A subset of the pot soil was oven-dried at 105 °C for 24 h and ground for the analysis of total C and N concentrations measured with an elemental analyzer (vario EL cube; Elementar Japan Ltd., Yokohama, Japan).

Bacterial and fungal abundances quantified by real-time PCR

Total DNA was extracted from 250 mg of moist soil using a Fast DNA SPIN Kit for Soil (Q-Biogene, Ohio, USA) following the manufacturer's instructions. Subsequently, all DNAs were quantified using QuantiFluor™ dsDNA System (Promega, Madison, USA) and DNA concentration for each extraction was

standardized to 20 ng μL^{-1}. The relative abundances of bacterial and fungal communities of each pot were assessed for each DNA extract by qPCR using a StepOne™ Real-Time PCR system (Applied Biosystems, Waltham, USA). For bacteria, a fragment of the 16S ribosomal ribonucleic acid (rRNA) gene was amplified using the Eub338/Eub518 primer pair (Fierer et al. 2005). For fungi, a fragment of the 18S rRNA gene was amplified using FR1/FF390 primers (Chemidlin Prévost-Bouré et al. 2011). Each 20 μL reaction contained 10 μL THUNDERBIRD™ Next SYBR® qPCR Mix (TOYOBO, Osaka, Japan), 0.4 μL per primer (10 μM), 2 μL template DNA (2 ng), and 7.2 μL H$_2$O. All samples were analyzed in duplicate using PCR strip tubes (Axygen, Thermo Fisher Scientific Inc., Waltham, USA). PCR amplification condition was set as follows: for bacteria; 95 °C for 2 min followed by 40 cycles of 95 °C for 15 s, 60 °C for 60 s (two-step), and for fungi; 95 °C for 15 min followed by 40 cycles of 95 °C for 60 s, 58 °C for 30 s, and 72 °C for 60 s. After amplification, melting curve and gel electrophoresis were performed to confirm that the amplified products were of the appropriate size. The qPCR efficiencies were 156.923% (R^2=0.947) for bacteria, and 100.648% (R^2=0.977) for fungi.

Standards for the qPCR assays were generated by PCR, amplifying each gene of interest from the genomic DNA of *Escherichia coli* clones containing plasmids that carried the respective PCR target fragment as an insert of a soil bacterial (unknown taxon) and fungal (*Botrytis cinerea* 20,201,009) strain using the primers previously described for each kingdom. The PCR products were confirmed on an agarose gel and cloned using a TA-Enhancer Cloning Kit (Nippon Gene, Toyama, Japan) following the manufacturer's instructions. Positive clones were further amplified using KOD One PCR Master Mix (TOYOBO, Osaka, Japan) and primers previously described for each kingdom. The thermal cycle program comprised 25 cycles of 98 °C for 10 sec, 55 °C for 5 sec, and 72 °C for 10 sec. Serial dilutions of each plasmid DNA were prepared, and bacterial and fungal gene copy numbers were calculated using a regression equation for each assay, relating the cycle threshold (Ct) value to the known number of copies in the standards, as described (Qian et al. 2007). The copy numbers of bacterial 16S rRNA and fungal 18S rRNA genes were expressed as copy number log 10 transformed per gram of dry weight soil. The fungi/bacteria (F/B) ratio was calculated for each pot based on the number of copies of the 16S rRNA or 18S rRNA genes log-transformed.

Nematode extraction and observation

Nematodes were extracted from 100 g of fresh soil samples from each pot by decanting and sieving, following Cobb's method (van Bezooijen 2006). Each soil sample was placed in a 2 L beaker and mixed with tap water. The water suspensions were stirred with a plastic spatula and decanted immediately into another 2 L beaker covered with a 1 mm mesh sieve (15 cm in diameter) to screen out stones and roots. The water suspensions were further mixed and decanted through successive 75 μm and 25 μm mesh sieves (15 cm in diameter). Finally, the remnants on each mesh sieve were carefully collected and pooled into a 50 mL beaker. The remaining sample matter was transferred into individual funnels (9 cm in diameter) covered with a paper-cleaning cloth (Prowipe S200; Elleair, Tokyo, Japan) and further processed to extract nematodes using the Baermann funnel technique for 24 h at 25 °C (Baermann 1917). The extracted nematodes were transferred into a Petri dish filled with distilled water and counted under a stereomicroscope to estimate their density (per gram of dried soil). Nematodes were then transferred to glass slides with vertical lines, and up to the first 100 individuals encountered in each sample (some samples contained as few as 80 nematodes) were identified at 100–400× magnification under a compound light microscope (BX53, Olympus, Tokyo, Japan). Nematodes were identified to the genus/family level following Bongers (1988) and divided into four trophic groups (bacterivorous, fungivorous, herbivorous, and predatory-omnivorous) based on the structural characteristics of their oral parts (Yeates et al. 1993).

Data and statistical analysis

To compare nematode densities among the treatments, the Steel–Dwass test was performed using the NSM3 package (Schneider et al. 2021) in R software version 4.3.1 (R Development Core Team 2023). We generated a non-metric multidimensional scaling (NMDS) scatter plot based on the Chao dissimilarity index using nematode taxonomic data, by generating 20 permutations using the metaMDS function in the vegan package (Oksanen et al. 2022) in R. In addition, permutational multivariate analysis of variance (PERMANOVA) was performed to determine whether the nematode

community structures differed among the treatments; 9999 permutations were conducted using the adonis function in vegan. The effects of soil, plant, and microbial properties on nematode community structure were determined by conducting 9999 permutations using the envfit function in vegan. Indicator species analysis (Dufrêne and Legendre 1997) was performed to determine whether any characteristic nematode genera were present among the treatments. This analysis was performed using indicator values for each nematode genus, and statistical significance was tested using a Monte Carlo test (9999 permutations). These analyses were performed using the indicspecies package (Cáceres and Legendre 2009) in R.

A structural equation model was constructed to provide a mechanistic understanding of how soil origin and tree species affect the trophic groups of nematodes. Structural equation modeling is a multivariate statistical method that allows for hypothesis testing of complex path-relation networks under any conditions (Grace et al. 2007). The full initial model (Fig. S2) was constructed a priori based on the hypotheses that (1) soil origins and tree species affected soil abiotic factors, root biomass, F/B ratio, and the abundance of nematode trophic groups; (2) soil abiotic factors affected root biomass, F/B ratio, and the abundance of nematode trophic groups; (3) F/B ratio affected bacterivorous and fungivorous nematodes; (4) root biomass affected herbivorous nematodes; (5) predatory and omnivorous nematodes feed on bacterivorous, fungivorous, and herbivorous ones. We added double headed arrows specifying residual covariance

(Bacterivores < − > Fungivores, Bacterivores < − > Herbivores, Fungivores < − > Herbivores) because the prey-predator interaction was fundamentally unknown. The model was constructed using data from all pots ($n = 96$). The analysis was performed using the piecewise SEM package (Lefcheck 2016) in R. In this analysis, soil origin and tree species were indicated as categorical explanatory variables, that is, soil origin: *C. japonica* (1) and *Q. serrata* (2) and tree species: *C. japonica* (1) and *Q. serrata* (2). Principal component analysis (PCA) was performed to reduce the dimensions of the soil abiotic factors, i.e., soil pH and C/N. The first principal component of soil properties (Soil PC1) was negatively correlated with soil pH and the C/N ratio (Fig. S3). First, all non-significant paths ($P > 0.05$) were removed from the initial model. We then compared several models that incorporated all or part of the significant paths. The overall fit of the piecewise SEM was assessed using Shipley's test of d-separation, which combines the *P*-values associated with each of the k independence claims in Fisher's C statistics (Shipley 2009). For all analyses, the significance level was set at $P < 0.05$, unless otherwise stated.

Results

Plant biomass, root traits, and mycorrhizal colonization

Shoot biomass values were significantly greater with CC (24.2 ± 0.3 g) and QC than CQ and QQ (Table 1,

Table 1 Seedling biomass of *Cryptomeria japonica* and *Quercus serrata*, root trais, soil environmental factors and microbial abundance of four pot treatments

Treatment codes	CC	CQ	QC	QQ
Soil origins	*C. japonica*	*C. japonica*	*Q. serrata*	*Q. serrata*
Tree species	*C. japonica*	*Q. serrata*	*C. japonica*	*Q. serrata*
Shoot biomass (g)	24.2 ± 0.3a [*]	19.8 ± 0.2b	24.3 ± 0.4a	20.1 ± 0.3a
Root biomass (g)	5.79 ± 0.26a	5.50 ± 0.51a	4.91 ± 0.21a	3.44 ± 0.41b
Fine root (g)	5.11 ± 0.23a	1.71 ± 0.2b	4.24 ± 0.17a	0.95 ± 0.14c
Specific root length	41.6 ± 1.7b	116.4 ± 10.0a	40.2 ± 1.5b	122.6 ± 8.4a
Soil pH (H_2O)	5.80 ± 0.03a	5.60 ± 0.03b	4.38 ± 0.03c	4.18 ± 0.03d
Soil C (%)	5.91 ± 0.16a	6.29 ± 0.17a	4.76 ± 0.25b	3.63 ± 0.15c
Soil N (%)	0.29 ± 0.01a	0.30 ± 0.01a	0.27 ± 0.01a	0.20 ± 0.01b
C/N ratio	19.8 ± 0.1b	20.5 ± 0.2a	16.9 ± 0.4c	16.4 ± 0.7c
Bacterial copy ($\log^{10}$)	20.71 ± 0.07ab	19.43 ± 0.19c	20.63 ± 0.15a	20.32 ± 0.11a
Fungal copy ($\log^{10}$)	8.13 ± 0.04c	7.81 ± 0.09d	8.59 ± 0.08b	8.89 ± 0.06a
F/B ratio	0.392 ± 0.002c	0.402 ± 0.003c	0.416 ± 0.003ab	0.438 ± 0.004a

[*]Data showed means $\pm$ SE ($n = 24$), and different characters next to the values indicated significant differences in measured items among four treatments (Steel–Dwass test, $P < 0.05$)

Steel–Dwass, $P < 0.05$), but root biomass values were significantly greater with CC (5.7 ± 0.3 g), CQ and QC than QQ (Table 1, Steel–Dwass, $P < 0.05$). Fine root biomass values were significantly greater with CC (5.1 ± 0.2 g) and QC than CQ and QQ (Table 1, Steel–Dwass, $P < 0.05$). SRL values were significantly greater with CQ and QQ than CC and QC (Table 1, Steel–Dwass, $P < 0.05$). In the CQ and QQ treatments, ECM formation was confirmed in all the seedlings. The number of *Q. serrata* root tips was not significantly different between CQ (241 ± 5) and QQ (241 ± 6) (Wilcoxon rank sum test, W = 322, $P = 0.48$), and ECM root frequencies were not significantly different between CQ ($68.9 \pm 2.7\%$) and QQ ($62.8 \pm 2.8\%$) (W = 360, $P = 0.14$), respectively.

Soil environmental conditions

The soil pH of each pot treatment ranged from 4.18 ± 0.03 to 5.80 ± 0.03, and CC was significantly the highest among the four treatments (Table 1, Steel–Dwass, $P < 0.05$). The total C was significantly higher at CC and CQ than at other treatments (Table 1, Steel–Dwass, $P < 0.05$), and the total N was significantly higher at CC, CQ, and QC than at QQ (Table 1, Steel-Dwass, $P < 0.05$). The C/ N ratio ranged from $16.4 \pm 0.7 - 20.5 \pm 0.2$ and CQ had the highest value (Table 1, Steel–Dwass, $P < 0.05$).

Bacterial and fungal DNA abundance

Bacterial gene copy numbers log 10 transformed per gram dry weight soil were significantly greater at CC, QC, and QQ than that at CQ. Fungal gene copy numbers were significantly the highest in QQ (Table 1, Steel–Dwass, $P < 0.05$). The F/B ratio was significantly the highest in QQ (Table 1, Steel–Dwass, $P < 0.05$).

Nematode abundance of each trophic group and community structure

The abundance of total nematodes (number per 100 g dry soil) in pots ranged from 212 ± 28 to 620 ± 64 and the number was significantly highest in QC (Fig. 1, Steel–Dwass, $P < 0.05$). The abundance of herbivorous nematodes was significantly highest in QC (Fig. 1, Steel–Dwass, $P < 0.05$). The abundance of fungivorous nematodes were significantly higher in QQ and QC than the others (Fig. 1, Steel–Dwass,
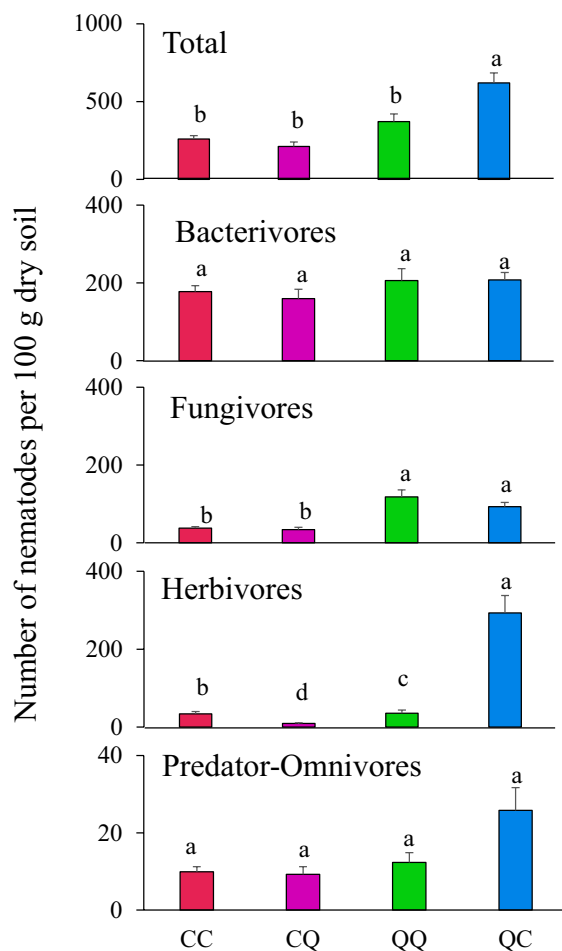

Fig. 1 Number of total nematodes and four trophic groups per 100-g dry soil at four different treatments. Columns are means ($n = 24$) with vertical bars of standard errors, and different characters upper to the bars indicated significant differences in nematode numbers among the treatments (Steel–Dwass test, $P < 0.05$). Treatment codes show *Cryptomeria japonica* soil with *C. japonica* seedlings (CC); *Quercus serrata* soil with *C. japonica* seedlings (QC); *C. japonica* soil with *Q. serrata* seedlings (CQ); *Q. serrata* soil with *Q. serrata* seedlings (QQ)

$P < 0.05$). Bacterivorous and predatory-omnivorous nematodes were not significantly different among pots (Fig. 1, Steel–Dwass, $P > 0.05$).

The NMDS scatter plot shows that the nematode community structures were significantly clustered among the four pot treatments (Fig. 2; stress value = 0.223, PERMANOVA, permutation 9999, $P < 0.001$, $R^2 = 0.70$). Among the environmental factors measured, soil origin, tree species, shoot biomass, root biomass, fine roots, SRL, soil pH, soil C, soil N, C/N ratio, bacterial and fungal gene copy numbers,
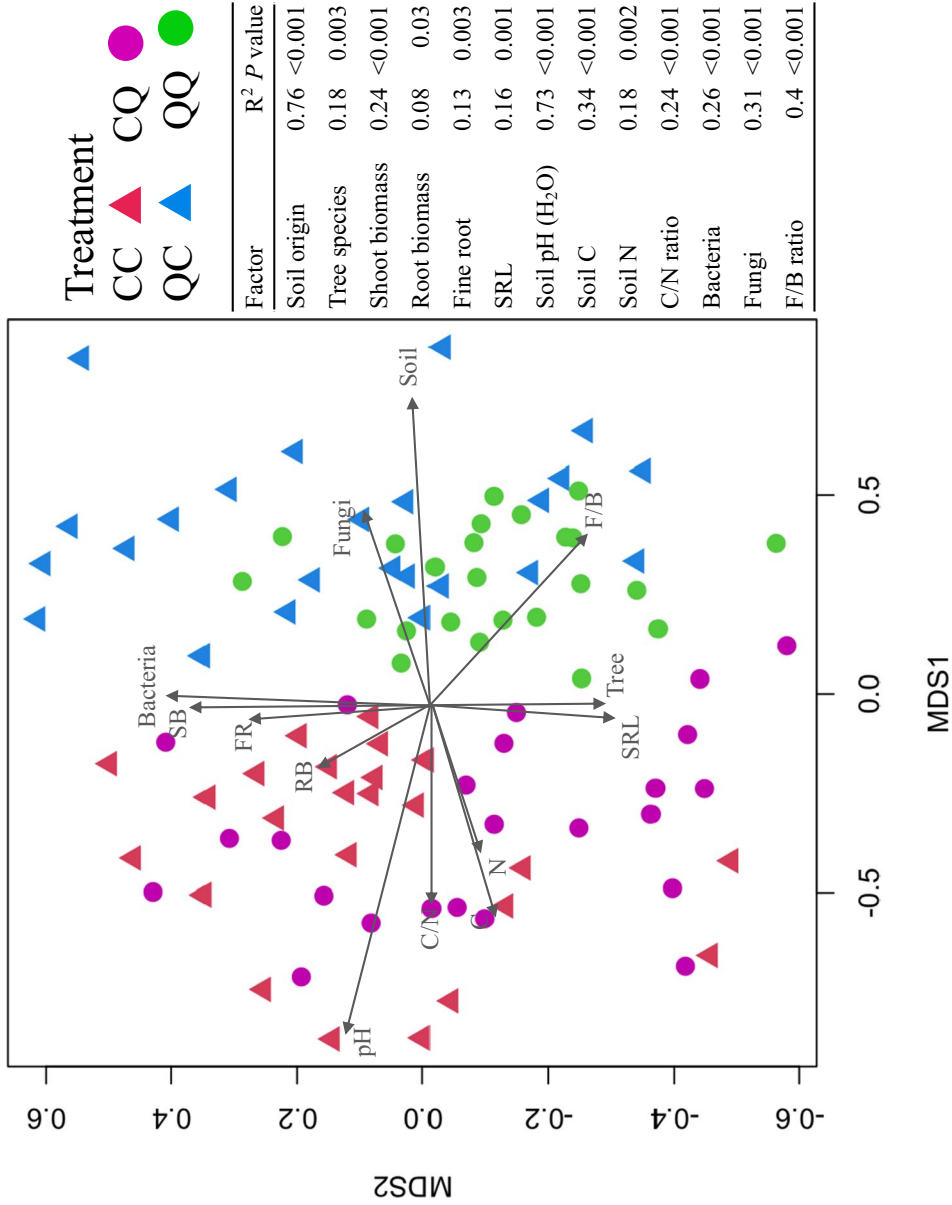
Fig. 2 Non-metric multidimensional scaling scatterplot of Chao dissimilarity based on the abundance of nematode taxa derived from four treatments. Stress value = 0.223. Nematode community structures were clustered significantly into *C. japonica* soil with *Cryptomeria. japonica* seedlings (CC); *Quercus serrata* soil with *C. japonica* seedlings (QC); *C. japonica* soil with *Q. serrata* seedlings (CQ); *Q. serrata* soil with *Q. serrata* seedlings (QQ) (PERMANOVA, $P < 0.001$, $R^2 = 0.70$). Soil origins, Tree species, Shoot biomass (SB), Root biomass (RB), Fine root biomass (FR), Specific root length (SRL), soil pH, C, N, C/N ratio, Bacterial and fungal DNA copy number and Fungi/Bacteria (F/B) ratio showed significant influences on nematode communities (Envfit, permutation 9999 times, $P < 0.05$)

Factor	R^2	P value
Soil origin	0.76	<0.001
Tree species	0.18	0.003
Shoot biomass	0.24	<0.001
Root biomass	0.08	0.03
Fine root	0.13	0.003
SRL	0.16	0.001
Soil pH (H$_2$O)	0.73	<0.001
Soil C	0.34	<0.001
Soil N	0.18	0.002
C/N ratio	0.24	<0.001
Bacteria	0.26	<0.001
Fungi	0.31	<0.001
F/B ratio	0.4	<0.001

and the F/B ratio significantly influenced the nematode community structure. Across all treatments, soil origin accounted for the most variation ($R^2=0.76$) in the nematode communities. Moreover, tree species also accounted for the variation in nematode communities ($R^2=0.18$, among the treatments).

Indicator species analysis was performed for each pot treatment (Table 2). Eleven taxa (*Acrobeles*, *Acrobeloides*, *Aphanolaimus*, Criconematidae, *Diphtherophora*, *Ecphyadophora*, Heteroderidae, *Helicotylenchus*, *Plectus*, *Teratocephalus* and *Wilsonema*) were selected as indicator taxa for CC ($P<0.05$), four taxa (*Miconchus*, *Monhystera*, Rhabditidae and *Rhabdolaimus*) for CQ, Trichodoridae and *Tylencholaimellus* for QC, and four taxa (*Cephalobus*, *Ditylenchus*, *Filenchus*/*Tylenchus* and *Mylonchulus*) for QQ.

Structural equation modeling (SEM) analysis

The final structural equation model adequately fitted the obtained dataset. The model explained the effects of soil origin and tree species on soil PC1, root biomass, F/B ratio, and nematode trophic group abundance (Fig. 3; Fisher's C=27.844, df=32, $P=0.677$, AICc=73.844). Soil PC1 was significantly positively correlated with *Q. serrata* soil. The F/B ratio was significantly positively correlated with *Q. serrata* soil and trees, whereas root biomass was significantly positively correlated with *C. japonica* soil and trees. The abundance of fungivorous nematodes was significantly positively correlated with *Q. serrata* soils but not with the F/B ratio. There was a positive covariance between the nematode abundance of bacterivores and fungivores. The abundance of herbivorous nematodes was significantly and positively correlated with *Q. serrata* soils and *C. japonica* trees, but not with root biomass. Herbivorous nematode abundance had a significant positive relationship with predator-omnivore abundance.

Discussion

Effects of tree species identity and soil origin on nematode community structures

Nematode community structures were significantly different between the tree species examined (Fig. 2), which agrees with the findings of previous studies (Cesarz et al. 2013; Gilarte et al. 2021). Moreover, the

nematode community structure with trees is apparently shifted and altered into different ones without trees (Fig. S4). Tree species identity is a major factor affecting root-associated microbial communities (Sawada et al. 2021; Tanikawa et al. 2023) and nematode diversity (Li et al. 2023). Since nematodes are involved in nutrient cycling by feeding on bacteria, fungi (Ingham et al. 1985) and roots (Wilschut and Geisen 2021), nematode communities are possibly tightly connected with microbial and root trait responses driven by tree species. For example, finer root systems enhance the complexity of nematode communities by increasing the relative abundance of high-trophic-level omnivores and predators (Zhang et al. 2022). Tree species identity can affect soil fertility by regulating soil nematode communities in coniferous and broad-leaved forests (Liu et al. 2023). Moreover, the nematode community structures differed significantly between soil origins obtained from either coniferous *C. japonica* or broad-leaved *Q. serrata* forests (Fig. 2). Previous studies have reported that nematode community structures are affected by soil origin (e.g., Richter et al. 2023). In the present study, nematode community structures were significantly coordinated by several proximate factors, particularly soil pH and C/N. These are generally related to both abiotic and biotic factors, that is, resource quality and quantity, which may indirectly influence nematode community structures (Kitagami et al. 2020; Liu et al. 2019). From our findings, the more fungal biomass present in *Q. serrata* forest soils, which can influence nematode community structures by changing fungivorous nematode abundance. Thus, nematode community structures are shaped by cascading effects of tree species identities on soil properties (e.g., microbial biomass) through root traits.

Direct and indirect effects of tree species identity and soil origin on nematode trophic compositions

The abundance of nematodes was significantly the highest in QC among all treatments (Fig. 1). Moreover, nematode densities with trees tended to be higher than those without trees (Fig. S5). Root biomass is well documented to have positive effects on nematode densities, particularly on herbivorous ones (Keith et al. 2009; Salamon and Wolters 2009). The proportion of herbivorous nematodes in the trophic composition was higher than that in other treatments.

Table 2 Relative frequencies (%) and index values of nematode taxa at four pot treatments

Trophic groups	Taxon	Pot treatments				Indicator values				*P*
		CC [a]	CQ	QQ	QC	CC	CQ	QQ	QC	value [d]
Bacterivores		68.5	72.4	54.5	36.3					
	Achromadora	0.36 [b]	0.27	0.10	0.10	0.33 [c]	0.23	0.10	0.10	0.292
	Acrobeles	1.07	0.80	0.05	0.50	**0.49**	0.33	0.03	0.27	0.015
	Acrobeloides	21.62	20.09	8.29	7.83	**0.61**	0.58	0.39	0.35	0.000
	Alaimus	1.98	1.87	2.01	2.72	0.40	0.36	0.43	0.45	0.833
	Aphanolaimus	1.32	0.91	0.05	0.00	**0.50**	0.42	0.03	0.00	0.008
	Bastiania	0.25	0.05	0.05	0.25	0.26	0.06	0.06	0.26	0.616
	Cephalobus	5.33	5.40	11.28	8.87	0.41	0.38	**0.60**	0.53	0.005
	Monhystera	0.15	0.43	0.00	0.00	0.15	**0.39**	0.00	0.00	0.030
	Plectus	2.89	1.87	1.47	0.84	**0.54**	0.40	0.35	0.19	0.033
	Prismatolaimus	10.76	8.44	19.08	9.31	0.47	0.40	**0.64**	0.43	0.000
	Prodesmodora	0.61	1.01	0.05	0.40	0.32	0.44	0.03	0.24	0.063
	Rhabditidae	12.84	22.65	11.57	4.51	0.48	**0.65**	0.48	0.27	0.000
	Rhabdolaimus	3.71	5.98	0.34	0.35	0.54	**0.72**	0.08	0.09	0.000
	Teratocephalus	2.23	1.50	0.05	0.30	**0.68**	0.45	0.02	0.11	0.000
	Wilsonema	3.40	1.12	0.10	0.35	**0.70**	0.33	0.04	0.09	0.000
Fungivores		15.13	17.57	32.56	17.14					
	Aphelenchoididae	9.49	9.78	10.69	3.52	0.53	0.52	0.55	0.28	0.194
	Diphterophora	0.56	0.05	0.00	0.10	**0.51**	0.05	0.00	0.11	0.002
	Ditylenchus	0.00	0.48	3.43	2.08	0.00	0.15	**0.56**	0.42	0.002
	Filenchus/Tylenchus	3.15	5.93	17.17	8.12	0.29	0.38	**0.71**	0.48	0.000
	Tylencholaimellus	1.93	1.34	1.28	3.32	0.36	0.28	0.33	**0.63**	0.000
Herbivores		11.62	3.90	9.17	42.79					
	Criconematidae	1.42	0.00	0.05	0.05	**0.56**	0.00	0.04	0.04	0.000
	Ecphyadophora	6.04	1.82	0.64	0.50	**0.80**	0.39	0.18	0.13	0.000
	Heteroderidae	1.17	0.85	0.29	0.00	**0.55**	0.30	0.11	0.00	0.001
	Helicotylenchus	1.47	0.91	0.00	0.15	**0.63**	0.40	0.00	0.09	0.000
	Longidoridae	0.30	0.11	0.29	0.59	0.22	0.08	0.20	0.31	0.444
	Trichodoridae	1.22	0.21	7.90	41.51	0.11	0.03	0.37	**0.90**	0.000
Predators&		4.16	5.07	3.78	3.76					
Omnivores	*Miconchus*	0.51	0.59	2.50	1.44	0.17	0.17	**0.58**	0.33	0.003
	Mylonchulus	0.81	1.92	0.00	0.35	0.35	**0.55**	0.00	0.16	0.003
	Paractinolaimus	0.00	0.16	0.00	0.05	0.00	0.25	0.00	0.10	0.424
	Qudsianematidae	2.84	2.40	1.28	1.93	0.50	0.49	0.30	0.41	0.309
Total number of nematodes [e]		1970	1872	2039	2019					

[a]See treatment codes for Table 1

[b]Relative frequency (%)=(number of nematodes in a certain genus)/ (total number of nematodes observed in each microhabitat)×100

[c]Indicator values were calculated based on Dufrêne and Legendre (1997). Bold values indicate significant detection of taxa in four microhabitats

[d]*P*-values (Monte Carlo tests, permutation 9999 times)

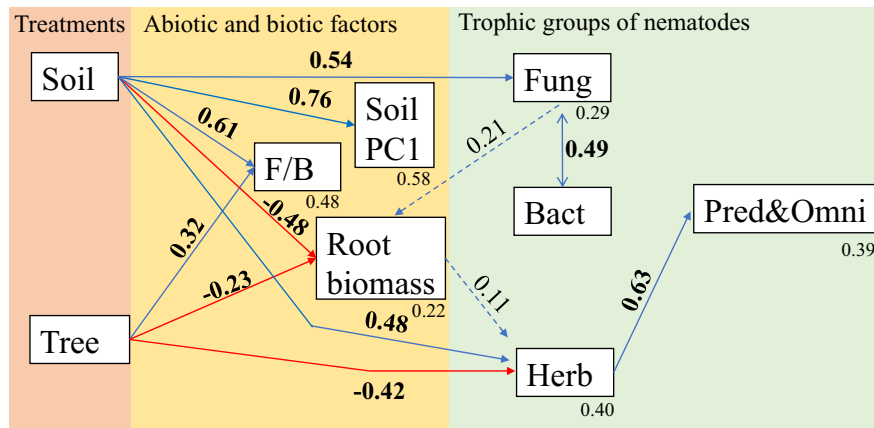[e]Total observed number of nematodes was summed up from a total of 24 samples

Fig. 3 Structural equation model of effects of soil origins and tree species on soil abiotic factors, root biomass, F/B ratio and the abundance of nematode trophic groups (Fisher's C = 27.844, df = 32, P = 0.677, AICc = 73.844). R squared values for endogenous variables are noted at the bottom of each factor. Numbers on arrows are standardized path coefficients. Solid and dashed lines represent significant and non-significant pathways, respectively. Soil origins and tree species were indicated as a categorical explanatory variable, i.e. soil origins; *Cryptomeria japonica* (1) and *Quercus serrata* (2), tree species; *C. japonica* (1) and *Q. serrata* (2). Principal component analysis (PCA) was performed to reduce the dimensions of soil abiotic factors, i.e., soil pH and C/N. The first principal component of soil properties (Soil PC1) was negatively correlated with soil pH and C/N ratio (see Fig. S3). Bact, abundance of bacterivores; Fung, abundance of fungivores; Herb, abundance of herbivores; Pred&Omni, abundance of predators and omnivores

Among these, Trichodoridae was the most dominant taxon (Table 2), which could be naturally maintained at a low density in *Q. serrata* forest soils. Members of this taxon may have possibly increased due to a bottom-up effect of the increase in *C. japonica* fine roots in the QC treatment. This result suggests that Trichodoridae fed on *C. japonica* roots, because some species Trichodoridae are frequently found in various tree rhizosphere species, including *C. japonica* (Mamiya 1967). Under low plant diversity conditions, specialist herbivorous nematodes can play an important role by contributing to negative plant–soil feedback toward a certain dominant plant species (Wilschut and Geisen 2021). In such a situation, the living fine root tissue is consumed by herbivorous nematodes, leading to the deterioration of the absorptive function of root systems (Maboreke et al. 2017; Saucet et al. 2016). There was no significant difference in the shoot and root biomass of *C. japonica* grown in the soils of either tree species. This result showed that damage by Trichodoridae had a negligible effect on host growth and there was no negative feedback to the host plant. Regarding root traits, a low root tissue density (i.e., cells are soft and easily penetrate the nematode stylet) resulted in increased herbivorous nematode density (de Deyn et al. 2008;

Wilschut and Geisen 2021), and herbivorous nematode abundance also increased in *C. japonica*, a tree with low root tissue density (Table 2). The diameters of fine roots in coniferous trees, including *C. japonica* were greater than those in broad-leaved trees (Wada et al. 2019); therefore, feeding area for herbivorous nematodes was large, which may have led to significant increments. Feeding by herbivorous nematodes also indirectly benefit plant performance by inducing increased plant exudation that stimulates microbial activity, enhancing N and P availability (Gebremikael et al. 2016). Other trophic groups of nematodes are distributed across the entire soil and rhizosphere food web (Bonkowski et al. 2009), and structure the rhizobiome, with potential positive feedback to plant performance (Thakur and Geisen 2019).

Soil origin exhibited significant effects on fungivore abundance, which was higher under *Q. serrata* soils than under *C. japonica* soils (Fig. 1), which was possibly due to intimate mycorrhizal associations between *Q. serrata* and ECM fungi (Matsuda et al. 2013). In the SEM analysis (Fig. 3), *Q. serrata* soils and their tree species positively affected the F/B ratio, and more than half of the root tips of *Q. serrata* seedlings showed ECM formation in both soil origins, which may contribute to fungal biomass.

Although a significant path from F/B to fungivorous nematodes was not selected, the *Q. serrata* soil may have contained many potential food resources for fungivorous nematodes. In support of this idea, girdling of *Picea obovata* stems decreased the abundance of fungivorous nematodes by decreasing the amount of extramatrical mycelia derived from ECM fungi, which are the food resource of fungivorous nematodes (Kudrin et al. 2021). The extramatrical hyphae of ECM fungi extending into soils may provide a food resource, thus improving the habitat quality of fungivorous nematodes (Kitagami and Matsuda 2020). The community structures of bacteria, fungi, and nematodes varied between the tree species and mycorrhizal symbionts, suggesting adaptation of microbial communities. Easily degradable substrates can be provided under trees associated with AM fungi, and recalcitrant substrates associated with ECM fungi (Eagar et al. 2022; Heděnec et al. 2020). Fungal community compositions differed between *C. japonica* plantations and natural forests in soils; for example, saprophytic, endophytic, and plant pathogenic fungi dominated in *C. japonica* plantations, whereas ECM fungi were predominant in natural forests (Sawada et al. 2021). The fungivorous nematode Aphelenchoididae was dominant in all treatments, suggesting that the nematodes fed on saprophytic or ECM fungi, regardless of the fungal ecological type. These nematode groups have a wide range of food resources because they can proliferate by feeding on saprophytic or ECM fungi (Kitagami and Matsuda 2022; Ruess et al. 2000). In the indicator species analysis, the fungivorous *Ditylenchus* and *Filenchus/Tylenchus* were selected as significant indicator species in QQ. ECM fungi may be suitable food sources for the reproduction of these nematodes. Selective grazing by fungivorous nematodes may facilitate the compensation of fungal growth, inducing to initial decomposition (Mamilov and Dilly 2002). Bacterivorous and fungivorous nematodes can influence microbe-mediated ecosystem processes by affecting microbial population size and traits (Thakur and Geisen 2019). Thus, fungivorous nematode abundance is influenced by mycorrhizal types as well as fungal ecological types in forest ecosystems.

An increase in the abundance of herbivorous, bacterivorous, and fungivorous nematodes, which are lower trophic groups, increases the abundance of predatory and omnivorous nematodes, which are higher trophic groups (Kitagami and Matsuda 2020; Zhang et al. 2020). In the SEM analysis, there was a tight connection in the abundance of nematode trophic groups between herbivorous and predatory-omnivorous nematodes. This is possibly explained by the feeding relationships between these two groups and suggests that predatory-omnivorous nematodes feed specifically on herbivorous nematodes. In fact, field experiments and molecular gut analyses have suggested that some predatory-omnivorous nematodes feed on herbivorous nematodes (Bilgrami et al. 2008; Cabos et al. 2013). Herbivorous nematodes are poorly motile and most of the ones recorded in this study are ectoparasitic, i.e., prey on epidermal and cortical root cells (Wyss 1997), which may have made it easier for predatory-omnivorous nematodes to approach and feed on herbivorous nematodes.

Conclusion

Our study revealed that tree species identity and soil origin synergistically influence nematode communities. Herbivorous nematodes significantly increased at *C. japonica* tree species in *Q. serrata* forest soils. Fungivorous nematodes were significantly greater in *Q. serrata* soils than in *C. japonica* soils because of the mycorrhizal associations between *Q. serrata* and ECM fungi. Moreover, there was a covariation between the abundance of herbivorous and predatory-omnivorous nematodes. Our findings suggest that tree species identity modifies soil micro-food webs by affecting microbial abundance and nematode trophic composition. However, our results do not necessarily reflect community patterns of soil organisms in field environments because the present experiments were performed in a controlled greenhouse using the early stages of tree seedlings. Nevertheless, our results will help us better understand the effects of tree species identity on belowground biodiversity and functioning. Further research integrating multi-dimensional root traits and manipulating tree symbiont partners is needed to generalize of multi-trophic interactions among trees, microbes, and soil animals. Besides, the monitoring soil communities over time after being converted to coniferous-broadleaf mixed forests would provide insights into the structure and stability of soil micro-food webs.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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