Direct and Indirect Effects on Soil Nematode Communities Differ Between Facilitative and Allelopathic Plants

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Abstract

Plants are expected to affect soil nematode communities. However, comparative studies on the direct and indirect ways dominant plants influence soil nematode communities are rare. In this study, we compared the effects of a dominant allelopathic plant, *Ligularia virgaurea*, and a dominant facilitative plant, *Dasiphora fruticosa*, on soil nematode richness and community composition in an alpine meadow of the Tibetan plateau. Our result indicated that 1) *D. fruticosa* significantly increased nematode richness whereas *L. virgaurea* had no significant effect; 2) *D. fruticosa* had no significant impact on bacterial and fungal richness, but *L. virgaurea* increased fungal richness; 3) *D. fruticosa* had strong positive direct, and weak positive indirect, effects on nematode richness, mainly mediated by a marginal decrease in fungal richness. By contrast, *L. virgaurea* had no significant direct effect on soil nematode richness but had strong indirect effects, mainly mediated by changes in soil pH and soil organic carbon content; 4) *L. virgaurea* influenced soil nematode community composition predominantly through direct effects but also indirectly through soil organic carbon. By contrast, *D. fruticosa* affected nematode communities through changes in understory plant communities, soil physiochemical, and microbial communities. Both facilitative and allelopathic plants thus influence soil nematode richness and community composition but seemingly in different ways. These highlight the importance of plants in determining soil community diversity and provide new insight to disentangle the complex above- and belowground linkages.

Introduction

Soil organisms play a major role in ecosystem functions, including plant productivity, nutrient mineralization and decomposition (Bongiorno et al. 2019; Neher 1999b). Soil nematodes are small semi-aquatic multicellular animals that occupy a central position in the soil food web linking primary producers and primary consumers with higher trophic levels (Li et al. 2014; Yeates 2010), and they are distributed across all trophic levels (Li et al. 2014; Neher 2001). Moreover, nematodes influence the growth, distribution and metabolic activities of microorganisms (Grewa and Wright 1992; Ruess and Dighton 1996) and microbial community composition (Djigal et al. 2004), thereby regulating the decomposition pathways (Hu et al. 2015), decomposition rate (De Mesel et al. 2003) and nutrient cycling (Chen et al. 2018; Sohlenius et al. 1988). Plant parasitic nematodes directly influence plant productivity (Lafonta et al. 2007), while omnivores and predators feed on other soils biota, which can affect the community composition of soil biota communities more broadly (Laakso and Setälä 1999).

There is an increasing interest in the linkages between plants and belowground communities given the observed effects on ecosystem functioning (Abgrall et al. 2018; Shao et al. 2018; Wang et al. 2018). The communities of soil nematode are highly diverse both spatially and temporally (Pen-Mouratov et al. 2004) and has attracted much attention as bio-indicators (Neher 2001). Nematode community composition is driven by the spatiotemporal variability in vegetation, soil properties, and microbial communities (Kardol et al. 2010; Kerfahi et al. 2016; Neher 1999a; Wilschut et al. 2019). Vegetation composition influence nematode communities through multiple pathways (De Deyn et al. 2004; Wang et al. 2018). For example, Yeates (1999) found that changes in the aboveground plant community alters

nematode community composition, particularly plant-feeding nematodes, but also fungivores and bacterivores due to changes in microbial communities (Yeates et al. 1993). Wang et al. (2019b) demonstrated that soil nitrogen (N) content, ammonium and pH negatively affected the biomass of fungivores, while soil C and N positively and negatively affect omnivores-predators biomass, respectively. A recent global scale study found that soil characteristics explain most of the variation in nematode abundances, with greater numbers in soils with high organic C content and lesser when soil pH is low (van den Hoogen et al. 2019). Moreover, increased soil water content has a positive effect on the abundance of plant-feeding nematode (Ruan et al. 2012).

Certain plants have functional traits that increase their influences on the surrounding environment. Facilitative plants can promote seed germination, survival, and growth of neighboring plants by ameliorating the harsh local environment, or by promoting beneficial microbes or suppressing plant pests and pathogens (Callaway 2007). For example, McIntire and Fajardo (2014) found that shading by facilitative plants reduce soil temperatures and increase soil moisture content in warm and arid environments, providing a more suitable microenvironment for other plants. Facilitative plants have also been found to cause shifts in microbial communities. For example, the facilitative plant *Retema sphaerocarpa* increase bacterial evenness, the relative abundance of *Gammaproteobacteria* (Hortal et al. 2015) and the relative abundance of *Arthrobacter* (Rodríguez-Echeverría et al. 2013).

By contrast, allelopathic plants release compounds that serves as protection against herbivores, parasites and pathogens, but can also reduce seed germination and growth of neighboring plants when leached into the soil (Casanova-Katny et al. 2011; Cheng and Cheng 2015; Hortal et al. 2015). Similarly, allelopathic effects on soil microbes are well known; for example, the allelochemical coumarin decrease soil bacterial and fungal richness (Niro et al. 2016). Allelopathic rice seeds reduce the cultivable microbial community and total soil phospholipid fatty acids (PLFAs) (Kong et al. 2008). And Qu et al. (2021) illuminated the root extract of *Rhus typhina*, an invasive plant that produces allelochemicals, appreciably inhibit soil microbial activity.. Many previous studies have shown that plants can release allelopathic compounds that act as nematicides, thereby playing an important role in chemical defense against parasites (Hooks et al. 2010). Although the effect of allelopathic and facilitative plants on soil biota has been explored by many studies (Jabran et al. 2015; Rodríguez-Echeverría et al. 2013; Tewksbury and Lloyd 2001), few studies have compared the direct and indirect effects of allelopathic and facilitative plants on soil nematode communities.

In this study, we compared the effects of a dominant allelopathic plant, *Ligularia virgaurea*, and a dominant facilitative plant, *Dasiphora fruticosa*, on the soil nematode community in an alpine meadow on the Tibetan plateau. We used high-throughput sequencing methods to identify the richness and composition of soil microbes as well as soil nematodes. Morphological identification of nematodes is time-consuming and requires excellent taxonomic skills, and is generally limited by incomplete description of local nematode species (Morise et al. 2012). High-throughput sequencing technology has been shown to overcome these weaknesses (Geisen et al. 2018; Kerfahi et al. 2016; Wilschut et al. 2019). We applied structural equation modeling (SEM) to assess the direct and indirect effects of two

contrasting dominant plants on nematode community composition through changes in the understory plant community, soil properties as well as soil microbial communities. We hypothesized that: i) *Dasiphora fruticosa* and *Ligularia virgaurea* increase and reduce nematode richness, respectively, because *Dasiphora fruticosa* can protect understory plants thereby increasing resource availability, while allelochemicals released by *Ligularia virgaurea* may be poisonous to nematodes and reduce the richness of nematodes. ii) *Dasiphora fruticosa* and *Ligularia virgaurea* differ in their direct and indirect influences on soil nematode communities, with *Dasiphora fruticosa* influencing soil nematode communities mainly through biotic factors (understory composition and microbial communities), while *Ligularia virgaurea* increase soil nutrient and soil fungal richness, but decrease understory plant richness, and directly and indirectly affect soil nematode.

Materials And Methods

Study site

The experiment was conducted in a relatively flat alpine meadow of the Research Station of the Alpine Meadow and Wetland Ecosystems of Lanzhou University (Azi Branch Station) in Maqu (33°40'N, 101°51'E), Gannan Tibetan Autonomous Prefecture on the eastern edge of the Tibetan Plateau, Gansu Province. Azi Branch Station is located 3500 m above sea level. The annual precipitation is 620 mm, and the rain falls mainly during the short, cool summer. There are approximately 2580 h of cloud-free solar radiation annually (Wang et al. 2018). The experimental plot is a typical sub-alpine meadow dominated a few shrubs, including the two focal shrubs, and annual herbaceous plants.

Experimental design

In June 2016, a grazed field site with a healthy population of both *Dasiphora fruticosa* and *Ligularia virgaurea* was selected for the study. Within this area, we randomly allocated fifteen 30 cm × 30 cm plots, 5 with *D. fruticosa* (abbreviation: *Dasiphora*), 5 with *L. virgaurea* (abbreviation: *Ligularia*) and 5 without *D. fruticosa* and *L. virgaurea* (hereafter “control”), respectively.

Soil sampling and vegetation survey

In August 2016, at the end of growing season, we collected three soil cores from the center of each plot (within a 30 cm × 30 cm quadrat) using a soil auger (4 cm diameter, 20 cm depth), picked out stones and then hand-mixed soil in plastic bags. Soils were kept at 4 ℃ until processing. A subsample of the soil from the mixed sample was transferred to a sterile 15mL centrifuge tube and stored at -80 ℃ for molecular analyses. Prior to soil sampling, we recorded the species and number of plants within the same 30 cm × 30 cm quadrate.

Soil properties

Soil water content was measured by drying 30 g soil for 72 h at 105 ℃. The remaining soil was air-dried, avoiding direct sunlight following removal of gravel and plant residues by hand, and then sieved through

a 100 mesh (0.15 mm). Soil pH was measured in a 1:2.5 soil: deionized water slurry using a pH meter (PHSJ-3F, Shanghai INESA Scientific Instrument Co., Ltd, China). Soil organic matter was measured based on dichromate oxidation procedure (Kalembasa and Jenkinson 1973). Soil total nitrogen and phosphorus were both digested by concentrated H_2SO_4, and measured by semi-micro Kjeldahl and Mo-Sb antispetrophotography, respectively, using an auto chemistry analyzer (SmartChem 200, AMS Alliance) (Baillie 1990; Hendershot 1985). Soil ammonium and nitrate nitrogen were measured based on heating digestion method.

Soil microbial identification

Genomic DNA was extracted from 0.25 g soil according to the method on the DNeasy PowerSoil Kit (QIAGEN) (MoBio Laboratories, Carlsbad, CA, USA). Then we measured the DNA concentration using NanoDrop and performed 1% agarose gel electrophoresis on the DNA sample to ensure that the DNA samples can be used in subsequent experiments. The DNA samples were sequenced using Illumina Miseq PE300 High-Throughput Sequencing. The primer pairs 341F (CCTACGGGNGGCWGCAG) and 785R (GACTACHVGGGTATCTAATCC) with barcodes were used for amplifying bacterial V3-V4 fragments (Klindworth et al. 2013). ITS1F (GATTGAATGGCTTAGAGG) and ITS2R (CTGCGTTCTTCATCGAT) with barcodes were used for amplifying fungal partial rDNA and ITS fragments (McGuire et al. 2013). The primers included Illumina adapters with the reverse primers also having an error-correcting 12-bp barcode unique to each sample to permit multiplexing of samples (Barberan et al. 2015). Quality-filtering was consistent with nematode methods. The remaining sequences were clustered into OTUs using the uparse software (http://www.drive5.com/usearch/manual/uparseotu_algo.html) according to their similarities, and 97% similarity level was selected, which generally represent microbial taxonomy at the species level. For bacteria, the RDP database (http://rdp.cme.msu.edu/misc/resources.jsp) was compared, and the fungal ITS area was compared with the Unite database (https://unite.ut.ee/index.php). We used the RDP classifier to compare the OTU representative sequence with the corresponding database to obtain the OTU species information, at confidence threshold of 80%.

Soil nematode identification

Nematode sequences were similarly amplified from the genomic DNA. In order to improve amplification efficiency, a higher proportion of nematode sequences can be obtained without nematode enrichment, we repeated DNA amplification before sequencing. The primers NemF and 18Sr2b (Sikder et al. 2020) were used in a pre-amplification step followed by amplification with primers NF1 and 18Sr2b in a semi-nested procedure (Sapkota and Nicolaisen 2015) (Table S1). NF1 and 18Sr2b were tag encoded using the forward primer 5 -CGTATCGCCTCCCTCGCGCCATCAG-MID-NF1- 3 and the reverse primer 5 -CTATGCGCCTTGCCAGCCCGCTCAG-18Sr2b-3 (Sapkota and Nicolaisen 2015). Reactions contained 12.5µl of 2 × Taq PCR mixture with loading dye reaction buffer (GenStar), 2.5µl each of forward primer and reverse primer, 1 µl of DNA template, and 6.5µl ddH_2O in a final volume of 25 µl. Amplification with NemF and 18Sr2b used an initial DNA denaturation step of 94°C for 5 min, followed by 20 cycles at 94°C for 30 sec, 53°C for 30 sec, 72°C for 1 min and a final elongation at 72°C for 10 min (Sapkota and

Nicolaisen 2015). After amplification, DNA samples were subjected to 1% agarose gel electrophoresis to check whether they can be used in subsequent experiments. DNA was sequenced using Illumina Miseq PE300 High-Throughput sequencing if the DNA sample is qualified.

We used QIIME for quality-filtering (Caporaso et al. 2010). To remove the interference sequence, we 1) split the sequence into samples according to the barcode and removed the barcode; 2) deduplicated the double-end sequences by the “Trimmomatic” software: removed bases with a tail quality value lower than 25; a 50bp sliding window was set, with a 1bp step, and the average base quality in the window was not less than 25; sequences less than 100bp were removed; 3) connected high-quality double-end sequences, with a minimum overlap region of 10bp and a maximum mismatch rate of 0.2, then removed sequences containing ambiguous base N by the “flash” software. Valid sequences without chimeras were subsequently clustered into different OTUs (Operational Taxonomic Units) by uparse (http://www.drive5.com/usearch/manual/uparseotu_algo.html) according to their similarities, and 99% similarity level was selected here. The RDP classifier was used to compare the OTU representative sequence with the Silva 18S (version 123) database to obtain OTU species information. The confidence threshold used by the RDP classifier to compare species databases was 80%.

Data analyses

We calculated OTUs richness for soil microbes and nematodes. For plants, we calculated understory species richness. We used Levene's test in the “car” package to test the homogeneity of variance and Shapiro-Wilk test to test the normality of data. If the data fitted the normal distribution and homogeneity of variance, the nematode richness, soil variables, microbial richness and understory species richness were assessed for differences between treatments using one-way analysis of variance (ANOVA) followed by Tukey-test when main effects were observed. We used permutation analysis of variance tests in “lmPerm” package if the data did not conform to the assumptions of normal distribution and variance homogeneity followed by multiple comparisons by “kruskalmc” function belong to “pgirmess” package. Non-metric multidimensional scaling (NMDS) based on the “Bray-Curtis” dissimilarity index in “vegan” package was used to visualize the spatial distance arrangement of the nematodes, plants, bacteria and fungi. Non-parametric multivariate analysis of variance (PerMANOVA) with 9999 permutations in “vegan” package was used to assess differences in community composition between plant treatments. We conducted a classification Random Forest analysis using the “randomForest” package to identify the relative importance of soil physicochemical properties variables in explaining nematode richness by measuring the increase in the mean square error (MSE) between the observed value and the OOB predicted value. The prediction accuracy was averaged across all trees (10000 trees) to produce the final importance measure (Delgado-Baquerizo et al. 2016), and we then selected the two most important properties for the constructing of structural equation modeling (SEM). Structural equation modeling (SEM) in “lavaan” package was applied to explore the influence ways of the different treatments on soil nematode community composition. The model fit was evaluated through χ^2 test and root mean square error of approximation (RMSEA) test. The figures were plotted using the ‘ggplot2’ package. And all data were analyzed using R software, version 3.6.3 (R Core Team).

We conducted structural equation modeling (SEM) analyses according to a *priori* model (Fig. S1) with following these premises: (1) soil nematode richness and communities composition can be affected by soil physicochemical properties, understory plant richness and communities composition, soil microbe richness and communities composition, and dominant plant species (Wang et al. 2018; Yeates et al. 1993); (2) soil microbe richness and communities composition can be affected by soil physicochemical properties, understory plant richness and communities composition, and dominant plant species (Hortal et al. 2015); (3) soil physicochemical properties can be affected by dominant plant (Wang et al. 2018); (4) understory plant richness and communities composition can be affected by dominant plant (Wang et al. 2019a). The a priori model provide a framework for the actual SEM analysis (Veen et al. 2010).

Results

There was no significant difference in the effects of *L. virgaurea* and *D. fruticosa* on understory plant richness (Fig. 1b), but non-metric multidimensional scaling (NMDS) and non-parametric multivariate analysis of variance (PerMANOVA) results showed that plant community composition based on presence, significantly differed between *D. fruticosa* and the control treatment (Fig. 2b, $P<0.01$), and marginally differed between *L. virgaurea* and the control treatment (Fig. 2b, $P<0.1$).

Soil water content, soil total phosphorus, soil total nitrogen, soil organic carbon, and soil ammonium nitrogen ($P<0.01$) was greater in the presence of *L. virgaurea* relative to the control treatment, while soil pH ($P<0.01$) and soil nitrate nitrogen was lower. Similarly, the presence of *D. fruticosa* was associated with greater soil total phosphorus, soil total nitrogen ($P<0.05$), soil organic carbon ($P<0.05$), soil ammonium nitrogen ($P<0.01$), and lower soil pH ($P<0.01$). However, *D. fruticosa* increased soil nitrate nitrogen and decreased soil water content, which is opposite to the effect of *L. virgaurea* (Table 1).

Table 1
Effects of different plant types on soil physicochemical properties. Abbreviation: SWC, soil water content (g/g); TP, total phosphorus (mg/g); TN, total nitrogen (mg/g); SOC, soil carbon content (mg/g); NO_3^--N, nitrate nitrogen (mg/g); NH_4^+-N, ammonium nitrogen (mg/g). Letters after each value indicate results of pair-wise comparisons. Different letters indicate significant differences between treatments (P>0.05).

	Control	*L. virgaurea*	*D. fruticosa*	P-value
SWC	0.431±0.021	0.444±0.017	0.387±0.031	0.241
TP	0.886±0.048	0.893±0.028	0.97±0.013	0.177
TN	**11.135±0.742a**	**11.91±0.460ab**	**13.459±0.510b**	**0.044**
SOC	**98.056±9.004a**	**120.212±7.366ab**	**132.062±7.709b**	**0.033**
pH	**6.772±0.038b**	**6.626±0.054ab**	**6.47±0.031a**	**0.001**
NO_3^--N	2.959±0.379	2.229±0.119	2.988±0.23	0.112
NH_4^+-N	**0.112±0.039a**	**0.417±0.063b**	**0.402±0.055b**	**0.002**

For bacteria, we retained a total of 683830 sequences after filtering and removing of chimeras. The total number of bases was 313003151, and the average sequence length 457.72 at 97% similarity. For fungi, we retained a total of 657833 sequences after filtering and removing of chimeras. The total number of bases was 224765243, and the average sequence length 341.68 at 97% similarity. We found there was no significant difference in the effects of *L. virgaurea* and *D. fruticosa* on bacterial richness (Fig. 1c). *L. virgaurea* increased fungal richness significantly (Fig. 1d, P<0.01), while fungal richness was not significantly affected by *D. fruticosa* (Fig. 1d). Non-metric multidimensional scaling (NMDS) and non-parametric multivariate analysis of variance (PerMANOVA) results showed that bacterial community composition under *D. fruticosa* was significantly different from that under control (Fig. 2c, P<0.05). However, there was no significant difference of fungal community composition among different dominant plant types and the control treatment (Fig. 2d). The presence of *D. fruticosa* increased the relative abundance of Proteobacteria, Bacteroidetes and Nitrospirae, and the presence of *L. virgaurea* increased the relative abundance of Proteobacteria, Verrucomicrobia (Fig. S3c). *L. virgaurea* decreased the relative abundance of Ascomycota and *D. fruticosa* decreased the relative abundance of Glomeromycota (Fig. S3d).

For Eukarya, we retained a total of 4143079 sequences after filtering and removing chimeras. The total number of bases was 1536595586, and the average sequence length 370.88 at 99% similarity. Following classification of OTUs, we found that the average nematode content was 41.81%, and other metazoan and fungi was 58.19% (Fig. S3a). We found a significant positive effect of *D. fruticosa* on nematode richness (Fig. 1a, P<0.001), but *L. virgaurea* had no effect on nematode richness (Fig. 1a). Although the

richness of soil nematodes was not significantly affected by *L. virgaurea*, the community composition of nematodes was significantly changed. Interestingly, as opposed to *L. virgaurea*, *D. fruticosa* increased the nematode richness but there was no significant effect of nematode communities composition (Fig. 1a, 2a). There were different responses of soil nematode species to the allelopathic *L. virgaurea* and the facilitative *D. fruticosa*. Compared with the control treatment, the presence of both *L. virgaurea* and *D. fruticosa* had a positive effect on the proportion of Diplogasterida and a negative effect the proportion of Tylenchida and Triplonchida. The proportion of Rhabditida was increased in the presence of *L. virgaurea* and reduced in the presence of *D. fruticosa*. In addition, the presence of *D. fruticosa* increased the proportion of Araeolaimida and Enoplida (Fig. S3b).

Random Forest results indicated soil organic carbon (34.87% IncMSE) and soil pH (22.85% IncMSE) were the two most important edaphic variables in explaining variations in nematode richness (Fig. S2). Soil pH can be considered as an indicator of soil environment and soil organic carbon can be considered as an indicator of soil nutrition.

The SEM model (n=10) assessing the effects of *L. virgaurea* explained 84.7% of the variation in soil nematode richness. There were highly significant relationships between soil organic carbon, soil pH and understory plant richness and nematode richness. Soil organic carbon and pH was positively related to nematode richness whereas understory plant richness was negatively related to nematode richness. The direct effect of *L. virgaurea* on nematode richness was not significant. However, there was a negative indirect effect of *L. virgaurea* on nematode richness through soil pH and a positive indirect effect through soil organic carbon. Although nematode richness was significantly negatively related to understory plant richness, there was no significant relationship between understory plant richness and *L. virgaurea*. This indicated that *L. virgaurea* affected nematode richness mainly indirectly through changes in abiotic factors (Fig. 3a).

The SEM model (n=10) assessing the effects of *D. fruticosa* explained 91.8% of the variation in soil nematode richness. The SEM showed not only a significant direct positive effect of *D. fruticosa* on nematode richness, but also an indirect effect of *D. fruticosa* on nematode richness through fungal richness. Although nematode richness was marginally negatively related to bacterial richness, there was no relationship between bacterial richness and *D. fruticosa*. Also, *D. fruticosa* significantly affected soil pH and soil organic carbon, but there was no correlation between soil pH and soil organic carbon and nematode richness. This indicated that *D. fruticosa* affected nematode richness both through direct and indirect ways, and then predominantly through the biotic factors (Fig. 3b). Both *L. virgaurea* and *D. fruticosa* can reduce soil pH and increase soil organic carbon content. These characteristics had significant effects on the nematode richness under *L. virgaurea* but not under *D. fruticosa* (Fig. 3).

The SEM (n=10) assessing the effects of *L. virgaurea* explained 83.2% of the variation in the nematode community composition. The SEM indicated that *L. virgaurea* had significant direct effects on nematode community composition and indirect effects through its influence on soil organic carbon (Fig. 4a). Similarly, the SEM (n=10) assessing the effects of *D. fruticose* explained 90.6% of the variation of

nematode community composition. There were highly significant relationships between soil pH, soil organic carbon and understory plant community composition and nematode community composition under *D. fruticosa*. Interestingly, with the presence of *D. fruticosa*, in addition to the direct effect, soil pH and organic carbon indirectly affect nematode community composition through changes in soil fungal community composition, while understory plant community composition affect soil nematode community composition indirectly through changes in soil bacterial community composition (Fig. 4b).

Discussion

Our results provide new insights into the influences of facilitative and allelopathic plants on belowground communities. We found that the facilitative plant *D. fruticosa* increased nematode richness in part driven by an increase in fungal richness, but contrary to our hypothesis the allelopathic plant *L. virgaurea* had no main effect on nematode richness. However, *L. virgaurea* indirectly affected soil nematode richness both through a positive effect of soil organic carbon and a negative effect of pH, indicating that the drivers of nematode richness may have changed despite the lack of a main effect. Moreover, *L. virgaurea* had a significant direct effect on soil nematode community composition and an indirect effect through its influence on soil organic carbon. By contrast, *D. fruticosa* had no net effect on nematode community composition because the effects of biotic factors and abiotic factors offset each other. Our study provides evidence that dominant plants can have contrasting effects on soil nematode communities that should be explored in more detail in future studies.

The effects of L. virgaurea on soil nematode communities

Allelopathic plants release chemical compounds into the soil that can affect the germination of seeds and the growth of neighbor plants (Luo et al. 2005; Vokou et al. 2003; Wang et al. 2020) as well as soil bacteria and soil fungi (Kalemba and Kunicka 2003). *L. virgaurea* has been shown to affect soil fungi community rhizodeposition (Shi et al. 2011) and host-specific fungal endophytes (Aschehoug et al. 2014). Although the allelopathic plants did not significantly affect the soil bacterial community in our study, we found similar results to (Liang et al. 2021), who found that *L. virgaurea* increased the relative abundance of Proteobacteria which is known to play a key role in soil C, N and sulphur cycling (Kersters et al. 2006) in alpine meadow ecosystems.

The opposing influences of *L. virgaurea* on soil pH and organic carbon resulted in no net effect of *L. virgaurea* on soil nematode richness. Nematode abundance have been observed to both be positively (Räty and Huhta 2003) and negatively (Nielsen et al. 2011) correlated with pH, but the effect is likely related to the gradient of pH studied; i.e. the relationship with pH is unimodal with abundances peaking at intermediate soil pH (van den Hoogen et al. 2020). Nematodes of different feeding types respond differently to soil pH. For example, the ratio of bacterivorous to fungivorous nematodes was markedly higher after manipulation of pH by liming (Räty and Huhta 2003). Our results showed that pH significantly increased soil nematode richness under *L. virgaurea* (Fig. 3a), and significantly changed the composition of nematode community under *D. fruticosa* (Fig. 4b). Soil nematodes are particularly

abundant in habitats with greater organic carbon contents and inputs (Bongers and Ferris 1999) because most feed on soil organisms that utilize organic matter (Moens et al. 2002). The negative correlation between understory plant richness and soil nematode richness may be due to the specificity of food selectivity of herbivorous nematode (Ruess and Dighton 1996). As is shown in the Figure S3b, *L. virgaurea* decreased the relative abundance of Tylenchida, Araeolaimida and Enoplida.

In addition to the indirect effects associated with changes in soil organic carbon, the composition of soil nematode communities is directly affected by *L. virgaurea*. The root exudates of the allelopathic plant *Lantana camara L. (Verbinaceae)* has been shown to cause mortality of *M. javanica* juveniles (Shaukat et al. 2003) and marigold (*Tagetes patula*) can produce allelopathic compounds toxic to plant-parasitic nematodes (Marahatta et al. 2012). We speculate that *L. virgaurea* release chemical compounds that affect the community composition of soil nematode given that the relative abundance of all nematode species was reduced, except Diplogasterida and Other. In particular, Araeolaimida were significantly reduced (Table S2). While our study indicate that allelopathic plants can affect soil nematode communities further work is required to verify how leachate from *L. virguarea* affect nematode communities and which compounds might be involved.

The effects of D. fruticosa **on soil nematode communities**

The facilitative plant *D. fruticosa* had a significant positive direct effect on soil nematode richness, and indirectly changed soil nematode richness mainly through biotic factors, especially fungal OTU richness. Wang et al. (2018) demonstrated a similar direct effect of *D. fruticosa* on soil nematode abundance at the same site. Dominant species can affect plant hosts and resource inputs (van der Putten and van der Stoel 1998), so the direct effect may be caused by increasing root activity, root leachate and plant litter. The positive response of nematode richness to *D. fruticosa* is likely through root exudates (Bais et al. 2006) and input of litter (Chauvin et al. 2015; Chen et al. 2007), which affect soil biomes and through this nematodes. For example, Gao et al. (2019) found that *D. fruticosa* can enhanced nutrient availability, particularly phosphorus because *D. fruticosa* can raise P from subsoil to the topsoil.

Many studies have shown feeding preferences in nematodes (Liu et al. 2018; Manwaring et al. 2020). For instance, Ruess et al. (2000) found that the nematode *Aphelenchoides sp.* selectivity grazing of fungal food resources and Hasna et al. (2007) revealed that the nematode *Aphelenchus avenae* was preferentially attracted to *Verticillium dahliae*. Similarly, the direct effects of *D. fruticose* on nematode community composition may be related to nematode feeding preferences.

D. fruticosa directly and indirectly affect soil nematode community composition, and the indirect influence can be through both biotic and abiotic factors. In our results, *D. fruticosa* increased the relative abundance of Araeolaimida, Diplogasterid, Enoplida and some unidentified nematodes (expressed as “Other”). The results showed that *D. fruticosa* has a wide range of effects on the nematode community composition, both positive and negative, but the effect on the nematode community composition is not significant, which may be due to positive and negative effects offsetting. Our results are consistent with those of Hortal et al. (2013), who found that the presence of the facilitative plant *Retama sphaerocarpa*

had no distinct effect on bacterial richness but influenced bacterial community composition. Specifically, the presence of *R. sphaerocarpa* increased the relative abundance of the gram-negative Proteobacteria and Bacteroidetes. A higher relative abundance of Proteobacteria and Bacteroidetes suggests that the soil communities are less disturbed and are considered a better resource for microbial grazers (Fierer et al. 2007).

Conclusion

In conclusion, our study discovered that dominant plants with contrasting functional characteristics have markedly different impacts on soil nematode communities. The the facilitative plant *D. fruticosa* affects soil nematode richness both directly and indirectly through its influences on soil fungal richness, while the allelopathic plant *L. virguarea* had no overall effect on nematode richness. Moreover, both species influence nematode community composition directly and through their influences on edaphic and biological properties. Specifically, *L. virgaurea* impacted nematode communities through its influences on soil organic carbon, while *D. fruticosa* impacted communities through its influences on soil organic carbon, pH, and understory plant commnunity, and the soil microbial communities. Our study highlights the importance of dominant plants in determining soil community diversity and provides new insight to disentangle the complex above- and below-ground relationship.

Declarations

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Competing Interests

No potential conflict of interest was reported by the authors!

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Hongxian Song, Sa Xiao, Xiaoli Yang, Ziyang Liu, Jingwei Chen, Hanwen Cui, Yajun Wang, Jiajia Wang, Kun Liu, Shuyan Chen, Lizhe An, and Uffe N Nielsen. The first draft of the manuscript was written by Hongxian Song and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. We are grateful to Limin Zhang and Aifeng Guo for their assistance in laboratory work.

Data Availability

The datasets generated during and/or analysed during the current study are available in the DRYAD repository, https://doi.org/10.5061/dryad.j0zpc86g0.

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Figures

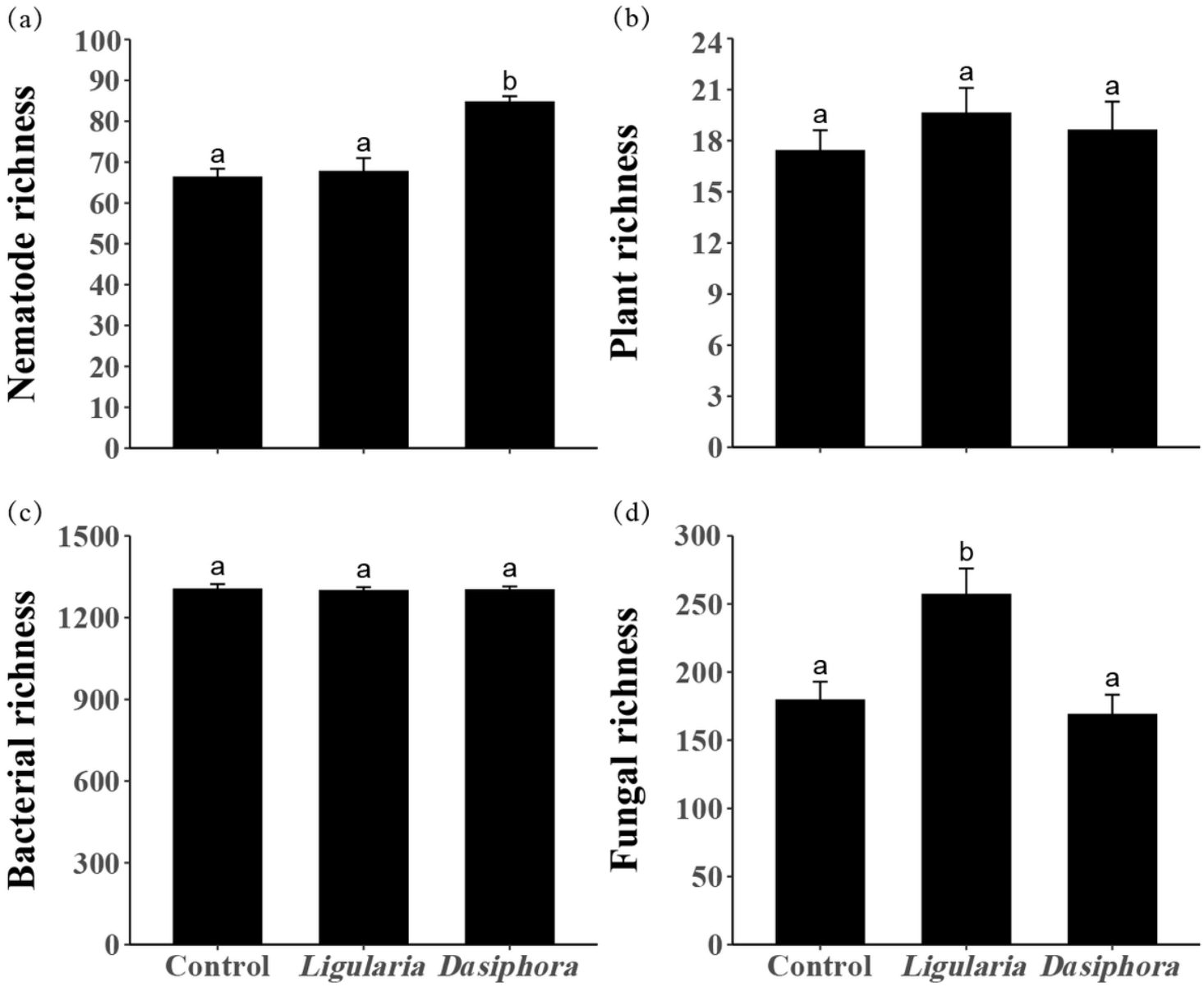

Figure 1

Mean (± SE) (a) nematode OTU richness, (b) understory plant richness, (c) bacterial OTU richness and (d) fungi OTU richness across the treatments. Different letters indicate significant differences between treatments ($P < 0.05$). Abbreviation: Control, without L. virgaurea and D. fruticosa; Ligularia, L. virgaurea; Dasiphora, D. fruticosa.

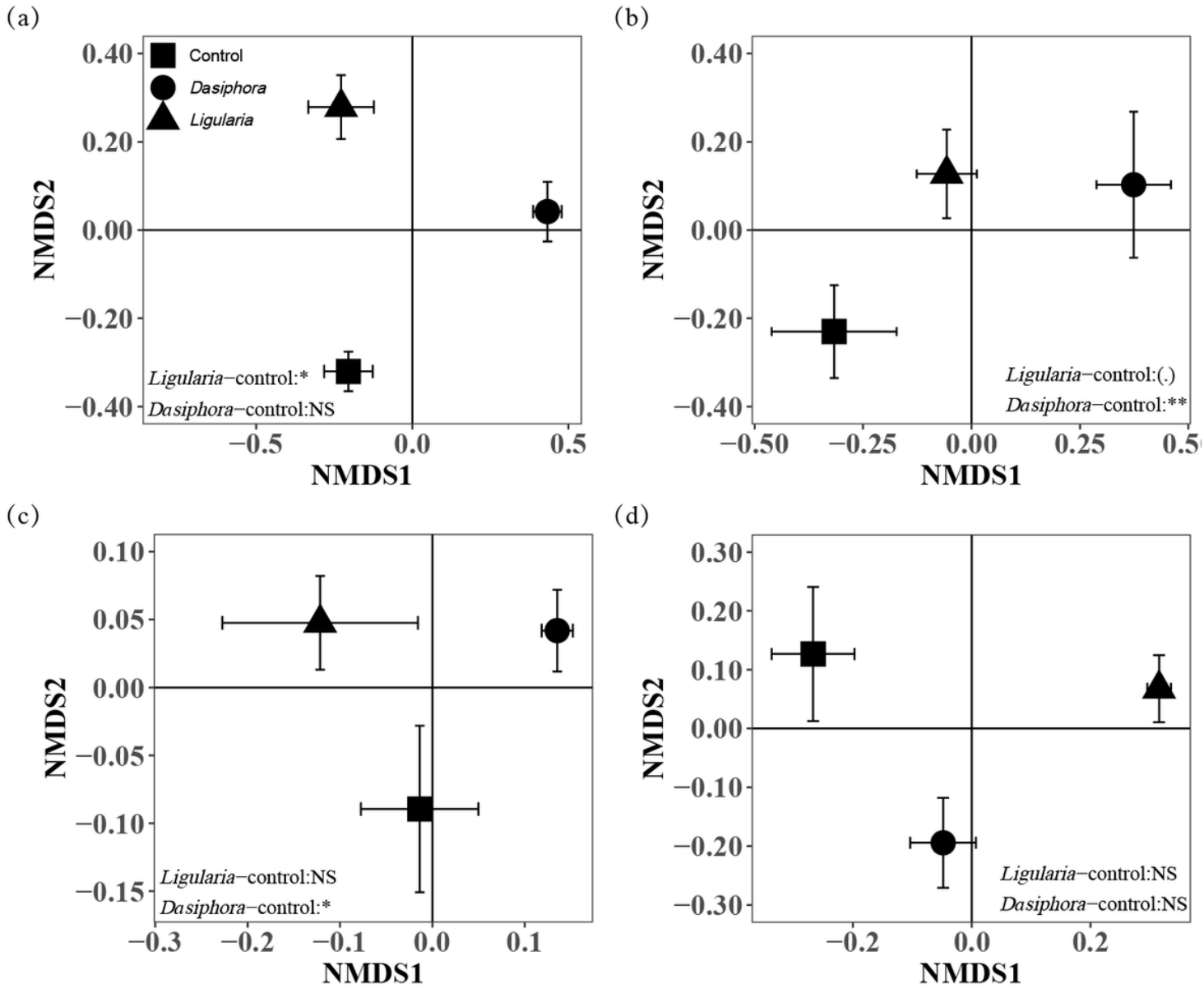

Figure 2

Community composition of (a) nematodes, (b) understory plants, (c) bacteria and (d) fungi associated with each plant treatment (i.e. L. virgaurea and D. fruticosa) based on non-metric multidimensional scaling (NMDS) using Bray-Curtis similarity index (stress<0.2). Significant results of one-way non-parametric multivariate analysis of variance (PerMANOVA) using Bray-Curtis similarity index are indicated on the right or left bottom part of each graph. **: P<0.01, *: P<0.05, NS: P>0.05. Abbreviation: Control, without L. virgaurea and D. fruticosa; Ligularia, L. virgaurea; Dasiphora, D. fruticosa.

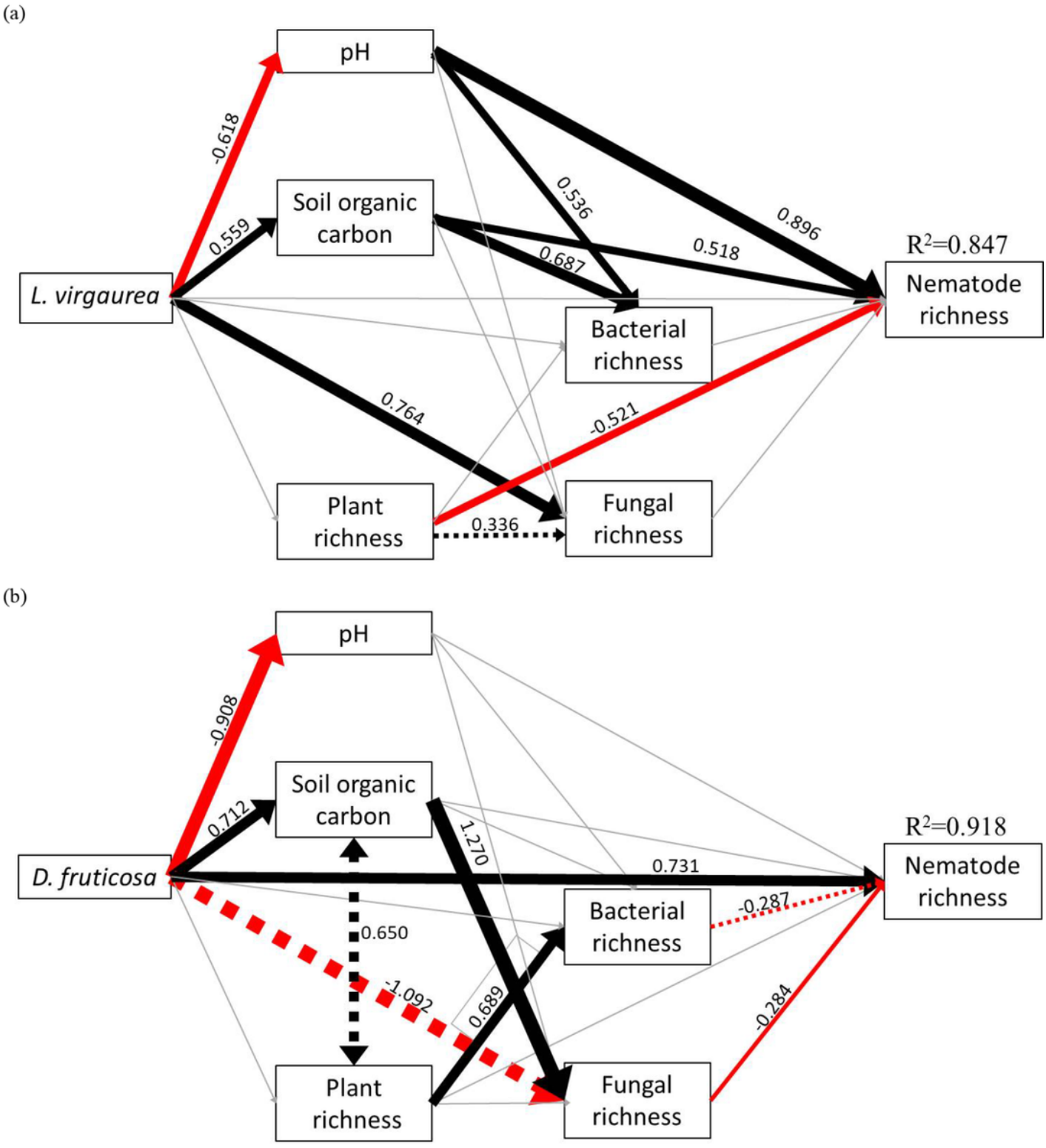

Figure 3

Results of the SEM analyses indicating direct and indirect effects of (a) L. virgaurea (P=0.423, df=4, R2=0.847, P(RMSEA)=0.437), (b) D. fruticosa (P=0.375, df =3, R2=0.918, P(RMSEA)=0.386) on nematode richness. Square boxes display variables included in the model: Plant richness, understory plant richness. Black means positive correlation; red means negative correlation; grey mean no significant correlation. Solid arrows indicate significant effects (at the level P < 0.05), and dashed arrows indicate marginally

significant effects (0.05< P < 0.1). Arrow width corresponds directly to the standardized path coefficient. R2 values associated with response variables indicate the proportion of explained variation by relationships with other variables. Values associated with solid arrows and dashed arrows represent standardized path coefficients.

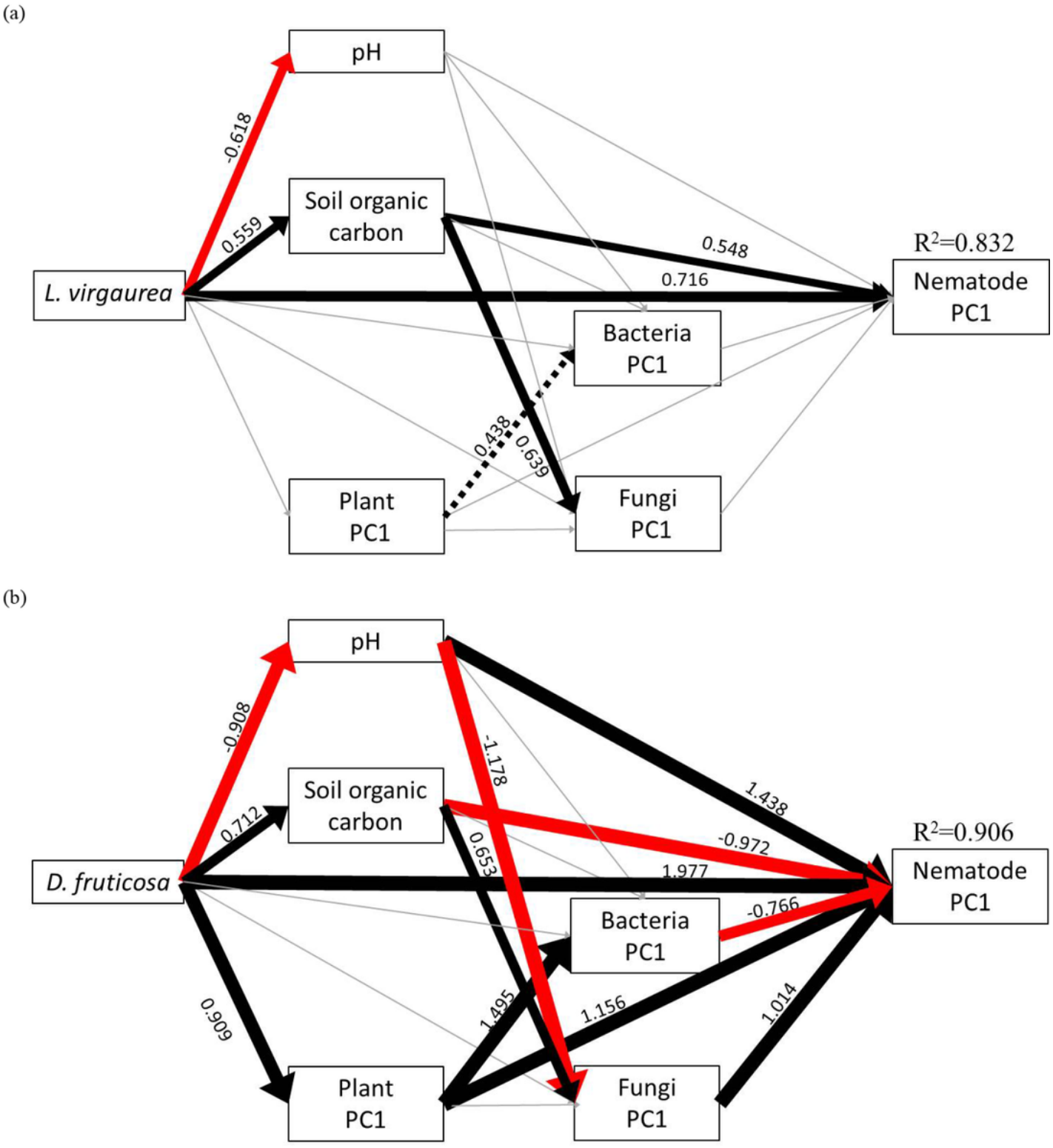

Figure 4

Results of the SEM analyses indicating direct and indirect effects of (a) L. virgaurea (P=0.938, df=4, R2=0.842, P(RMSEA)=0.940), (b) D. fruticosa (P=0.836, df =4, R2=0.906, P(RMSEA)=0.843) on nematode community composition (PC1). Square boxes display variables included in the model: Plant PC1, understory plant community composition (PC1); Bacteria PC1, bacterial community composition (PC1); Fungi PC1, fungal community composition (PC1); Nematode PC1, nematode community composition (PC1). Black means positive correlation; red means negative correlation; grey mean no significant correlation. Solid arrows indicate significant effects (at the level P < 0.05), and dashed arrows indicate marginally significant effects (0.05< P < 0.1). Arrow width corresponds directly to the standardized path coefficient. R2 values associated with response variables indicate the proportion of explained variation by relationships with other variables. Values associated with solid arrows and dashed arrows represent standardized path coefficients.

Supplementary Files

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