



Differences in the effects of broadleaf and coniferous trees on soil nematode communities and soil fertility across successional stages

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Abstract

Purpose Soil nematodes are among the most important fauna in soils and participate actively in soil ecological processes. However, whether and how soil nematodes are involved in the effects of tree species type on soil fertility remain unclear, especially during subalpine forest secondary succession.

Methods A monoculture pot experiment of two broadleaf (*Betula platyphylla* and *Betula albosinensis*) and two coniferous (*Picea asperata* and *Abies faxoniana*) trees, using sterilized soils inoculated with

unsterilized soils beneath dominant plants from different successional stages, was conducted in a greenhouse. After a period of plant growth, soil nematode communities and soil fertility in each pot were investigated.

Results Significant differences were noted in nematode community composition under the broadleaf and coniferous trees. Coniferous trees accumulated more abundant microbivores and omnivore-predators than broadleaf trees. Moreover, the contrasting effects of tree species type on soil nematode communities were associated with successional stages, with the greatest differences noted in the early successional stages. In addition, soil nematodes might play a significant mediating role in the effects of broadleaf and coniferous trees on soil fertility. However, the indirect regulatory effects induced by soil nematodes weakened with the successional stages.

Conclusion Overall, our study suggested that tree species type might affect soil fertility by regulating soil nematode communities across successional stages. Compared with broadleaf trees, more abundant microbivores under coniferous trees might contribute to the improvement of soil nitrogen mineralization but not to the increase in soil carbon storage, which might be limited by new carbon input into soils.

Jia Liu and Xiaohu Wang contributed equally to this work.

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Introduction

Forests are one of the largest terrestrial carbon reservoirs and play an important role in the global carbon cycle (Pan et al. 2011). In evaluating the carbon sequestration potential of forests, forest type and tree identity have been found to be crucial determining factors (Mayer et al. 2020). Soil nitrogen, which serves as the basic nutrient for plant growth, also affects plant species composition and ecosystem functions, particularly in some N-limited subalpine forests (Högberg et al. 2017; Zou et al. 2017). A number of studies have demonstrated that tree species and functional groups have significant effects on soil fertility, including soil carbon and nitrogen storage (Dawud et al. 2017; Peng et al. 2020). Additionally, tree species have strong effects on soil bacterial and fungal communities (Rožek et al. 2020; Tedersoo et al. 2016), by which tree species might indirectly influence soil fertility (Wang et al. 2016). As one of the most important components in the soil ecosystem, soil nematodes participate directly or indirectly in the decomposition of organic substances and mineralization of nutrients (Ranoarisoa et al. 2018; Wang et al. 2017). However, how tree species types, such as broadleaf and coniferous trees, affect soil nematode communities and thus soil fertility remains unclear.

Due to the differences in the quality and quantity of plant litter and exudates, tree species have been recognized to have notably different influences on soil fertility (Dawud et al. 2017; Peng et al. 2020; Stefanowicz et al. 2021). For example, the soil soluble organic nitrogen content was found to be higher under broadleaf trees than under coniferous trees (Błońska et al. 2016; Xing et al. 2010). Through a quantitative review of common garden experiments, Hüblová and Frouz (2021) showed that broadleaf and coniferous trees had opposite influences on soil carbon storage, with greater carbon storage under broadleaf trees in immature post-mining soils and greater carbon storage under coniferous trees in mature forest soils. In contrast, Chiti et al. (2012), Peng et al. (2020) and Su et al. (2021) suggested that broadleaf trees had greater soil carbon storage than coniferous trees in forest soils, indicating the controversy of broadleaf and coniferous trees affecting soil carbon storage. In addition, broadleaf and coniferous trees differ in their influences on soil bacterial and fungal communities

(Awad et al. 2019; Guo et al. 2016; Li et al. 2021). Given the important contributions of soil microbial communities to carbon sequestration (Zhang et al. 2013), it is reasonable to consider that the effects of tree species on soil fertility could be substantially associated with soil microfauna (Frouz et al. 2013). It is well established that soil nematode communities are also significantly regulated by plant species (De Deyn et al. 2004; Viketoft et al. 2009), and the effects of tree species on soil nematode communities vary with nematode trophic groups (Yan et al. 2021). As such, broadleaf and coniferous trees may also have different influences on the soil nematode community structure. More importantly, it is essential and urgent to explore whether the effects of broadleaf and coniferous trees on soil fertility could be mediated by soil nematode communities.

Recent studies have shown that the variations in soil fertility under broadleaf and coniferous trees might be related to the stage of soil development represented by soils with different previous land uses (Hüblová and Frouz 2021). It is well known that strong ecological linkages exist between above- and belowground communities (De Deyn and Van der Putten 2005; Wardle et al. 2004). Particularly in the process of secondary succession, the plant community serves as an important driver governing the soil biota community (Lozano et al. 2014; Qiang et al. 2021). Broadleaf and coniferous trees, which generally dominate at the late successional stage, would also establish and distribute their populations at the early and middle successional stages. Given the heterogeneous patterns of soil nematode communities among different vegetation types (Li et al. 2015; Mondino et al. 2011), the effects of tree species on soil nematode communities might also vary with successional stages. For example, Gilarte et al. (2021) demonstrated that nitrogen fixing and non-fixing trees had different effects on soil nematode communities across successional stages. However, it remains unknown about the effects of broadleaf and coniferous trees on soil nematode communities across successional stages, particularly when these effects might contribute to the divergent variations in soil fertility under broadleaf and coniferous trees. Therefore, exploring whether and how broadleaf and coniferous trees influence soil fertility by regulating soil nematode communities across successional stages facilitates our further understanding of soil fertility,

particularly soil carbon and nitrogen sequestration potential and mechanisms of the forests.

The alteration of soil biotic and abiotic characteristics induced by plants can in turn influence the performance of future plants growing in the same soil, which is known as plant-soil feedbacks (PSFs) (van der Putten et al. 2013; Wilschut et al. 2019). It is well recognized that the PSFs are important drivers of the shift in plant community composition and, thus, succession (Kardol et al. 2007; Pugnaire et al. 2019). Previous studies showed that early successional plant species tend to generate negative PSFs that facilitate the establishment of later successional species and finally replace the early successional species, while the PSFs shifted from negative to positive with succession and allow for a stable climax community of later successional species (Kardol et al. 2006; terHorst and Zee 2016). However, most PSF studies were performed using soils conditioned by plant species in the greenhouse (Semchenko et al. 2018; Wilschut et al. 2019) or in mesocosms (Hannula et al. 2021), while studies using field conditioned soils are lacking.

In this study, we conducted a pot experiment in a greenhouse with a constant temperature (~19 °C), humidity and illumination regulation (12 h of daytime). The seedlings of two broadleaf trees (*Betula platyphylla* and *Betula albosinensis*) or two coniferous trees (*Picea asperata* and *Abies faxoniana*) were planted in monospecific pots, using sterilized soils inoculated with unsterilized soils beneath dominant plants from early, middle and late successional stages. This monoculture of the pot experiment in the greenhouse could be useful in concentrating 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 the field experiments (Stefanowicz et al. 2021). More importantly, we used field conditioned soils rather than greenhouse conditioned soils in our pot experiment, which could provide a novel research case for PSF studies (Kulmatiski et al. 2008). The purposes of this study were as follows: (1) to determine the effects of broadleaf and coniferous trees on nematode communities across successional stages and (2) to explore whether the shifts in soil nematode communities were involved in the regulatory effects of broadleaf and coniferous trees on soil fertility. We hypothesized that (1) there were

marked differences in the effects of broadleaf and coniferous trees on soil nematode communities across successional stages, with the greatest differences of tree effects in the early successional stage; and (2) soil nematode communities contributed to the regulatory effects of broadleaf and coniferous trees on soil fertility.

Materials and methods

Study species and soil preparation

To examine the effects of broadleaf and coniferous trees on soil nematode communities and soil fertility across successional stages, we selected tree species from the Miyaluo forest region of Lixian County, eastern Tibetan Plateau, Sichuan, China. This subalpine forest region has undergone a continuous secondary succession since historical logging in the last century (Liu 2002; Qiang et al. 2021). Herbs dominated in the early successional stage, including *Poa annua*, *Koeleria macrantha* and *Anemone rivularis*; shrubs dominated in the middle successional stage, including *Berberis sichuanica* and *Rhododendron fortunei*; and trees dominated in the late successional stage, including *B. platyphylla*, *Betula albosinensis*, *Picea asperata* and *Abies faxoniana*. We focused on the two broadleaf trees (*B. platyphylla* and *B. albosinensis*) and two coniferous trees (*P. asperata* and *A. faxoniana*). The seeds of these trees were collected in the Miyaluo forest region and grown into seedlings in the laboratory, which were prepared for the following pot experiment.

To examine whether the tree effects change with secondary succession, we collected plenty of soils beneath dominant plants of the early, middle and late successional stages (i.e., three herbs, two shrubs and four trees as stated above) at 0–20 cm depths in the Miyaluo forest region. We also collected soils at 0–20 cm depths in the adjacent degraded areas. The collected soils were passed through a 2 mm sieve in the laboratory, and the soils of degraded areas were sterilized using the gamma ray method. Then, the mixture of unsterilized soils beneath each dominant plant and sterilized soils of the degraded areas (mass ratio: 7% to 93%) were used as experimental potting soils. The mixtures of 9 unsterilized soils and sterilized soils were kept separate, i.e., a total

of 9 soil preparations. Since these herbs, shrubs and trees coexisted respectively at the early, middle and late successional stages, the nematode communities in the soils of the herbs, shrubs and trees could be considered as those respectively from early, middle and late successional stages. In a sense, each soil preparation contained a random sample of the nematode community from each corresponding successional stage. Because our study focused on the effects of broadleaf and coniferous trees on soil nematode communities across successional stages, we further pooled the 9 soil preparations into 3 factor levels (i.e., early, middle and late successional stages) in the following analyses. The soil preparation using the independent soil sampling method in our study was acceptable for our research background and goals regarding forest succession, while avoiding the use of pseudoreplications (Gundale et al. 2019). The low inoculation proportion of unsterilized soil could minimize the interference of the potential differences in initial soil fertility in the experimental soils, while providing the soil nematode communities from each successional stage at a basic level (Wang et al. 2019; Zhao et al. 2021).

Experimental design

In the greenhouse with a regulated microclimate, the monoculture of each broadleaf or coniferous tree seedling was conducted in the experimental pots. The same quantity (700 g) of mixed soils representing different successional stages was put into each pot (9.8×11.6×11.6 cm) that was placed on a plastic dish. Broadleaf and coniferous seedlings with similar growth periods (approximately 4 weeks) were selected and transplanted into the corresponding pots. There were eight replications for each pot treatment. All pots were watered periodically, and rearranged to eliminate subregion effects. When the plant roots occupied the entirety of the potting soil indicating the effects of plants on the potting soil system were expected to be sufficient, the collection of plant materials and soil samples was conducted. Thus, the fast-growing broadleaf and slow-growing coniferous seedlings were allowed to grow for 5 and 13 months, respectively. For each pot treatment, five replications were selected randomly for the collection of plant materials and soil samples, i.e., a total of 180 pots (4 tree seedlings × 9 potting soils × 5 replications).

Then, the above- and belowground parts of the plants in these selected pots were harvested. Every plant part was oven-dried at 65 °C until constant weight to calculate biomass. The residual soils in each experimental pot were collected and divided into two subsamples. One subsample was used for soil nematode extraction, and the other one was used for soil fertility measurement.

Nematode community analysis

Soil nematodes were extracted from 100 g fresh soil using a modification of the shallow dish method (Mao et al. 2004). Briefly, 100 g fresh soil was mixed and stirred slightly with approximately 1 L deionized water and then passed through an 80-mesh sieve (180 µm aperture) and a 500-mesh sieve (30 µm aperture). This operation was repeated three times. The residues on the sieves were washed and transferred to an 18-mesh sieve (1 mm aperture) covered with a layer of nematode filter in a shallow dish. Deionized water was added to the dish until the residues on the filter were soaked. After two days, the water in the dish was collected and transferred to the beaker. After sitting for another 2 hours, approximately 3 ml of liquid was collected from the bottom and fixed by the addition of an equivalent 4% formalin solution. All fixed soil nematodes were counted under a dissecting microscope (BXT-1304, Bingyu, China) to calculate nematode abundance (individuals per 100 g dry soil). Then, 100 randomly selected nematodes, or all individuals if fewer than 100, from each sample were identified to the genus level based on nematode morphological characteristics using an optical microscope (XTL-208C, Jintong, China). According to Yeates et al. (1993), the identified nematodes were classified into four trophic groups: bacterivores (Ba), fungivores (Fu), herbivores (He) and omnivore-predators (Op). The abundance of each trophic group was also expressed as individuals per 100 g dry soil.

The Shannon-Wiener index, $H' = -\sum p(i) \times \ln p(i)$, was used as an indicator of soil nematode diversity, where $p(i)$ is the proportion of the i th genus in a sample (Freckman and Ettema 1993). Two nematode maturity indices were also used for the assessment of the soil nematode community structure, i.e., the maturity index (MI) and the plant parasitic index (PPI). The MI was calculated based on the abundance

of free-living nematodes (i.e., nonherbivores), with a low value representing a highly disturbed environment, while the PPI, calculated exclusively based on herbivorous nematodes, assessed the extent of feeding and parasitism on plant roots (Shaw et al. 2019). To calculate the two indices, the identified nematode genera were assigned a colonizer-persister (c-p) value ranging from enrichment colonizers (c-p 1) and disturbance colonizers (c-p 2) to persisters (c-p 5) (Bongers 1990; Shaw et al. 2019). Then, MI and PPI were calculated using the same formula: MI (PPI) = $\sum v(i) \times p(i)$, where $v(i)$ is the c-p value of genus i (Bongers 1990).

Soil chemical analysis

To calculate nematode abundance based on dry weight, the soil water content was measured by oven-drying 20 g fresh soil samples at 105 °C for 24 hours. Soil pH was measured in a 1:2.5 (w:v) soil: deionized water suspension using a digital pH meter (FE28-Standard, Mettler-Toledo, Switzerland). Soil organic carbon (SOC) was measured using the potassium dichromate heating method. Soil ammonium nitrogen ($\text{NH}_4^+\text{-N}$) and nitrate nitrogen ($\text{NO}_3^-\text{-N}$) were extracted using a 2 M KCl solution and were measured by colorimetry with a microplate reader (Varioskan LUX, Thermo Scientific, America).

Data analysis

Two-way ANOVAs were performed to examine the effects of tree species type (broadleaf and coniferous trees), successional stage (early, middle and late stages) and their interactions on the nematode abundances (total abundance and trophic group abundance), nematode ecological indices (genus richness, H' , MI and PPI) and soil fertility ($\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ and SOC). Post-hoc test was applied to compare the differences among different treatments, using the least significant difference (LSD) method ($P < 0.05$). Variation partitioning analysis (VPA) was performed to estimate the independent and shared contributions of tree species type, successional stage and nematode community to soil fertility via the “vegan” package of R (Oksanen et al. 2019). To examine whether the shifts in soil nematode communities were involved in the regulatory effects of broadleaf and coniferous trees on soil fertility,

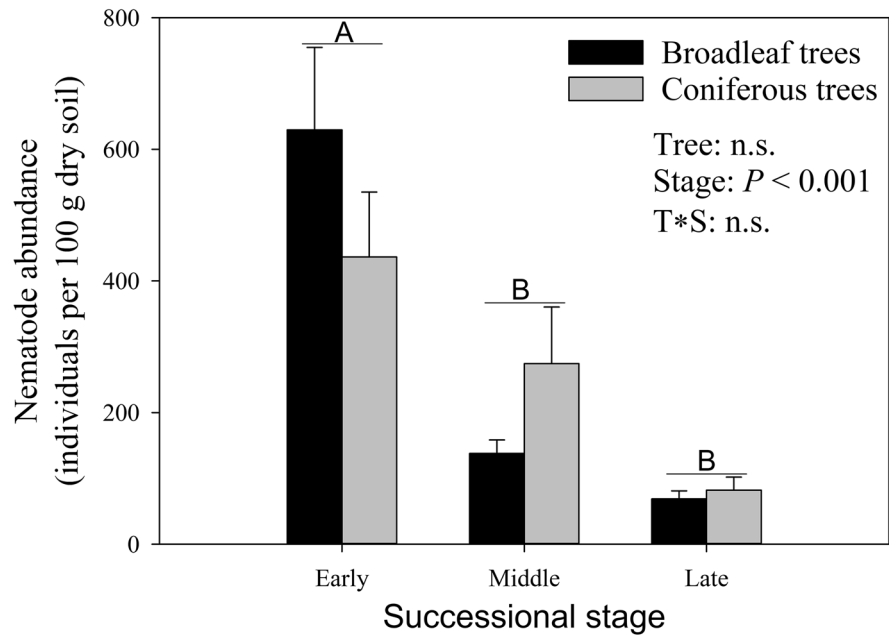
partial least squares path modelling (PLS-PM) was performed to illustrate the correlations among tree species type, soil nematodes and soil fertility at both the whole successional stages and each successional stage, using the function “innerplot” in the R package “plsmpm” (Sanchez et al. 2015). The latent variables in the PLS-PM studied here included tree species type, successional stage, soil nematodes and soil fertility. Each latent variable included one or more manifest variables, for example, soil nematodes including Ba, Fu, Op and He, soil fertility including SOC, $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$. Each manifest variable had a relative contribution degree shown below the manifest variable. Path coefficients represented the direction and strength of the linear relationships between latent variables and the explained variability (R^2) was also estimated in the PLS-PM. The models were evaluated using the goodness of fit (GOF) statistic. Data were checked for normality prior to analyses and converted logarithmically as needed. All data analyses were performed with the statistical analysis software R-4.0.3 (R Foundation for Statistical Computing, Frederiksberg, Denmark).

Results

Nematode community composition

The abundance of total nematodes was significantly related with successional stage alone ($P < 0.001$, Fig. 1), rather than tree species type. Broadleaf and coniferous trees often accumulated the highest nematode abundance in soils of the early successional stage and the lowest abundance in soils of the late stage. However, tree species type had significant effects on nematode trophic groups, and the tree effects were significantly related to successional stages (Fig. 2). In early-stage soils only, coniferous trees accumulated significantly more bacterivores and fungivores and fewer herbivores than broadleaf trees, whereas in soils of the middle and late stages, no significant differences were found in the abundance of the three trophic groups between broadleaf and coniferous trees ($P < 0.05$, Fig. 2A, B and D). In contrast, omnivore-predator abundance was significantly greater under coniferous trees than under broadleaf trees, regardless of successional stage ($P < 0.05$, Fig. 2C).

Fig. 1 The abundance of total soil nematodes in soils of different successional stages under broadleaf and coniferous trees. All the results are presented as the means \pm SE. Different uppercase letters indicate significant differences among different stage treatments ($P < 0.05$); ns, nonsignificant



Similar to nematode trophic groups, tree species type exhibited successional stage-dependent effects on nematode ecological indices (Table 1). In soils of the early and late stages, coniferous trees had significantly higher nematode diversity and genus richness than broadleaf trees ($P < 0.05$). In contrast, the MI was significantly higher under coniferous trees than under broadleaf trees ($P < 0.05$) in soils of the middle and late stages. Related to the relatively high herbivore abundance, broadleaf trees had the highest PPI in early-stage soils.

Soil fertility

SOC was significantly higher under broadleaf trees than under coniferous trees in soils of all stages ($P < 0.05$, Fig. 3A), with greater differences noted in soils of the middle and late stages than those of the early stage. In contrast, soil $\text{NH}_4^+\text{-N}$ was significantly lower under broadleaf trees than under coniferous trees, regardless of successional stage ($P < 0.05$, Fig. 3B). However, the effects of tree species type on soil $\text{NO}_3^-\text{-N}$ varied with successional stages, with significantly lower $\text{NO}_3^-\text{-N}$ in early-stage soils and higher $\text{NO}_3^-\text{-N}$ in late-stage soils under broadleaf trees than under coniferous trees ($P < 0.05$, Fig. 3C). In middle-stage soils, no significant difference was found for soil $\text{NO}_3^-\text{-N}$ between broadleaf and coniferous trees (Fig. 3C).

Contributions of tree species type, successional stage and nematode community to soil fertility

VPA showed that tree species type was the strongest predictor (22.7%) of variations in soil fertility, followed by the nematode community (19.5%) and successional stage (13.7%) (Fig. 4). Specifically, tree species type independently accounted for the highest percentage (12.3%) of variations in soil fertility, followed by the shared contribution (9.4%) of tree species type and nematode community. PLS-PM at the whole successional stages showed that soil nematodes might not be involved in the effects of tree species type and successional stage on soil fertility (Fig. 5A). However, PLS-PM at each successional stage further suggested that tree species type exhibited significant indirect effects via soil nematodes on soil fertility, and these effects varied with successional stages (Fig. 5B, C and D). With secondary succession from the early and middle to late stages, the indirect effects of tree species on soil fertility via soil nematodes became weaker, with stronger indirect effects in early-stage soils (path coefficient: 0.20, Fig. 5B), weaker indirect effects in middle-stage soils (-0.13 , Fig. 5C) and minimal indirect effects in late-stage soils (0.006, Fig. 5D), compared with the direct effects of tree species on soil fertility (0.45, -0.69 and -0.80 for early-, middle- and late-stage soils, respectively, Fig. 5).

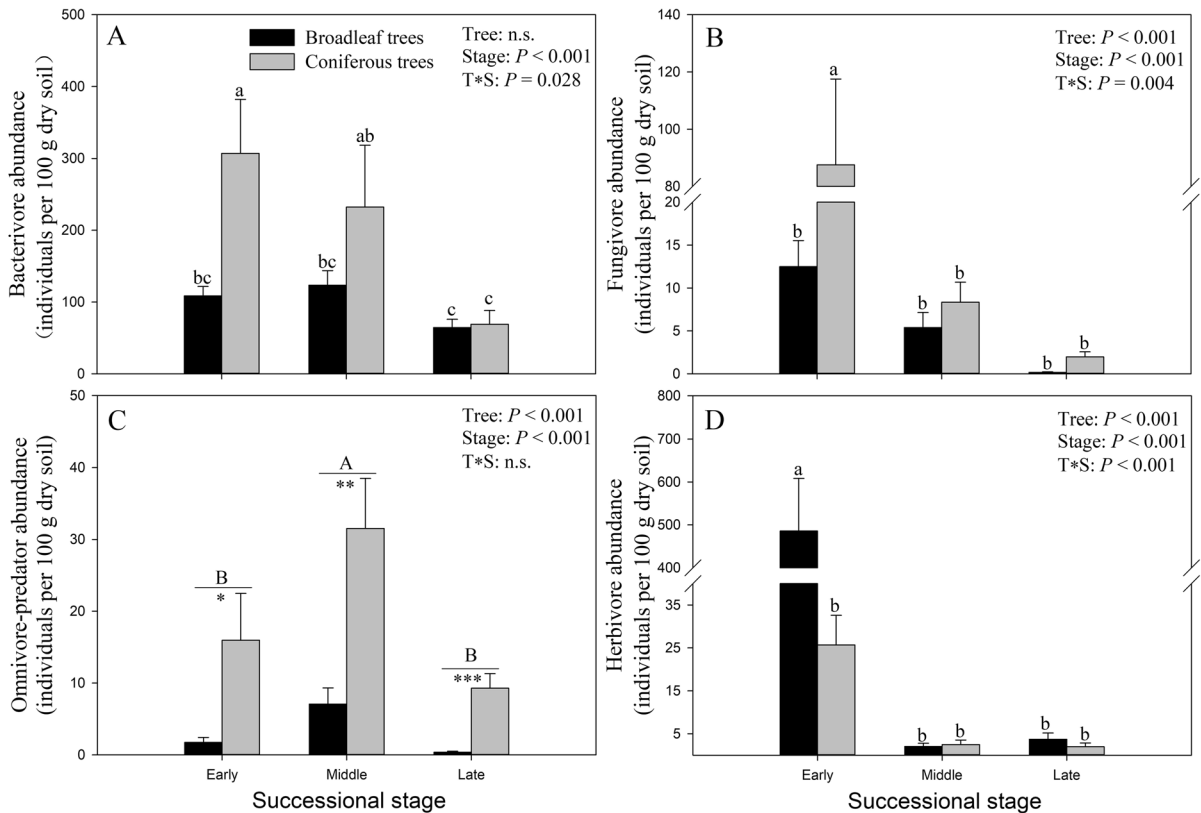


Fig. 2 The abundances of nematode trophic groups in soils of different successional stages under broadleaf and coniferous trees, including (A) bacterivores, (B) fungivores, (C) omnivore-predators and (D) herbivores. All the results are presented as the means ± SE. Different lowercase letters indicate significant differences among all the treatments ($P < 0.05$) in (A), (B) and (D) where significant interaction effects occur.

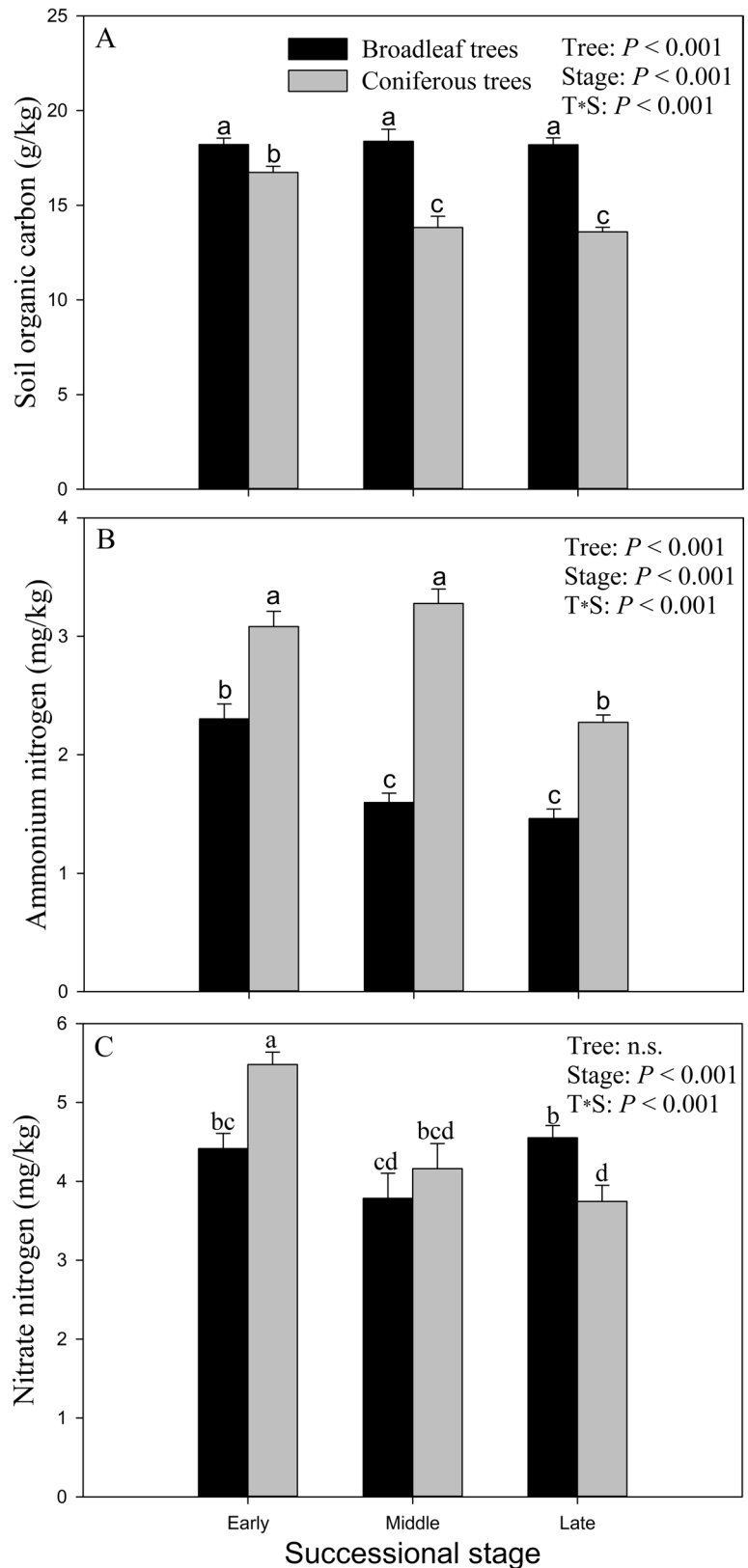
In (C) where no significant interaction effects occur, different uppercase letters indicate significant differences among different stage treatments ($P < 0.05$) and asterisks indicate significant differences between broadleaf and coniferous trees in each stage treatment; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, nonsignificant

Table 1 The ecological indices of soil nematodes under broadleaf and coniferous trees in soils of different successional stages

Successional stage	Tree species type	Ecological indices			
		H'	GR	MI	PPI
Early stage	Broadleaf	0.70(0.07)	5.13(0.28)c	2.01(0.02)b	3.06(0.03)
	Conifer	0.96(0.08)	7.17(0.43)a	2.09(0.04)b	2.75(0.17)
Middle stage	Broadleaf	0.60(0.08)	5.70(0.56)bc	2.07(0.04)b	1.20(0.34)
	Conifer	0.68(0.08)	6.60(0.46)ab	3.04(0.22)a	0.99(0.28)
Late stage	Broadleaf	0.14(0.03)	2.08(0.20)e	2.02(0.02)b	1.20(0.24)
	Conifer	0.42(0.05)	4.08(0.34)d	2.85(0.17)a	0.65(0.19)
P value	S	< 0.001	< 0.001	< 0.001	0.04
	T	< 0.001	< 0.001	< 0.001	< 0.001
	S × T	n.s.	0.043	0.002	n.s.

H', Shannon-Wiener index; GR, genus richness; MI, maturity index; PPI, plant parasitic index; S, successional stage effect; T, tree species type effect; S × T, successional stage and tree species type interaction effect. Values are means with one SE in parentheses. Different lowercase letters indicate significant differences among all the treatments ($P < 0.05$); n.s., nonsignificant

Fig. 3 Soil fertility in soils of different successional stages under broadleaf and coniferous trees, including (A) soil organic carbon, (B) soil ammonium nitrogen, and (C) soil nitrate nitrogen. All the results are presented as the means \pm SE. Different lowercase letters indicate significant differences among all the treatments ($P < 0.05$); ns, nonsignificant



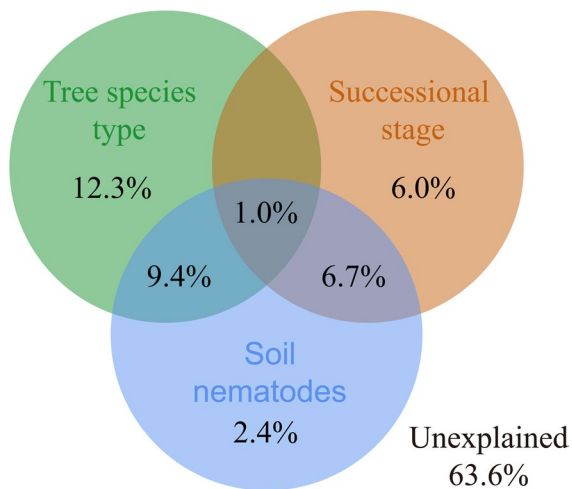


Fig. 4 Relative proportions of the explained variances of tree species type, successional stage and soil nematodes to the variances in soil fertility for all samples using variation partitioning analysis (VPA). The number outside the overlaps of the circle represents the independent contribution of the factor. The numbers in the overlaps of two or three circles represented the shared contributions of the two or three factors

Discussion

Contrasting effects of tree species type on nematode communities across successional stages

Different from field studies susceptible to interferences from various environmental factors (Stefanowicz et al. 2021), our study focused on the dominant effects of broadleaf and coniferous trees on soil nematode communities through a monoculture pot experiment. Our results showed that there was no significant difference in the effects of broadleaf and coniferous trees on total nematode abundance in soils of all successional stages. However, broadleaf and coniferous trees exhibited significantly different effects on nematode trophic groups, which supported the common view that tree species play an important role in affecting soil nematode community composition (Viketoft et al. 2009; Yan et al. 2021). For example, Cesarz et al. (2013) found that three target tree species in a temperate deciduous forest significantly affected the nematode trophic structure rather than total nematode abundance. Among nematode trophic groups, significant differences in the effects of broadleaf and coniferous trees on the abundance of omnivore-predators were noted,

regardless of successional stages, indicating strong influences of tree species type on soil nematodes at the high trophic level, such as *Prodorylaimus* and *Mesodorylaimus* (Table S1). Tree species type also exhibited significant effects on fungivore abundance, with significantly higher fungivore abundance under coniferous trees than broadleaf trees in soils of early successional stage, which might be due to the presence of strong symbiotic relationships between the coniferous trees (*P. asperata* and *A. faxoniana*) and ectomycorrhizal fungi (Zhang et al. 2018). The omnivore-predators, with high c-p values, play an important role in maintaining the complex structure and stability of the soil food web and show great sensitivity to environmental disturbance (Guan et al. 2018; Ruan et al. 2012). Compared with broadleaf trees, a higher abundance of omnivore-predators under coniferous trees might contribute to a fairly stable microbial community and soil ecosystem under coniferous forests (Žifčáková et al. 2016), which could also be implied by our results that coniferous trees had greater nematode diversity, genus richness and MI than broadleaf trees. In contrast, the large-scale geographic distribution patterns of soil nematodes provided by Song et al. (2017) and van den Hoogen et al. (2019) showed that temperate broadleaf forests had greater nematode density and genus richness than temperate coniferous forests. This is probably related to the study area, given that the experimental soils and trees in our study were collected in the subalpine zone with harsh climate conditions. Thus, the stronger cold hardiness of coniferous trees might be conducive to maintaining more diverse nematode communities than broadleaf trees (Chang et al. 2021).

Additionally, consistent with our first hypothesis, we found that the differences in the effects of broadleaf and coniferous trees on the soil nematode communities were associated with successional stages. Compared with late-stage soils, greater differences in the effects of broadleaf and coniferous trees on nematode trophic groups were found in the early-stage soils. This is probably due to the interrelations between plant communities and soil nematode communities across successional stages (Li et al. 2015). Specifically, since our target tree species dominated and coexisted in the late successional stage, they established relatively stable interrelations with nematode communities in late-stage soils. However, the target tree species showed different

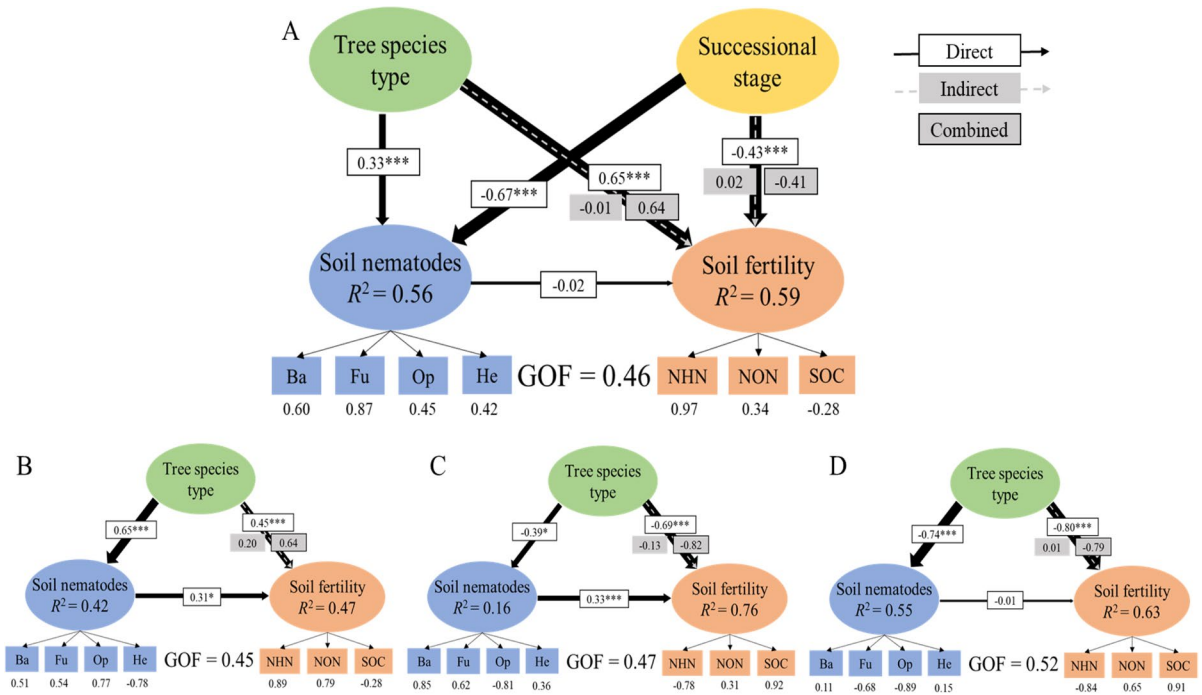


Fig. 5 Direct and indirect effects of tree species type, successional stage and soil nematodes on soil fertility explored by partial least squares path modelling (PLS-PM) in soils of (A) all, (B) early, (C) middle and (D) late stages. The width of the arrows indicates the strength of the causal relationships supplemented by standardized path coefficients (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). R^2 values indicate the explained variance of response variables. The models were evaluated using the goodness of fit (GOF) statistic. Ba, bacterivore; Fu, fungivore; Op, omnivore-predator; He, herbivore; NHN, ammonium nitrogen; NON, nitrate nitrogen; SOC, soil organic carbon

effects on soil nematode communities that were associated with herbs in early-stage soils, with more microbivorous nematodes and fewer herbivorous nematodes under coniferous trees than under broadleaf trees. According to the results of Liu et al. (2022), fewer microbivorous nematodes and more herbivorous nematodes were found in early-stage soils than in late-stage soils. Therefore, we speculated that compared with broadleaf trees, coniferous trees might have stronger regulatory effects on soil nematodes and might be more successful in accumulating beneficial microbivores and inhibiting harmful herbivores.

Contrasting effects of tree species type on soil fertility across successional stages

In this study, significant differences were noted in the effects of tree species type on soil fertility, including soil organic carbon, ammonium nitrogen and nitrate nitrogen. Regardless of successional stage,

the soil organic carbon content under broadleaf trees was significantly higher than that under coniferous trees. This result reinforced the findings of previous studies that broadleaf forests generally have larger soil organic carbon stocks than coniferous forests (Chiti et al. 2012; Peng et al. 2020; Su et al. 2021). In addition, we found that the content of soil ammonium nitrogen under broadleaf trees was significantly lower than that under coniferous trees, which is consistent with previous studies in the field (Cheng et al. 2014; Kang et al. 2018). The promoting effects of coniferous trees on soil ammonium nitrogen could be particularly important in our sampling area characterized by N-limitation (Zhang et al. 2017). Although broadleaf trees were reported to show higher uptake of nitrate nitrogen than coniferous trees, which indicated that soil nitrate nitrogen content under broadleaf trees might be lower than that under coniferous trees (Li et al. 2016), our results showed that soil nitrate under broadleaf and coniferous trees exhibited inconsistent

variations in soils of different stages. These results implied that in addition to soil carbon (Hübllová and Frouz 2021), the variations in soil nitrogen sequestration under broadleaf and coniferous trees might also be related to successional stages. However, given the ephemeral nature of soil inorganic nitrogen (i.e., ammonium volatilizes and nitrate leaches rapidly), there are limitations to the conclusions that can be drawn using a single time point measurement. However, the experimental pot with a plastic dish on the bottom could effectively avoid the nitrate leaching, while the constant temperature (~19 °C) in the experimental greenhouse was relatively low so that the ammonium volatilizing could be restrained to some extent. Since there are still some difficulties in the restoration of degraded forests after artificial afforestation, such as slow forest secondary succession, low ecological services of secondary forests (e.g., low forest productivity and water conservation), etc. (Liu et al. 2021), exploring the effects and potential mechanisms of tree species type on soil fertility might provide constructive insight in addressing these difficulties. Given the contrasting effects of broadleaf and coniferous trees on nematode communities across successional stages observed in our study, as well as the ecological functions of soil nematodes in the decomposition of soil organic matter and nutrient mineralization (Ranoarisoa et al. 2018; Wang et al. 2017), the regulatory roles of soil nematode communities in the effects of tree species type on soil fertility should not be ignored.

Roles of nematode community in the effects of tree species type on soil fertility

Our VPA results showed that tree species type had dominant effects on soil fertility, whereas the effects of soil nematode communities might also be nonnegligible, particularly the combined effects of tree species type and soil nematode communities. Previous studies have shown that the effects of tree species on soil properties might be substantially mediated by soil microbial communities (Frouz et al. 2013; Peng et al. 2020). Moreover, microbial activity was found to be a direct driving factor for plants affecting soil properties (Lange et al. 2015). Soil nematodes, with high trophic levels and serving as grazers of soil microbial communities, have important effects on enhancing microbial activity

and further improving the decomposition of soil organic matter (Zhou et al. 2013). Consistent with our second hypothesis, our results further suggested that soil nematode communities might play an indirect regulatory role in the effects of tree species type on soil fertility. Although it must be noted that the inoculation soil might introduce a small amount of soil microbes beside nematodes, the significant path coefficients among tree species type, soil nematodes and soil fertility (Fig. 5B and C) have demonstrated the existence of the mediating roles of soil nematodes to some extent. Accordingly, specific inoculation using nematode suspension is needed to further assess the mediating roles of soil nematodes in the effects of trees on soil fertility. Additionally, it is worth noting that the mediating roles of soil nematodes were related to the successional stage, which might be caused by the contrasting effects of tree species type on soil nematode communities across successional stages. Specifically, the indirect effects of tree species type on soil fertility via soil nematodes weakened with successional stages.

The regulatory influence of plants on soil biotic and abiotic characteristics is considered a fundamental phase of plant-soil feedbacks (van der Putten et al. 2013; Wilschut et al. 2019). The change in the indirect effects of tree species type on soil fertility via soil nematodes might, to some extent, alter the feedback effects of soil on vegetation dynamics during forest succession, which still need to be further confirmed in future studies. In addition, consistent with previous studies (Kardol et al. 2006; terHorst and Zee 2016), we found that late successional coniferous trees grow better in late-stage soils than early-stage soils (Fig. S1), implying a positive PSF from late successional plant species in contrast to a negative PSF from early successional species. By using field conditioned soils instead of greenhouse conditioned soils, our result still supported the view that the PSFs can drive plant community replacement through successional stages (Kardol et al. 2007; Pugnaire et al. 2019). However, the broadleaf trees were found to grow better in middle-stage soils than in other soils (Fig. S1). This might be due to the fact that the broadleaf trees used in our study were pioneer tree species in the late successional stage and the soil legacies of middle-successional shrubs were reported to have a facilitative effect on the pioneer tree seedling growth,

which could facilitate the successful establishment of pioneer tree species (Liang et al. 2022).

Although we observed a higher abundance of microbivorous nematodes that could promote the sizes and turnover rates of soil organic carbon pools (Jiang et al. 2018) under coniferous trees than under broadleaf trees, the root biomass of broadleaf trees was also found to be much greater than that of coniferous trees in our study (Fig. S1). Thus, the higher content of soil organic carbon under broadleaf trees than under coniferous trees might be caused by the root inputs of plants contributing predominantly to the soil organic carbon content (Mueller et al. 2012; Prescott and Vesterdal 2013). This result implied that the new carbon input into soils, such as plant roots, could have dominant effects on soil carbon storage, among which the roles of soil nematodes might be relatively limited. This is in parallel with the views of Lange et al. (2015) that the integration of new carbon into soil had greater contributions to the increase in soil carbon storage than the decomposition of existing soil carbon. However, the difference in the soil organic carbon content between broadleaf and coniferous trees was smallest in early-stage soils, which might be associated with the relatively higher abundance of microbivorous nematodes under coniferous trees in early-stage soils than soils of other stages, such as bacterivorous *Cephalobus* and fungivorous *Aphelenchoides* (Table S1). This might be caused by the potential advantages of coniferous trees accumulating more abundant microbivorous nematodes than broadleaf trees in our study. Despite the lower soil organic carbon content, the higher soil inorganic nitrogen content under coniferous trees than under broadleaf trees might reflect the important roles of soil nematodes in nutrient mineralization (Gebremikael et al. 2016). Given the positive effects of coniferous trees on microbivorous nematodes and soil mineral nitrogen, as well as the positive effects of broadleaf trees on soil carbon storage, mixed forests of broadleaf and coniferous trees might have greater potential in regulating soil nematode communities and soil fertility in favour of forest ecosystems. For example, Li et al. (2021) suggested that coniferous *Pinus massoniana* mixed with broadleaf *Schima superba* might contribute to soil quality improvement by altering soil fungal communities. Therefore, the roles of soil nematodes in the effects of trees on soil fertility could be promising

in providing scientific guidance for forest ecosystem management (such as artificial afforestation), which still needs to be further studied.

Conclusion

Collectively, our results showed that broadleaf and coniferous trees significantly differed in their effects on soil nematode community composition, particularly omnivore-predators, rather than total nematode abundance. The top-down effect induced by omnivore-predators might contribute to diverse and structured nematode communities under coniferous trees than under broadleaf trees. Moreover, the differences in the effects of broadleaf and coniferous trees on soil nematode communities were associated with secondary successional stages, with the greatest differences noted in the early successional stages. In addition, we found that soil nematode communities might have played indirect regulatory roles, that weakened with successional stages, in the effects of tree species type on soil fertility. It must be noted that extrapolating these results should be done with caution, given some limitations within the experimental design, such as the potential interferences caused by the potting soils and experimental duration. However, mutually corroborating with other studies, our results to some extent revealed the differences in the effects of broadleaf and coniferous trees on soil nematode communities and soil fertility across successional stages. Due to the potential advantages of accumulating beneficial microbivores, coniferous trees might have improved soil nutrient mineralization. In contrast, fast-growing broadleaf trees with larger root biomass might have caused the increase in the new carbon input into soils, which resulted in greater soil carbon storage than coniferous trees. Overall, our results implied that reconstructing mixed forests of broadleaf and coniferous trees might be a promising choice for forest ecosystem management (such as artificial afforestation), given their respective advantages in regulating soil nematode communities and soil fertility.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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

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