

Roots With Larger Specific Root Length and C: N Ratio Sustain More Complex Nematode Community

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Abstract

Aims Roots bridge above and belowground systems, and play a pivotal role in structuring root-associated organisms via influencing food resources and habitat conditions. Most studies focused on the relationships between plant identity and root-associated organisms, however, little is known about how root traits affect nematode communities within the rhizosphere.

Methods We investigated the relationships between root traits of four plant species and nematode diversity, community structure and trophic complexity in an ex-arable field.

Results While the relative abundance of herbivorous nematodes was negatively associated with specific root length (SRL), specific root area (SRA), root length density (RLD) and root C: N ratio, free-living nematodes were positively affected by these traits, implying a multifaceted effect of root traits on root-associated organisms. Importantly, we found that finer root systems promoted the complexity of the nematode community, by increasing the relative abundance of high trophic-level nematodes (i.e., omnivores and predators) and enhancing nematode diversity.

Conclusion Our findings suggest that root traits could be reliable indicators of soil community structure and interactions, and provide new insights into soil biodiversity and functional maintenance.

Introduction

Anthropogenic activities are known to have profound impacts on plant diversity and/or functional groups, which will in turn impact on the structure and functions of terrestrial ecosystem (Chen et al. 2021; Diaz et al. 2019). Most studies have so far focused on the responses of aboveground communities (Chen et al. 2018; Huang et al. 2020), yet the understanding of how belowground responses to changes in plant community is limited. Plants shape belowground communities through determining the characteristics of biomass production, litter quality, and belowground carbon allocation (Hobbie 2015; Yokobe et al 2021). Conceptually, taller or larger plants would allocate greater biomass and carbon (C) into soil, resulting in more microbes and subsequent grazers, than that of shorter and smaller plants (Chapin et al. 2011). Nevertheless, numerous studies have shown that greater plant biomass does not always lead to increases in the biomass or abundance of soil micro-organisms. Neutral and negative results have also been reported (Li et al. 2021; Zhou et al. 2020).

One of the key reasons for inconsistencies among the aforementioned studies lies in the underestimation of the effects of plant roots, which account for the majority of plant biomass for many biomes (Huang et al. 2021; Poorter et al. 2012). Roots are the key linkages between above and belowground communities, and play critical roles in maintaining multiple ecosystem functions (Bardgett and van der Putten 2014), such as energy flux (Legay et al. 2020), nutrient retention (De Deyn et al. 2008) and resistance to invasions (Herve and Erb 2019). Different plant species have contrasting root systems, including branching patterns, rooting depth, root longevity and turnover time, which together affect soil abiotic and biotic properties (Han et al. 2020). Divergent root systems create diverse habitats for soil biota (Legay et

al. 2020; Merino-Martín et al. 2020), suggesting that root patterns are important factors in explaining the variations in soil biota. Understanding plant root induced changes is critical to predict the dynamics of belowground communities, and root traits were proposed as a useful tool for this (Bardgett et al. 2014; Violle et al. 2007). Such trait-based approaches have increasingly been used to probe alterations in belowground communities (Han et al. 2020; Spitzer et al. 2021). For example, roots with high specific root length (SRL) and low root diameter or root tissue density (RTD) are often associated with high root turnover and short life span, and reduce the colonization of root-associated microbes (Bergmann et al. 2020; Qiu et al. 2021). Recent studies, however, explored the relationships between root traits and soil biota focus on microbes, such as bacteria and fungi (Spitzer et al. 2021; Sweeney et al. 2021), while it remains largely unknown how root traits affect soil fauna and the soil food web.

Nematodes are the most diverse and abundant metazoan, and appear in a wide array of trophic levels including primary (herbivores), secondary (microbivores) and tertiary (predators) consumers (van den Hoogen et al. 2019). Thus, soil nematodes are assumed as a proxy for estimating the situation of soil food web under different environmental conditions (Neher 2001). Root traits could affect soil nematode communities via two major pathways. On the one hand, as live roots and root litter are major food resources, variations of root biomass would lead to fluctuations in nematode abundance (Cortois et al. 2017). Furthermore, roots with a higher N content may enhance palatability for certain herbivores, which would favour specific herbivores and result in low diversity of nematode community because of niche competition (Chase et al. 2002). Root traits may also affect abiotic and biotic aspects of the soil habitat conditions, with cascading effects on soil nematodes. For instance, distinct root diameters differentially alter soil moisture and porosity (Jin et al. 2017) which influences the behaviours of nematodes with different body sizes (Erktan et al. 2020), with finer root systems creating more pore-space adjacent to roots so aiding the survival of larger nematodes, such as omnivores and predators (Briar et al. 2011; Franco et al. 2019). Also, greater values of specific root length and specific root area (SRA) provide more available micro-habitats for microbes, thereby increasing the richness of microbivorous nematodes with different food preferences (Picot et al. 2019). In particular, previous studies have proposed that increases in high-trophic level soil biota would lead to a more complex soil food web (Levine et al. 2017). Therefore, root trait-based approaches may improve our understanding of nematode assemblages (Ritz and Trudgill 1999; Zhang et al. 2020).

Here, we tested the responses of nematode community composition and structure to changes in plant species with diverse root traits (including root biomass, root diameter, specific root length, specific root area, root length density, root tissue density and root C: N ratio) in an ex-arable field. We hypothesized that (1) roots with greater biomass could recruit more nematodes, whereas roots with lower N content or greater specific root length would suppress herbivores; and (2) roots with greater specific root length and area would enhance relative abundance of omnivores and predators through improving habitat conditions, thus facilitating the diversity and complexity of nematode community.

Materials And Methods

Experimental site description and plant species collection

The study site was an ex-arable field at Jiangxi Institute of Red Soil, Jiangxi Province, China (116°20′24″ E, 28°15′30″ N), with a subtropical climate of 18.1°C mean annual temperature and 1537 mm mean annual precipitation. The management of this field changed from crop cultivation (rotation of peanut and sweet potato) to abandonment in December 2014, resulting in natural germination of pioneer plant species. The soil is a quaternary red clay derived soil, classified as *Ultisols and Oxisols* according to Soil Survey Staff (1999). Initial soil physicochemical properties were characterized as: 17% sand, 56.9% silt, 26.1% clay, 5.3 pH (H₂O), 10.4 g kg⁻¹ total C, 1.0 g kg⁻¹ total N, and 19.4 mg kg⁻¹ mineral N.

A total of 20 species were identified by their morphological features (Table S1), which were pioneers following the agricultural field abandoned. Comprehensively based on the previous field investigation, we selected four representative species including *Setaria viridis* (L.) P. Beauv. (*S. viridis*; *Poaceae*), *Phytolacca americana* L. (*P. americana*; *Phytolaccaceae*), *Xanthium sibiricum* Patr. ex Widder (*X. sibiricum*; *Asteraceae*) and *Polygonum perfoliatum* L. (*P. perfoliatum*; *Polygonaceae*). They belong to four distinct taxonomic families and especially possessed distinct root traits (see the results below). Root samples were collected in June and September 2015, representing growth stage and maturity stage respectively. The plant samples were collected according to following criteria that (1) five patches of per species were selected as separately replicated sampling sites at the study site; and (2) each replicated patch of per plant species were distanced from each other by over 10 m; and (3) harvested well-developed individuals in the center of target species patches to exclude the confounding effects of other adjacent species. After excavation with spade (the depth was beyond 30 cm to ensure root system integrity) and gently shaking away loose soil from roots, samples were stored in labeled polyethylene bags respectively and were conveyed to laboratory and kept at 4°C straight away for further analysis.

Root-traits measurement

Before measuring root traits, rhizosphere soil samples (directly adhered to the root system) were removed into clean polyethylene bags after obtained through brushing and mixing. Root samples were washed clean in running water to remove soil adhered. All root samples were scanned with scanner (EPSON LA2400 Scanner) and measured with WINRHIZO software to get the values of root length, surface area, volume, and diameter. Then, plant roots were dried to a constant weight at 60°C to determine root biomass (g). Root length or surface area production per unit dry mass were described in terms of specific root length (SRL; m g⁻¹) or specific root length separately (SRA; cm² g⁻¹), root length density (RLD; m cm⁻³) calculated as the ratio between root total length and volume, and root tissue density (RTD; g cm⁻³) representing the fraction of vascular tissue in a single root segment was calculated as root dry mass divided by volume (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Ball-milled samples were analyzed by potassium dichromate oxidation-ferrous sulphate titration and the Kjeldahl digestion with

sulfuric acid and hydrogen peroxide to analyze root carbon content and root nitrogen content (Sparks et al. 1996).

Assessment of nematode community

Rhizosphere soil nematodes were extracted from 50g fresh soil with modified Baermann method followed by sugar centrifugal flotation (Liu et al. 2008). Nematodes were identified to genus with a light microscope 400× magnification (150 randomly-selected individuals per sample or all individuals in the condition of fewer than 150) after counted. Meanwhile, all nematodes identified were divided into bacterivores, fungivores, herbivores and omnivore-predators following Yeates et al. (1993). The abundance of total nematodes was expressed as individuals per 1 g dry weight soil.

We calculated indices to evaluate nematode community structure. First, the ratio between fungivores and bacterivores was calculated as FF/BF which could reflect the relative importance of energy channels in soil (Bardgett 2010; Wasilewska 1997). Also, the ratio between omnivore-predators and herbivores (OP/H) was used to indicate nematode community complexity, because the prevalence of omnivores and predators is advantage to balance distribution and increasing interactions in nematode community via grazing. (Thakur et al. 2014; Wasilewska 1997). Furthermore, the Maturity Index (MI) was calculated with the weighted mean of the individual colonizer-persister values (ranged from c-p 1 to c-p 5) of free-living nematodes as follows:

$$MI = \sum_{i=1}^n v(i) \cdot f(i)$$

where $v(i)$ is the c-p value of taxon i and $f(i)$ is the frequency of that taxon in a sample (Bongers 1990). The MI was used as an indicator of environmental disturbance and soil food web complexity, which high value reflected stable and complex conditions (Bongers and Bongers 1998; Siebert et al. 2020). The number of taxa was calculated to demonstrate nematode richness. Finally, nematode networks were presented to indicate the linkage density of taxa within nematode community.

Data analysis

All analyses were performed in R Version 4.0.5 (R Core Team, 2020). The relationships between nematode indices and comprehensive root traits were measured using simple regression analysis based on R^2 values using the function *lm* in R package base. Significant difference was determined at levels of $p < 0.05$, $p < 0.01$, and $p < 0.001$. Nematode association networks for each plant species were created by first creating a network meta-matrix using the standardized statistics of nematodes according to identification. Nematode network analyses were carried out using “Vegan” and “igraph” packages (Csardi and Nepusz, 2005; Oksanen et al., 2020). We removed poorly represented nematode taxa to facilitate the determination of the core community, and analyzed as following criteria: (1) taxa relative abundance >

0.1%; (2) presented in 3 samples at least; (3) Spearman's correlation coefficient (r) > 0.6; and (4) significant difference was determined at levels of <0.05. In order to describe the topology of the networks, we calculated average node connectivity, average path length, diameter, cumulative degree distribution, clustering coefficient and modularity. Visualization of networks were presented with the interactive platform gephi (Bastian et al., 2009).

Results

Root traits across plant species

At the growth stage, root biomass of *S. viridis* was significantly larger than other plant species, but lower than other plant species at the maturity stage ($p < 0.05$, Fig. 1a). *P. americana* presented the highest value of root diameter compared to other plant species ($p < 0.05$, Fig. 1b). Besides, SRL, SRA, RLD and root C: N ratio showed consistent and decreasing trends in the order of *S. viridis*, *X. sibiricum*, *P. perfoliatum* and *P. americana* at both growth and maturity stage ($p < 0.05$, Fig. 1c-e and Fig. 1g).

Soil nematode community

Total nematode individuals differed significantly among plant species at the maturity stage ($p < 0.05$; Fig. 2a), but were similar at the growth stage ($p > 0.05$; Fig. 2a). *S. viridis*, which had the highest values of SRL, SRA, RLD and root C: N ratio had significantly higher relative abundance of bacterivores and fungivores ($p < 0.05$; Fig. 2c-d), but lower relative abundance of herbivores than other plant species ($p < 0.05$; Fig. 2b). Besides, the value of FF/BF under *S. viridis* treatment was significantly higher than that of other plant species at the maturity stage ($p < 0.05$; Fig. 2f). Increase of SRL, SRA, RLD and root C: N ratio shifted nematode community towards a more richness community, as indicated by higher nematode taxa richness ($p < 0.05$; Fig. 1 and Fig. 2g). *S. viridis* and *X. sibiricum* presented significant higher values of MI and OP/H than other treatments at the growth stage, whereas *S. viridis* and *P. perfoliatum* showed higher values of MI and OP/H at the maturity stage, as indicated in Fig. 2h and Fig. 2i. Generally, plant species had significant effect on nematode community composition (Fig. 2).

Relations of nematode community composition with root traits

Total nematode abundance was negatively correlated with SRL ($R = -0.57$, $p < 0.05$; Table 1) and RLD ($R = -0.63$, $p < 0.05$) at the maturity stage. Besides, root biomass presented significantly relationships with relative abundance of herbivores, bacterivores and fungivores ($p < 0.05$), but such relationships were inconsistent at growth and maturity stage. Root traits including SRL, SRA, RLD and root C: N ratio were consistently and negatively related to the relative abundance of herbivores respectively, but positively related to the relative abundance of microbivorous nematodes ($p < 0.05$).

Table 1

Relations between nematode abundance and root traits. The R values followed with *, **, and *** indicate $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. Biomass- root biomass, Diameter- root diameter, SRL- specific root length, SRA- specific root area, RLD- root length density, RTD- root tissue density, C: N- root C: N ratio

	Biomass	Diameter	SRL	SRA	RLD	RTD	C: N
<i>Growth stage</i>							
Total nematode individuals	-0.14	0.31	0.08	0.27	-0.04	-0.32	-0.01
Relative abundance of bacterivores	0.74***	-0.04	0.55*	0.66**	0.76***	0.45*	0.46*
Relative abundance of fungivores	0.75***	-0.003	0.63**	0.79***	0.75***	0.36	0.69***
Relative abundance of herbivores	-0.53*	0.23	-0.81***	-0.76***	-0.85***	-0.26	-0.61**
Relative abundance of omnivore-predators	-0.10	-0.38	0.62**	0.34	0.45*	-0.12	0.27
<i>Maturity stage</i>							
Total nematode individuals	0.23	0.33	-0.57**	-0.41	-0.63**	0.23	-0.42
Relative abundance of bacterivores	-0.51*	-0.60**	0.63**	0.59**	0.66**	-0.36	0.64**
Relative abundance of fungivores	-0.68***	-0.50*	0.83***	0.69***	0.83***	-0.27	0.45*
Relative abundance of herbivores	0.76***	0.63**	-0.77***	-0.72***	-0.78***	0.46*	-0.56*
Relative abundance of omnivore-predators	-0.65**	-0.45*	0.43	0.48*	0.43	-0.48*	0.31

FF/BF was positively correlated with SRL ($R^2 = 0.17$, $p < 0.05$; Fig. 3), RLD ($R^2 = 0.15$, $p < 0.05$) at the maturity stage. Besides, MI was positively associated with root traits including SRL ($R^2 = 0.53$, $p < 0.001$), SRA ($R^2 = 0.43$, $p < 0.001$), RLD ($R^2 = 0.50$, $p < 0.001$) and root C: N ratio ($R^2 = 0.27$, $p < 0.001$), but negatively correlated with root biomass, root diameter and RTD at the maturity stage. Similar relationships were observed in the relations of nematode richness and OP/H with root traits separately ($p < 0.05$), however root C: N ratio was the only exception, presenting unremarkable relationship ($p > 0.05$).

Network complexity of nematode communities

The complexity of nematode communities was evaluated within taxa of identified nematode using a correlation network (Fig. 4). Generally, the numbers of network average nodes, edges declined in a particular order of treatments (*S. viridis* followed with *X. sibiricum*, *P. perfoliatum* and *P. americana*) which suggested the decrease of nematode community complexity, because greater network complexity often depended upon the number of taxa (nodes) and the linkage density (the number of edges) within the network (Table S2).

Discussion

Trait-based approaches are increasingly used to explore the relationships between plant and soil communities (Fry et al. 2018; Fujii et al. 2020). Since roots bridge above and belowground communities, understanding how root traits affect soil biota is of great importance in predicting plant-soil interactions, particularly under future global change scenarios (Han and Zhu 2021; Bardgett 2017). In this study, a trait-based approach was used to explore the relationships between root systems and nematode communities in an ex-arable field grown with four pioneer plant species. The results showed that root traits significantly affected nematode community composition and structure, with finer and greater C: N root systems supporting greater species richness and community complexity than in thicker and lower C: N root systems. These findings highlight that root traits could be used to predict soil nematode communities, and especially, would be an indicator for soil food-web structure without soil sampling when root traits are known for many plant species.

Although the total nematode individuals were largely unaffected by root biomass, which disproved our first hypothesis, our results suggested that the variation of root biomass would change the functional composition of nematode communities. The insignificant association between total nematode individuals and root biomass may attribute to different responses of nematodes in different trophic groups (De Deyn et al. 2004; Wardle et al. 2003). Interestingly, the relationships between the relative abundance of nematode (herbivores or microbivores) and root biomass were distinct at two stages. One possible explanation for this contrasting result may due to the senescence of the annual species (such as *S. viridis*) and continued growing of perennial species (such as *P. americana*) at the maturity stage, resulting in the discrepant tendency of root biomass among plant species between two stages. Such results emphasized the limitation with regard to the disentanglement of plant-soil interaction with considering root biomass only, and also, highlight for more dynamic investigations.

Our results demonstrated that the relative abundance of herbivores was negatively related to root C: N ratio, which was consistent with previous studies (Gough et al. 2021; Viketoft 2008). Given that root C: N ratio reflects structural defenses (e.g., the concentration of lignin) related to the relative investment of C and N at the tissue level (Ma et al. 2018), greater C: N might prevent certain herbivores from penetrating cells of roots and thereby restricting survival (Ramachandran et al. 2020; Yeates 1999). These results confirmed that both quantity and quality of food resources were potential drivers of community composition within the rhizosphere (De Deyn et al. 2004). More importantly, the negative relationships between the relative abundance of herbivores and root traits including specific root length, specific root

area and root length density suggest a multifaceted control of root traits on root-associated micro-organisms. Roots with greater values of specific root length were associated with greater nutrient uptake capacity and high turnover rates as well as shorter longevity (Roumet et al. 2006), which reduced survival time of herbivores. This result is inconsistent with a study conducted in a restoration chronosequence in a mixed-grass prairie (Otfinowski and Coffey 2020). Such discrepancies among these studies suggest the complex relationships between root traits and rhizosphere herbivore communities (Neher 2010), which call for the need to conduct more studies considering root exudates, biota-interactions and spatio-temporal heterogeneity (Sun et al. 2021; Thakur and Geisen 2019; Xiong et al. 2021). For example, root exudates, which were not considered in the current study, are thought to affect the performance of nematodes, and have been shown to attract or repel root herbivores (Sikder and Vestergard 2020). Specific root length, specific root area, root length density were positively related to the relative abundance of free-living nematodes in this study. In particular, a greater specific root area likely provides more niches for reproduction in root microbes that may cascade up to affect microbivorous nematodes and consumers in higher trophic levels (Bukovinszky et al. 2008). These results illustrate that different effects of multiple root traits on distinct trophic groups of soil micro-organisms, and further supports the idea that plants could affect the nematode abundance through different pathways (e.g., rhizosphere and litter pathways) (Zhang et al. 2019).

Consistent with our second hypothesis that roots with greater specific root length and area could result in greater complexity of nematode communities, we showed that the increases of complexity corresponded with increasing the relative abundance of high-trophic nematode (i.e., omnivores and predators) and nematode diversity. Finer root systems enhanced soil porosity in the processes of pushing soil particles aside for growth (Bardgett et al. 2014; Greinwald et al. 2021), and a greater specific root length has been proposed to improve root water-use ability and promote the water availability of rhizosphere soil (Fort et al. 2017). As such, high-trophic level nematodes (usually with large body size) could take advantages from habitat improvement with thicker water films around soil particles for their activities such as movement, predation, and reproduction (Franco et al. 2019; Wallace 1968; Xiong et al. 2019). Importantly, the increases in omnivores and predators could develop more interactions among trophic levels by feeding microbes, protists and other nematodes, thus increasing community complexity of nematode (Neutel et al. 2007; Siebert et al. 2020). Such positive effects of top-down control on community complexity have also been found in other studies (Shao et al. 2016; Thakur et al. 2014), and exert non-negligible effects on multiple ecosystem functions. On the other hand, increases in nematode diversity induced by denser, finer root system could also be an important driver in the enhancement of community complexity of nematode communities (Paine 1966). Increases in niche availability resulted from increases of specific root area could facilitate microbial coexistence and reproduction, which in turn reduced the risk of the disappearance of rare nematode species with specific food preferences (Picot et al. 2019; Yan et al. 2020). Given that rare nematode species may exert significant relationships to other micro-organisms that are often neglected in most studies, their contributions to the complexity of nematode community may be underestimated.

Conclusions And Outlook

Although there was limited sample size and trait assemblage in this study, our findings revealed that plants with different root traits exert contrasting effects on distinct nematode trophic groups. In particular, denser and finer root systems increased the community complexity of nematode by providing more available micro-habitats, which increased in relative abundance of higher trophic level nematodes (omnivores and predators) and nematode diversity. While our current work builds a bridge between plant roots and nematode communities from a trait perspective, these relationships were obtained from a single-site experiment and only based on four species, and hence requires further exploration across a wider range of species and environmental conditions. Based on our current findings and limitations, furthermore, a broader generalization of the presented findings requires further studies with greater sample numbers, from multiple sites, integrate multi-dimensional root trait variations, across different climatic conditions and accounting for coordination between plant roots and soil biota. This will help us to better understand the effects of plant communities on belowground biodiversity and functioning in a changing world.

Declarations

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Statements and Declarations

This work was supported by CARS-22-G-10 and 2018FY100300. The authors have no relevant financial or non-financial interests to disclose. All authors contributed to the study conception and design. Research design was performed by Xiaoyun Chen and Manqiang Liu. Experiment and data collection were performed by Wenqing Fan and Chongzhe Zhang. Data analysis was performed by Jingru Zhang, Chongzhe Zhang and Yiheng Tao. The first draft of the manuscript was written by Jingru Zhang and Zhengkun Hu, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

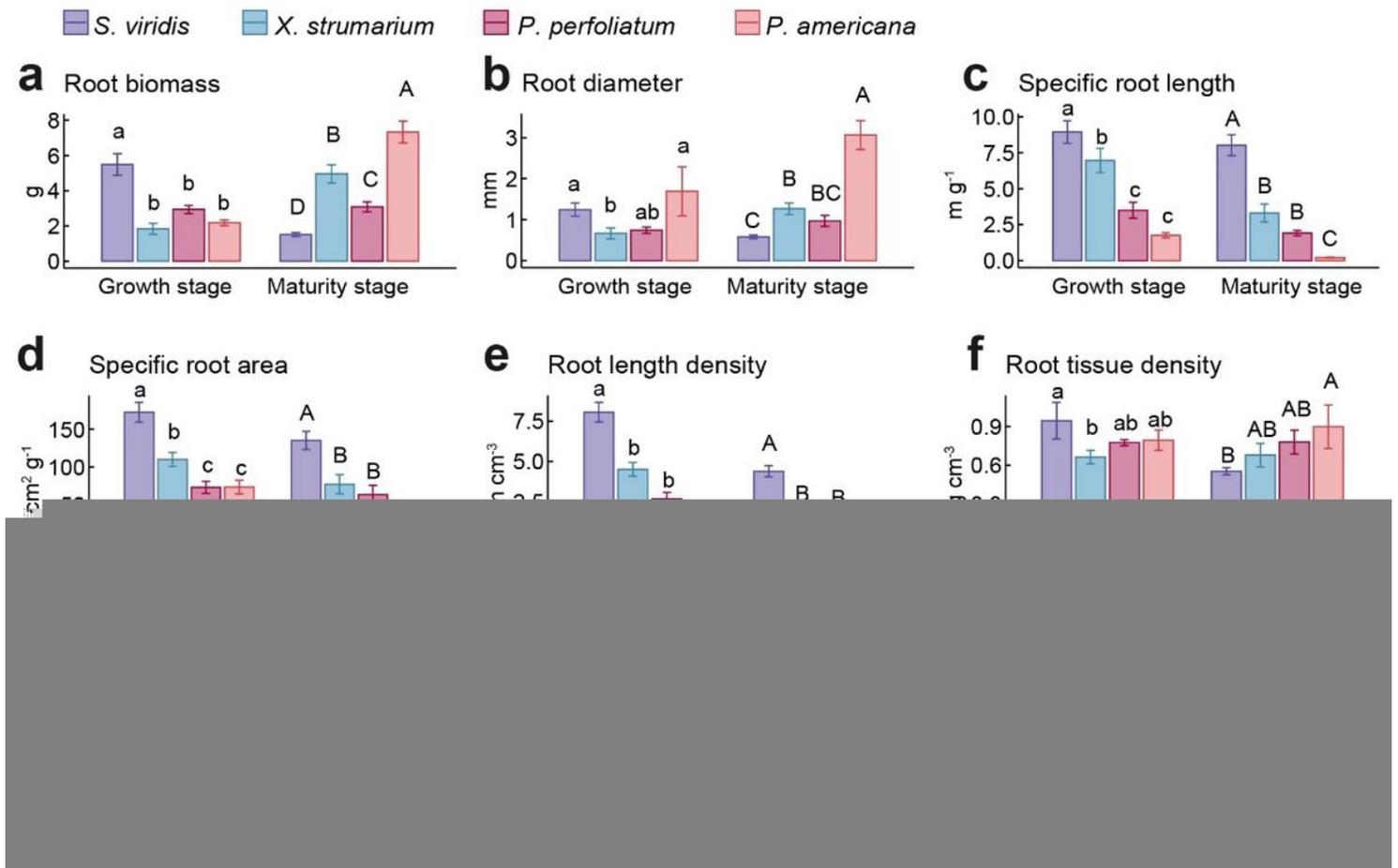


Figure 1

Effects of plant species on root biomass (a), root diameter (b), specific root length (c), specific root area (d) and root length density (e), root tissue density (f), root C: N ratio (g) in growth stage and maturity stage. Bars show means \pm standard errors within growth or maturity stage ($n = 5$). Significant differences between plant species in growth stage are presented by lowercase letters, while capital letters indicate significant differences between plant species in maturity stage (LSD test; $p < 0.05$). Effects of growth stages on root traits are listed in Table S2 with repeated measures ANOVA

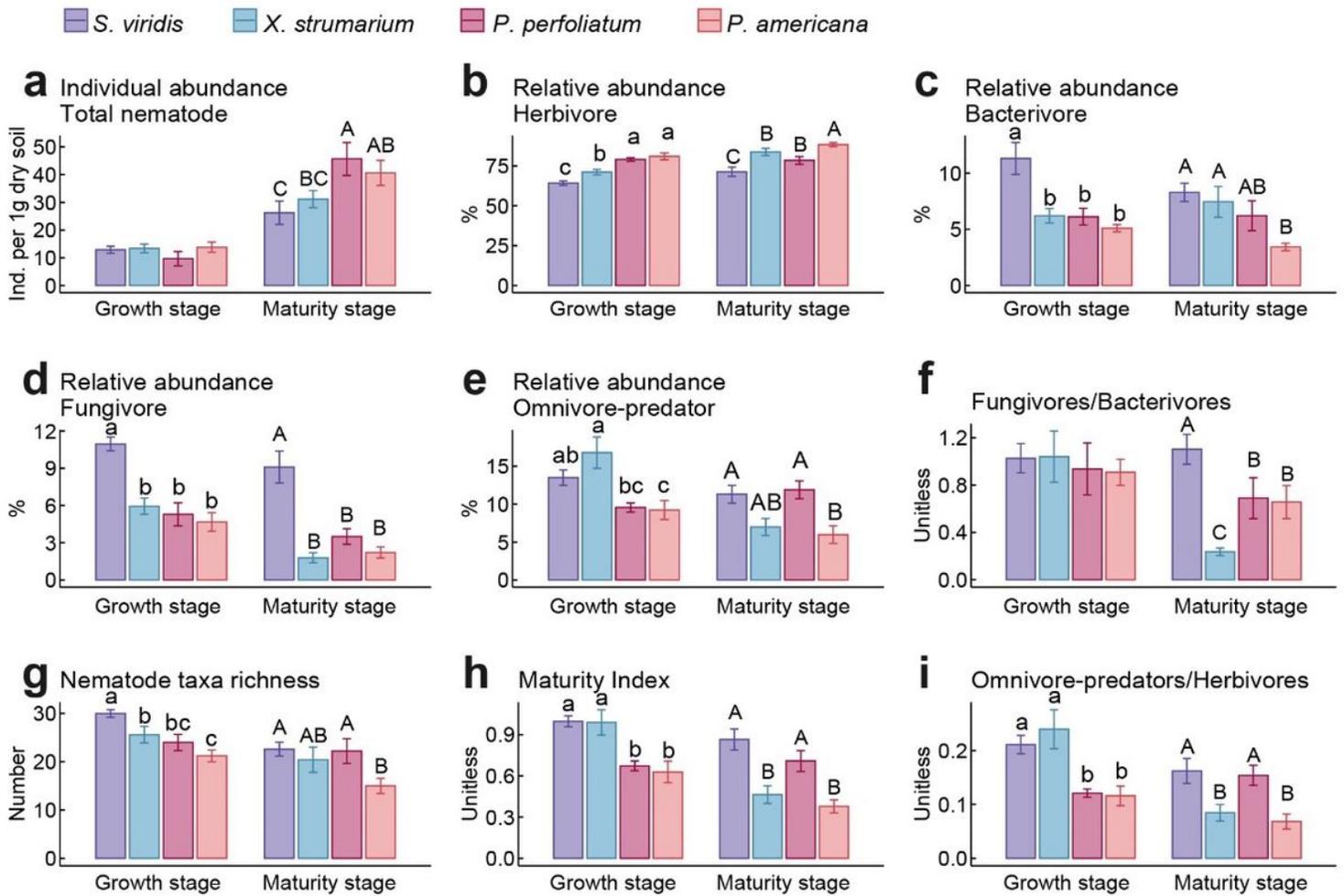


Figure 2

Effect of plant species on total nematode individuals (a), relative abundance of nematodes in different trophic groups (b-e), and ecological indices of nematode communities (f-i). Bars show means \pm standard errors within growth or maturity stage ($n = 5$). Significant differences between plant species in growth stage are presented by lowercase letters, while capital letters indicate significant differences between plant species in maturity stage (LSD test; $p < 0.05$). Effects of growth stages on nematode communities are listed in Table S2 with repeated measures ANOVA

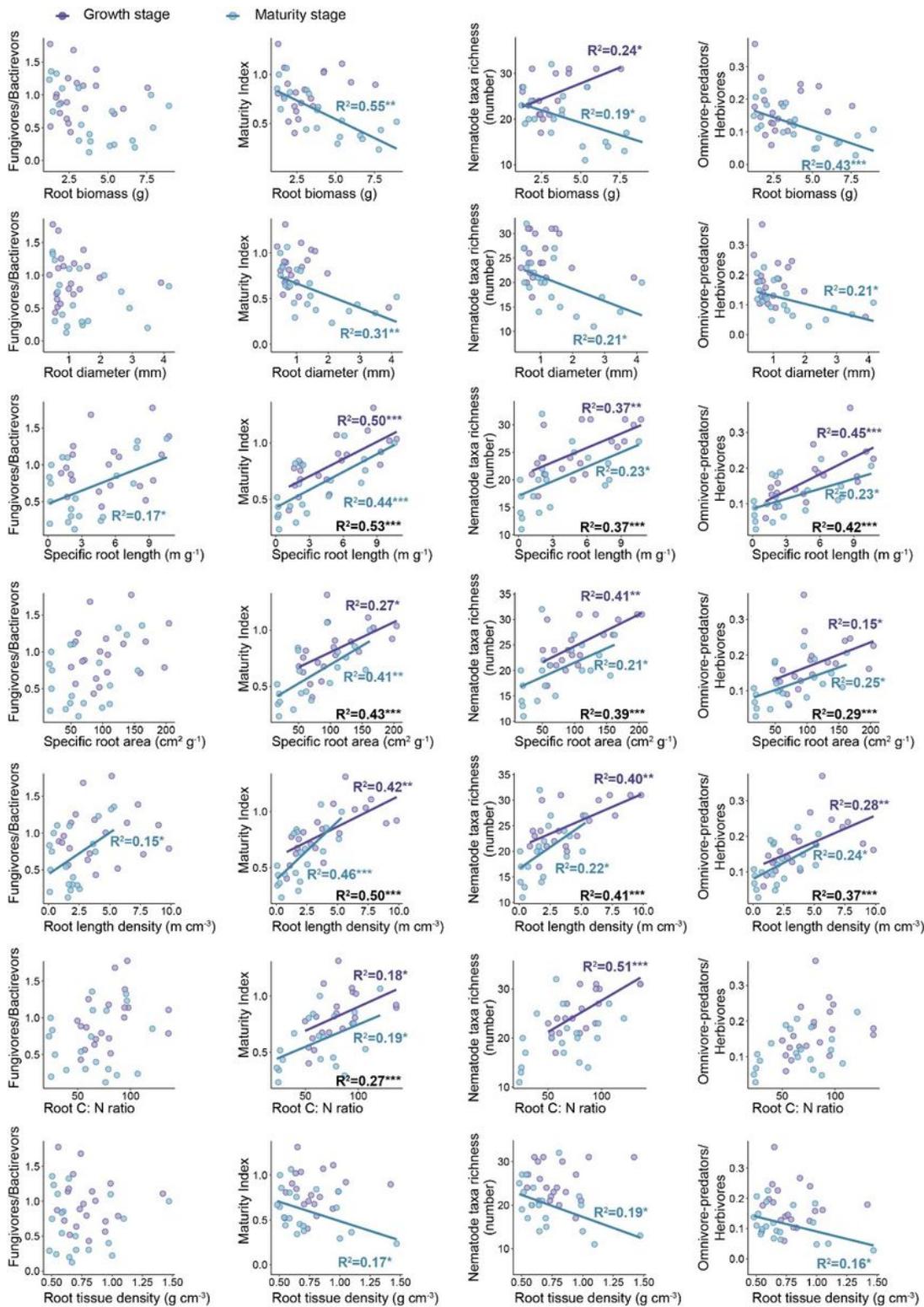


Figure 3

Separate relationships between ecological indices of soil nematode community and root traits at two stages (represented by different colours). R^2 is the coefficient of determination, and significance levels are $p < 0.05$, $p < 0.01$ and $p < 0.001$. R^2 in black indicates correlation coefficient, which

calculated by combined value of two stages for the consistent tendency of growth stage and maturity stage. Linear trend lines were only plotted for groups that got significance levels

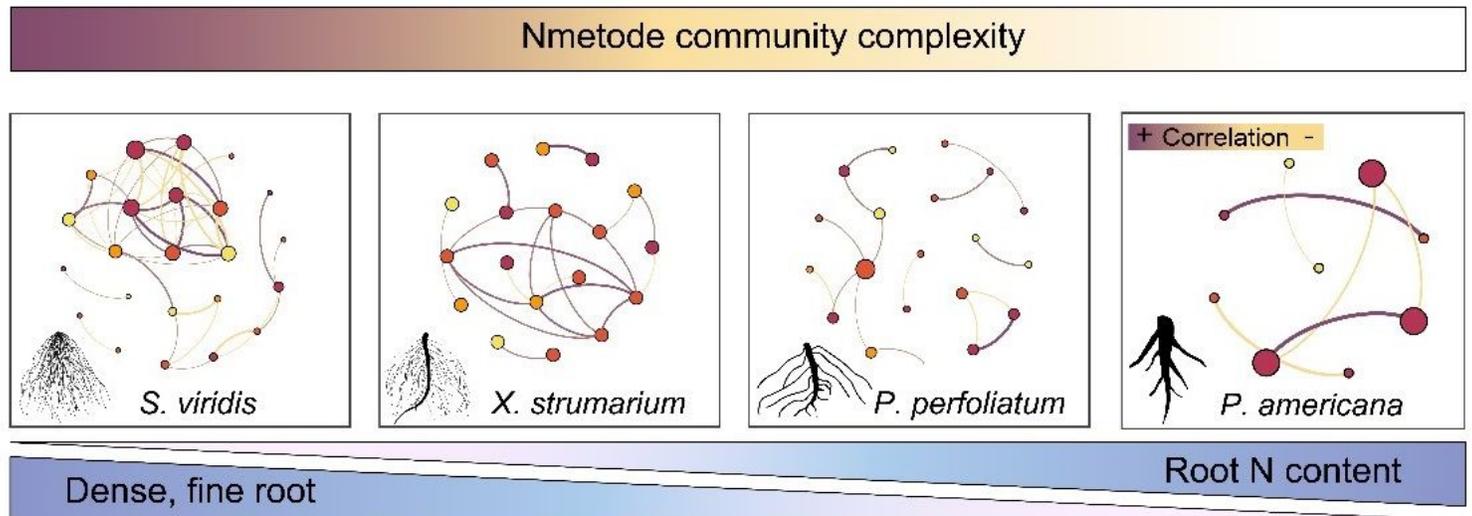


Figure 4

The relations between nematode community complexity and root traits according results in this study. Co-occurrence networks of different plant species were detected to predict nematode community complexity. Links were colored by the coefficient of correlation, and the width represents the absolute value of the correlation coefficient. The size of nodes is proportional to the average number of connections, and nematode trophic groups are shown in different colours. Data for Fig 4 include growth and maturity stages. Details of network topological attributes are listed in Table S1

Supplementary Files

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