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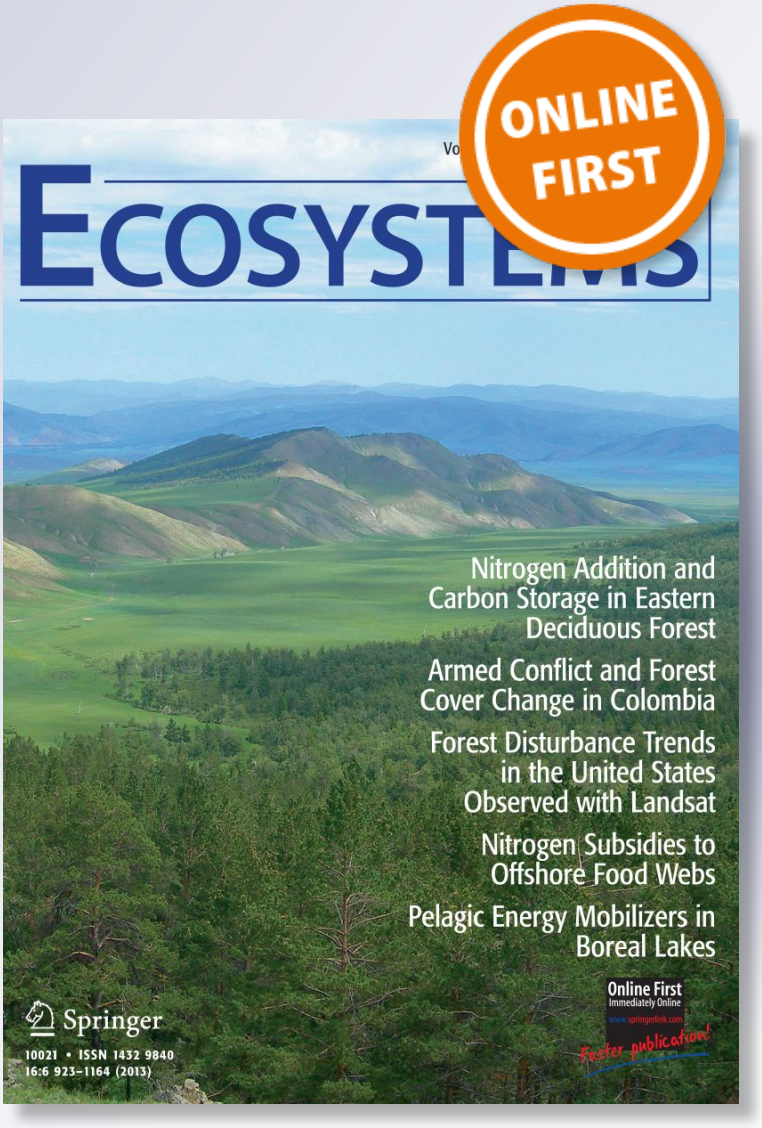

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The Impacts of Above- and Belowground Plant Input on Soil Microbiota: Invasive *Spartina alterniflora* Versus Native *Phragmites australis*

Pei Zhang,[1] Deborah A. Neher,[2] Bo Li,[1] and Jihua Wu[1]*

[1]*Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, Shanghai 200433, People's Republic of China;* [2]*Department of Plant and Soil Science, University of Vermont, Burlington, Vermont 05405, USA*

Abstract

Invasive plants affect soil food webs through various resource inputs including shoot litter, root litter and living root input. The net impact of invasive plants on soil biota has been recognized; however, the relative contributions of different resource input pathways have not been quantified. Through a 2 × 2 × 2 factorial field experiment, a pair of invasive and native plant species (*Spartina alterniflora* vs. *Phragmites australis*) was compared to determine the relative impacts of their living roots or shoots and root litter on soil microbial and nematode communities. Living root identity affected bacteria-to-fungi PLFA ratios, abundance of total nematodes, plant-feeding nematodes and omnivorous nematodes. Specifically, the plant-feeding nematodes were 627% less abundant when living roots of invasive *S. alterniflora* were present than those of native *P. australis*. Likewise, shoot and root biomass (within soil at 0–10 cm depth) of *S. alterniflora* was, respectively, 300 and 100% greater than those of *P. australis*. These findings support the enemy release hypothesis of plant invasion. Root litter identity affected other components of soil microbiota (that is, bacterial-feeding nematodes), which were 34% more abundant in the presence of root litter of *P. australis* than *S. alterniflora*. Overall, more variation associated with nematode community structure and function was explained by differences in living roots than root or shoot litter for this pair of plant species sharing a common habitat but contrasting invasion degrees. We conclude that belowground resource input is an important mechanism used by invasive plants to affect ecosystem structure and function.

Key words: aboveground–belowground interactions; exotic plants; nematodes; microbial PLFAs; saltmarsh; living root input; litter input.

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Author Contributions PZ and JHW conceived and designed the study. PZ conducted field research, lab measurements and statistical analyses. PZ, JHW, DN, BL wrote the paper.

**Corresponding author; e-mail:* jihuawu@fudan.edu.cn

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Introduction

Biotic interactions between above- and belowground systems are essential drivers of ecosystem functioning (Wardle and others 2004; Bardgett and Wardle 2010). Plants affect soil food webs by providing resources to soil organisms which, in turn, regulate soil nutrient cycling and feedback to aboveground systems by influencing nutrient acquisition and plant growth (Bardgett and Wardle 2010). Understanding how plants allocate resources to soil communities in these interacting processes is crucial because it is the origin of resource flow and regulation of soil community structure and function (Wardle and others 2004; Bardgett and Wardle 2010).

Plant-derived resources enter the soil through three main pathways: shoot litter, root litter and root exudates (Ruf and others 2006). It is well established that plant litter is a major resource input for soil decomposers (Scheu 2002; Moore and others 2004; Freschet and others 2013), and impacts microbial carbon use efficiency and decomposer abundance (Eisenhauer and Reich 2012). However, decomposing litter originating from shoot and root tissues influences soil biota differently (Freschet and others 2013; Zhao and others 2014; Sauvadet and others 2016). Decomposition rates are affected by relative concentrations of nutrients and recalcitrant compounds in the litter substrate which vary not only among plant species, but also between shoots and roots (Bird and Torn 2006; Zhao and others 2014). For many tree species, decomposition of root litter is slower and correlated with lower litter quality compared to shoot litter (Bird and Torn 2006; Hansson and others 2010; Steffens and others 2015). Root litter may have a greater contribution to the soil C budget simply because of its longer residence time (Bird and Torn 2006; Freschet and others 2013). These different impacts by litter type are also reflected in the structure of microbial communities and soil fauna (Zhao and others 2014; Sauvadet and others 2016). Thus, contrasting inputs of shoot or root litter of different plant species may support different soil communities. In addition to the resource input from decomposition of litter, a growing number of studies propose that living root-derived resources are another important driver of soil food web dynamics (Högberg and others 2001; Ruf and others 2006; Pollierer and others 2007). Soil organisms may utilize living root-derived resources more readily, because root exudates are forms of resources that are more labile than litter (Bardgett and others 2005). Therefore, the impact of plant species identity on soil biota composition corresponds with whether the resource originates from above- or belowground living or dead tissues (Keith and others 2009; De Deyn and others 2011; Eisenhauer and Reich 2012). However, the relative contribution of these three input pathways to soil communities remains controversial. It seems context dependent, for example, varying among ecosystem types (Bardgett and Wardle 2010) and among plant species (Keith and others 2009; Eissfeller and others 2013).

Plant invasion is one of the most important components of global change (Kourtev and others 2002; Ehrenfeld 2003). Interactions between soil biota and invasive plants and their roles in successful invasion have received much attention (Reinhart and Callaway 2006; Dawson and Schrama 2016). As predicted by the enemy release hypothesis, invasive plants may experience less pressure from soilborne herbivores than native plants, which indirectly favors the establishment and growth of invasive plants (van der Putten and others 2005; Morriën and others 2012). For example, Morriën and others (2012) compared soil under three invasive and nine native plant species in the invaded ranges and found invasive plants had, on average, fewer root-feeding nematodes per unit root biomass. Their subsequent studies validate that under greater herbivory pressure, there was stronger negative feedback to the root biomass of native than invasive plant species (Morriën and others 2012). Furthermore, invasive plants can change soil microbial and faunal abundance or composition and, consequently, influence ecosystem carbon stocks and nutrient dynamics in invaded ecosystems (Ehrenfeld 2003; Liao and others 2008). This is partially because invasive and native plants often contribute a different quantity and quality of resource inputs to the soil (Liao and others 2007; Ehrenfeld 2010), directly affecting the diet of soil biota no matter whether the resource input is through litter fall during the process of decomposition or root exudates during the growing season (Wardle and others 2004; Wolfe and Klironomos 2005). However, previous studies all focused on the net effects of plant invasion on belowground communities and have not discriminated the relative importance of diverse plant input pathways. Which type of input (shoot litter, root litter or living root) contributes most when invasive plants influence soil communities remains unknown. Furthermore, how differently trophic groups in the soil food web respond to these dif-

ferent plant inputs is unclear, although it is helpful to elucidate why some soil organisms are vulnerable to plant invasion, but others are not (McCary and others 2016).

Smooth cordgrass (*Spartina alterniflora*), native to the Atlantic and Gulf Coasts of North America, was introduced to China in 1979 to accelerate sedimentation and stabilize tidal flats, and has spread rapidly across the east coast of China (Chen and others 2004). In saltmarshes of the Yangtze estuary, *S. alterniflora* outcompeted native plants such as common reed *Phragmites australis* and has become a dominant plant species (Chen and others 2004). The extensive invasion of *S. alterniflora* has induced pronounced changes in soil community structure and functions (Li and others 2009). For instance, *S. alterniflora* invasion altered the community composition of soil bacteria (Wang and others 2007), nematodes (Chen and others 2007b) and macrofauna (Chen and others 2009). However, whether these consequences result from above- or belowground plant input and how identities of shoot litter, root litter and root exudates influence these processes are unclear and need further study.

Soil microbes and nematodes utilize plant resources from both litter input and root exudation, and are useful indicators for evaluating the effects of plant invasion on ecosystem structure and functions. Soil microbes are basal components of soil food webs (Moore and others 2005). We use phospholipid fatty acids (PLFAs) to measure the relative responses of bacteria and fungi to different plant inputs. The PLFAs method is useful for detecting responses of bacteria or fungi in the soil microbial community to a treatment (Ramsey and others 2006; Frostegård and others 2011). Nematodes occupy multiple trophic positions and play key roles in the soil food web through their regulatory functions in organic matter decomposition and nitrogen mineralization (Ritz and Trudgill 1999). Measurements of nematode communities have been proved to be useful tools to assess ecosystem diversity and function. Nematode metabolic footprint, which considers biomass and metabolic activities of the nematode community simultaneously, is also a useful tool for ecosystem assessment (Ferris 2010). It provides an effective way to assess the magnitude of C flow in the soil food web and estimate the contributions of nematodes to ecosystem function (Ferris 2010; Ferris and others 2012; Hodson and others 2014; Zhang and others 2015; Hu and others 2016).

In this study, we investigated the responses of soil microbes and nematodes to *S. alterniflora* invasion to answer two specific questions: (1) Which type of plant input (living root, root litter, shoot litter) contributes most to the differences in soil food web structure and functions between invasive *S. alterniflora* and native *P. australis*? (2) Do different components in the soil microbiota respond to varying plant input pathways differently? We hypothesize that the differences in living root inputs between *S. alterniflora* and *P. australis* are more important than litter input for inducing changes in soil microbiota (Ruf and others 2006; Pollierer and others 2007, 2012). Moreover, we hypothesize that different pathways of plant inputs differentially affect the soil community because of different dietary preferences of the myriad of soil species (Eissfeller and others 2013).

Materials and Methods

Study Site and Experimental Design

The study was conducted at Dongtan saltmarsh on Chongming Island, which is located in the Yangtze Estuary, China. It has a characteristic of semidiurnal meso-tide, and the mean tidal amplitude is 2.67 m (Chen and others 2004). We chose an unvegetated area of land (31°30′10″N, 121°58′37″E, ca. 600 m^2) to conduct the experiment. Both exotic *S. alterniflora* and native *P. australis* communities are found in the vicinity of this area. The unvegetated area is a bare mud flat without any previous higher plants, and we chose this area to avoid the legacy effects of plant communities on the performance of soil microbiota. The soil was a sandy clay loam with organic matter content of 4%, mean water content of 28% and pH of 6.57. In the unvegetated area, eight treatments were established, representing factorial combinations ($2 \times 2 \times 2 = 8$) of living plant identity, shoot litter input and root litter input of two plant species (*S. alterniflora* or *P. australis*) with four replicates (Table 1). The experimental design was inspired by Eisenhauer and Reich (2012).

To create living plant plots for *S. alterniflora* and *P. australis*, a total of 32 plots (1.2 m × 1.2 m each) were positioned randomly in the whole unvegetated area and the average interval was greater than 2 m between plots. On March 27–28, 2014, 20 plant ramets of *S. alterniflora* (about 30 cm high) for each plot were transplanted from four adjacent plant patches (ca. 9 m^2 each). Rhizosphere soil adhering to the roots was removed as much as possible after excavating ramets. Subsequently, ramets of *S. alterniflora* were transplanted and spaced uniformly in half of the plots. The same number of *P. australis* ramets in similar sizes was

Table 1. Treatments in the Complete 2 × 2 × 2 Factorial Design of Living Plant Identity (*Spartina alterniflora* or *Phragmites australis*), Shoot Litter Input (*S. alterniflora* or *P. australis)* and Root Litter Input (*S. alterniflora* or *P. australis*)

Treatment	Living plant identity	Shoot litter input	Root litter input
1	S	S	S
2	S	S	P
3	S	P	S
4	S	P	P
5	P	S	S
6	P	S	P
7	P	P	S
8	P	P	P

S = Spartina alterniflora; P = Phragmites australis.

transplanted into the remaining plots from another four adjacent plant patches (ca. 9 m^2 each). All transplanted plants were subject to natural growth without management.

Shoot and root litter of *S. alterniflora* and *P. australis* was harvested from adjacent vegetation patches on April 5, 2014. The litter represented decomposing plant materials from the previous year. Shoot litter including stems, sheath and leaves was cut with scissors at the soil surface and maintained as the natural composition in the field (biomass ratio between stems, sheath and leaves: *S. alterniflora* 2.18:1:1.56; *P. australis* 2.14:1:1.31). Root litter including rhizomes and roots with the natural composition in the field (biomass ratio between rhizomes and roots: *S. alterniflora* 3.66:1; *P. australis* 6.26:1) was collected using a PVC tube (i.d. 10 cm) to a depth of 20 cm below the ground after the aboveground residue was removed. All litter was rinsed with tap water, oven-dried to constant weight at 60°C and chopped into 2-cm-long pieces. A total of 32 litterbags (40 cm length, 5 cm width) of 1 mm mesh were prepared. Each litterbag contained a mixture of one kind of shoot litter and one kind of root litter (Table 1). Sixteen litterbags contained 25 g of shoot litter of *S. alterniflora* (C/N ratio 53.71) and another 16 litterbags contained 25 g shoot litter of *P. australis* (C/N ratio 39.28). In each litterbag, 25 g root litter of *S. alterniflora* or *P. australis* was mixed with shoot litter to represent four treatment combinations of litter (Table 1). The C/N ratios were 63.66 and 34.03 for root litter of *S. alterniflora* and *P. australis*, respectively. We mixed the shoot and root litter in one litterbag to minimize the spatial heterogeneity in soil biota distribution induced by different litter kinds (see Appendix Figure 1).

On June 26, 2014, we selected an individual plant from each plot which was healthy and taller than 1 m. The litterbag was folded to encircle the ramet. The litterbags were buried at a soil depth of 8 cm at a distance of 10 cm from the center of the ramet (Appendix Figure 1.). We attributed the effects of living plant identity mainly to the effects of living root identity because of limited new root litter production of transplant plants during the growing season.

Sampling and Procedures

On September 27, 2014, aboveground parts of the selected living plant in each plot were harvested by cutting with scissors at the soil surface. The belowground parts of plants were sampled with PVC tubes (i.d. 10 cm) to the depth of 10 cm below the soil surface after the aboveground parts were removed. All plant materials were washed and oven-dried to a constant weight at 60°C to measure the above- and belowground biomass. Litterbags were retrieved from the soil, carefully washed and dried at 60°C to estimate the decomposition rate based on mass loss. The shoot and root litter could not be well distinguished after decomposition, so we estimated the mass loss of the mixture of shoot and root litter for each litterbag.

As a proxy for salinity, electrical conductivity of soil in the experimental plots was determined in situ using a soil EC meter (2265FS, Spectrum Technologies, Inc., USA). Eight soil cores (3.2 cm internal diameter, 10 cm depth) were collected using PVC tubes from soil between the central living plant and litterbag in each plot. The soil from eight cores was homogenized to form a composite sample and then split into three subsamples: 270 g

soil was fixed in 4% hot formalin for nematode community analysis, 25 g soil was 45°C oven-dried to measure water content and then ignited at 550°C for 5 h in the muffle furnace to estimate organic matter content (Heiri and others 2001), and the remaining soil was freeze-dried to analyze microbial phospholipid fatty acids (PLFAs). Nematodes were extracted from soil using the Ludox TM flotation method (Griffiths and others 1990) and counted under a stereomicroscope. Over 100 nematode specimens in each sample were picked haphazardly and identified to genus using a compound microscope. Nematodes were assigned to one of the five trophic groups according to Yeates and others (1993), that is, algal-feeding, plant-feeding, bacterial-feeding, predaceous and omnivorous nematodes. The trophic diversity index (TD) was calculated as $TD = 1/\sum p_i^2$, where p_i is the proportion of trophic group i.

To estimate the amount of carbon entering the soil food web, the nematode metabolic footprint (F) in each plot was calculated as:

$$F = \sum N_t \left(0.1 \left(\frac{W_t}{m_t} \right) + 0.273 \left(W_t^{0.75} \right) \right),$$

where N_t, W_t and m_t are the number of individuals, fresh body weight and colonizer–persister (cp) value of taxon t (Bongers 1990; Ferris 2010). Three forms of nematode metabolic footprints were used in our study, that is, enrichment footprint (F_e), structure footprint (F_s) and functional metabolic footprint. F_e emphasizes the resource enrichment in the food web which is mainly reflected by the nematodes at lower trophic levels in the food chain (Ferris 2010; Zhang and others 2015). F_s reflects the regulatory functions of trophic levels higher in the food chain (Ferris and others 2012). The functional metabolic footprint was transformed to standardized carbon units using the formula $F_e \times F_s/2$, which reflects the ability of the ecosystem to support trophic groups higher in the food chain (Ferris and others 2012; Hodson and others 2014). Mean fresh body weight (W) of each nematode genus was assigned according to Ferris (2013). For a few genera that were not represented on the Web site, W values were estimated based on length (L) and maximum body diameter (D). The calculation of W was using the formula $W = (L \times D^2)/(1.6 \times 10^6)$ (Andrássy 1956).

Processes of lipid extraction from soil and PLFAs fractionation followed those of Bossio and Scow (1998). Subsequently, PLFAs were saponified and methylated yielding fatty acid methyl esters that were separated and quantified with an Agilent 6890 gas chromatograph and identified by a MIDI Sherlock Microbial Identification System (MIDI, Inc., Newark, DE) based on retention time. Specific PLFA biomarkers were grouped to represent bacteria and fungi, respectively (Frostegård and Bååth 1996; Bossio and Scow 1998).

Statistical Analyses

A three-way ANOVA was performed to examine the effects of living plant identity, shoot litter identity and root litter identity on microbial characteristics and soil nematode community properties. Data were $\log_{10}(x + 1)$-transformed to meet the assumptions of ANOVA where necessary (see Appendix Table 1). The ANOVA was conducted by general linear modeling (GLM). Details of the model and residuals are provided in Appendix Table 1. In addition, a non-metric multidimensional scaling (NMDS) followed by analysis of similarity (ANOSIM) was performed to compare nematode community composition among treatments. Briefly, nematode genus abundance was $\log_{10}(x + 1)$-transformed to produce a ranked similarity matrix based on Bray–Curtis similarity, and an ordination plot was created via NMDS. Then the ANOSIM (Clarke and Warwick 1994) was used to compare nematode community structure dissimilarities affected by living plant identity, shoot litter identity and root litter identity, respectively. Similarity percentage analysis (SIMPER) was conducted to identify the genera primarily responsible for the Bray–Curtis dissimilarity of nematode communities between *S. alterniflora* and *P. australis*. The three-way ANOVA was performed using Statistica 8.0 (StatSoft), and all multivariate analyses were performed in the PRIMER software package 5.2.

Results

The conductivity, water content and organic matter content of soil at the end of experiment were similar among all treatments. The above- and belowground biomasses of *S. alterniflora* (aboveground 57.76 ± 8.68 g/plant individual; belowground 0–10 cm depth 35.81 ± 5.90 g/plant individual, mean ± 1 SE) were 300 and 100%, respectively, greater than those of *P. australis* (aboveground 13.11 ± 2.74 g/plant individual; belowground 0–10 cm depth 15.42 ± 2.94 g/plant individual) in this experiment. The percentage of litter mass loss during our study period varied from 27 to 49% and was affected by root litter identity ($F_{1,24}$ = 10.24, P = 0.004, η_p^2 = 0.30). The mass loss containing *P. australis* root litter (42 ± 2%) was

greater than that containing *S. alterniflora* root litter (36 ± 1%).

There was high variation of bacterial PLFAs among the treatments but not significantly affected by shoot litter, root litter or living plant identity. However, the shoot litter identity (η_p^2 = 0.11) explained more of the variation of the bacterial PLFAs than root litter (η_p^2 = 0.08) or living plant identity (η_p^2 = 0.01) (Table 2). In most cases, the bacterial PLFAs values were lower in the presence of shoot litter of *S. alterniflora* (2151.38 ± 249.48 nmol/g) than that of *P. australis* (2605.99 ± 439.53 nmol/g) (Figure 1). The concentrations of fungal PLFAs were relatively small compared to those of bacterial PLFAs (Figure 1). Living plant, shoot and root litter identity had a significant interactive effect on fungal PLFAs (Table 2). The bacteria-to-fungi PLFA ratio was mainly affected by living plant identity ($F_{1,24}$ = 5.48, P = 0.03, η_p^2 = 0.22) (Table 2), with a lower value in the presence of living *S. alterniflora* plants (5.00 ± 0.95) than that of *P. australis* (7.06 ± 1.55) (Figure 1).

The abundance of total nematodes was greater in the presence of living *P. australis* plants than that of *S. alterniflora* (Table 3; Figure 2). On average, plots with living plants of *P. australis* supported 35.30% more nematodes than those with living *S. alterniflora* ($F_{1,24}$ = 6.47, P = 0.018, η_p^2 = 0.22). Similarly, the abundance of plant-feeding nematodes was 7.27 times higher with living plants of *P. australis* than those of *S. alterniflora* ($F_{1,24}$ = 34.50, P < 0.001, η_p^2 = 0.62). The abundance of omnivorous nematodes was affected most by living plant identity ($F_{1,24}$ = 5.28, P = 0.033, η_p^2 = 0.21), followed by

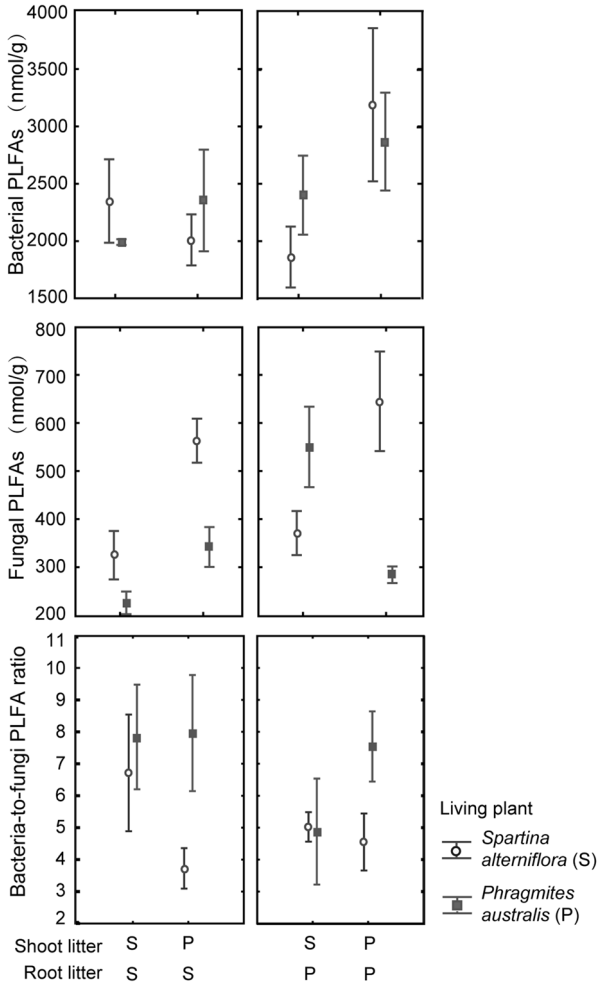

Figure 1. Bacterial PLFAs, fungal PLFAs and bacteria-to-fungi PLFA ratio. S = *Spartina alterniflora*, P = *Phragmites australis*. Data are illustrated as means ± 1 SE.

Table 2. Summary of Three-Way ANOVA Examining the Effects of Living Plant (LP), Shoot Litter (SL) and Root Litter (RL) Identity on Soil Microbial Characteristics (Bacterial PLFAs, Fungal PLFAs and Bacteria-to-Fungi PLFA Ratio)

	LP	SL	RL	LP × SL	LP × RL	SL × RL	LP × SL × RL
Bacterial PLFAs							
F	0.21	2.51	1.79	0.04	0.16	2.68	1.96
P	0.655	0.128	0.195	0.853	0.690	0.118	0.177
η_p^2	0.01	0.11	0.08	0.00	0.01	0.12	0.09
Fungal PLFAs							
F	**14.12**	**7.14**	**8.09**	**14.96**	1.85	**10.20**	**9.05**
P	**<0.001**	**0.013**	**0.009**	**0.001**	0.186	**0.004**	**0.006**
η_p^2	**0.37**	**0.23**	**0.25**	**0.38**	0.07	**0.30**	**0.27**
Bacteria-to-fungi PLFA ratio							
F	**5.48**	0.04	1.47	3.18	0.52	2.08	0.00
P	**0.030**	0.849	0.240	0.091	0.482	0.165	0.994
η_p^2	**0.22**	0.00	0.07	0.14	0.03	0.10	0.00

Significant differences (P < 0.05) are indicated in bold.

Table 3. Summary of Three-Way ANOVA Testing the Effects of Living Plant (LP), Shoot Litter (SL) and Root Litter (RL) Identity on the Variables of Soil Nematodes

	LP			SL			RL			LP × SL			LP × RL			SL × RL			LP × SL × RL		
	F	P	η_p^2	F	P	η_p^2	F	P	η_p^2	F	P	η_p^2	F	P	η_p^2	F	P	η_p^2	F	P	η_p^2
Abundance																					
Total nematodes	**6.47**	**0.018**	**0.22**	0.00	1.000	0.00	0.14	0.708	0.01	0.05	0.832	0.00	3.40	0.078	0.13	3.54	0.073	0.13	3.17	0.088	0.12
Algal-feeding nematodes	0.24	0.630	0.01	1.19	0.290	0.06	1.06	0.317	0.05	0.48	0.497	0.02	2.36	0.141	0.11	3.93	0.062	0.17	1.05	0.318	0.05
Bacterial-feeding nematodes	1.17	0.292	0.06	0.38	0.546	0.02	**5.45**	**0.030**	**0.21**	0.32	0.577	0.02	1.30	0.268	0.06	1.84	0.191	0.08	1.17	0.292	0.06
Predaceous nematodes	2.16	0.157	0.09	1.59	0.222	0.07	**5.90**	**0.024**	**0.22**	2.46	0.132	0.10	2.11	0.162	0.09	**10.13**	**0.004**	**0.33**	**5.33**	**0.031**	**0.20**
Omnivorous nematodes	**5.28**	**0.033**	**0.21**	2.88	0.105	0.13	0.41	0.528	0.02	2.27	0.148	0.10	0.65	0.429	0.03	3.75	0.067	0.16	1.67	0.211	0.08
Plant-feeding nematodes	**34.50**	**<0.001**	**0.62**	0.00	0.962	0.00	2.10	0.162	0.09	1.68	0.209	0.07	0.92	0.348	0.04	0.18	0.676	0.01	0.01	0.930	0.00
Ecological indices																					
Trophic diversity	**30.27**	**<0.001**	**0.56**	0.29	0.597	0.01	0.72	0.404	0.03	0.29	0.593	0.01	0.13	0.724	0.01	1.00	0.327	0.04	0.01	0.918	0.00
Enrichment footprint	0.09	0.762	0.01	0.00	0.954	0.00	0.48	0.497	0.02	0.50	0.487	0.02	0.94	0.341	0.04	1.38	0.252	0.06	0.38	0.543	0.02
Structure footprint	**4.51**	**0.046**	**0.18**	0.04	0.850	0.00	0.11	0.739	0.01	0.11	0.743	0.01	**8.23**	**0.010**	**0.29**	2.25	0.149	0.10	0.99	0.332	0.05
Functional footprint	**4.71**	**0.042**	**0.19**	0.02	0.893	0.00	0.42	0.525	0.02	0.15	0.670	0.01	**11.80**	**0.003**	**0.37**	3.24	0.087	0.14	0.41	0.530	0.02

Significant differences ($P < 0.05$) are indicated in bold.

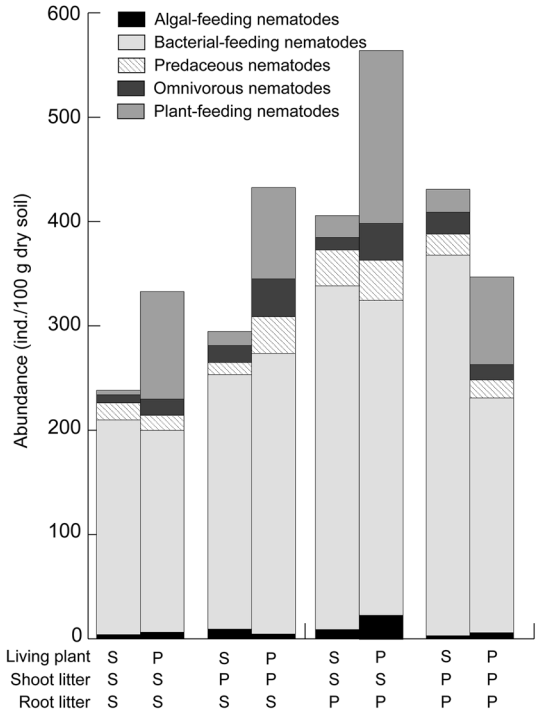

Figure 2. Composition of soil nematode trophic groups. S = *Spartina alterniflora*, P = *Phragmites australis*.

shoot litter identity ($F_{1,24} = 2.88$, $P = 0.105$, $\eta_p^2 = 0.13$) (Table 3). The abundance of omnivorous nematodes was highest (25.49 ± 3.79 ind./100 g dry soil) in the presence of living plants and shoot litter of *P. australis* (Figure 2). The identity of root litter had a significant effect on other specific trophic groups of nematodes (Table 3). The bacterial-feeding nematodes were more abundant in the presence of root litter of *P. australis* (305.21 ± 40.35 ind./100 g dry soil) than that of *S. alterniflora* (228.01 ± 50.79 ind./100 g dry soil) (Figure 2). There were complex interactive effects among treatments on the abundance of predaceous nematodes (Table 3). This indicated the main effect of root litter identity on predaceous nematodes was also influenced by living plant and shoot litter identity.

The species identity difference in living plants had a pronounced impact on nematode community structure and function (Table 3; Figure 4A). Trophic diversity values were smaller for nematode communities associated with living *S. alterniflora* plants (1.49 ± 0.12) than *P. australis* (2.16 ± 0.18) (Figure 3). The results of NMDS and ANOSIM also suggest that the structure of nematode communities differed between living plants of *S. alterniflora* and *P. australis* (see Figure 4A, Global R of ANOSIM = 0.169, $P = 0.002$). In contrast, the effects of shoot or root litter identity had a relatively weaker impact on the structure of the nematode community (shoot litter identity: Global R of ANOSIM = −0.046, $P = 0.874$; root litter identity: Global R of ANOSIM = 0.026; $P = 0.247$) (Figure 4B, C). Thus, the effect of living plant identity explained most of the variation in nematode community structure between *S. alterniflora* and *P. australis*. The results of SIMPER indicated *Tylenchus* contributed most to the structural dissimilarity of nematode communities between these two plant species, irrespective of resource input pathways. The living plant identity alone, and in combination with root litter identity, had significant impacts on

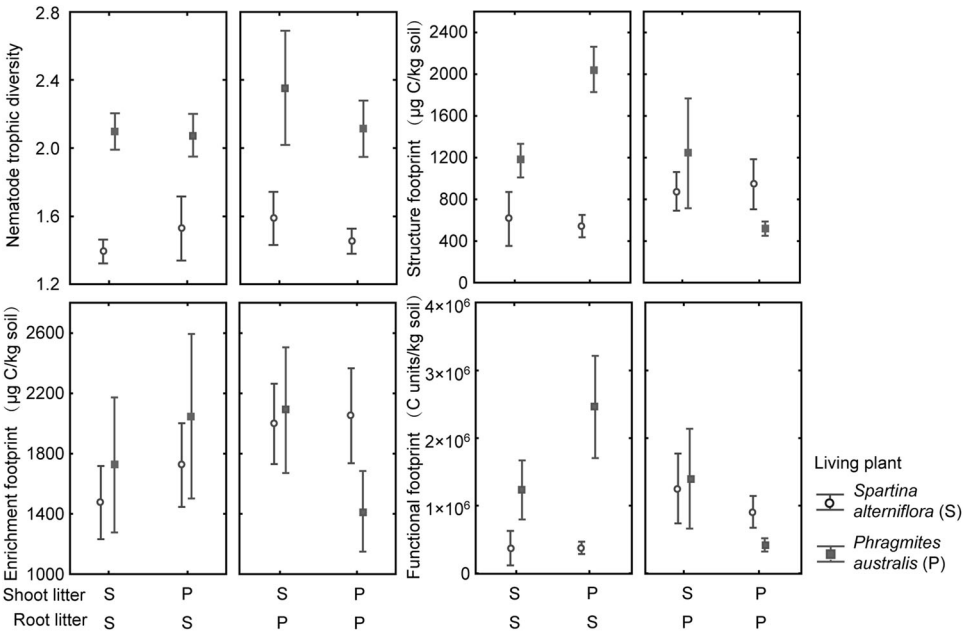

Figure 3. Nematode trophic diversity and metabolic footprints. S = *Spartina alterniflora*, P = *Phragmites australis*. Data are illustrated as means ± 1 SE.

structure and functional metabolic footprints of nematode communities (Table 3). Both structure and functional metabolic footprints of nematode communities were greater with living *P. australis* plants (structure footprint 1608.56 ± 189.39 μg C/kg dry soil; functional footprint 1.85 ± 0.60 10^6 C units/kg soil) than *S. alterniflora* (structure footprint 577.86 ± 182.92 μg C/kg dry soil; functional footprint 0.37 ± 0.17 × 10^6 C units/kg soil) in the presence of *S. alterniflora* root litter (Figure 3).

Discussion

Invasive plants affect the structure and functions of belowground communities via ecological interactions in the rhizosphere and litter input (Wolfe and Klironomos 2005). Although much evidence has revealed the considerable effects of plant invasions on soil biota (Ravit and others 2003; Chen and others 2007b), to the best of our knowledge, no study has distinguished the relative contributions of living roots, shoot litter and root litter input from invasive and native plants to soil communities in the field. Through comparing *S. alterniflora* and *P. australis* in a Chinese marsh, this study demonstrated that the identities of living roots, root litter and shoot litter between co-occurring invasive and native plants affected different components of the soil microbiota at differing magnitudes and these effects may interact with each other.

The Influence of Living Root Identity

Nutrient availability in the soil changes after plant invasion (Kourtev and others 2002). These alterations are reflected in modifications to the structure of microbial communities, such as shifts between a fungal-dominated community and a bacterial-dominated community, and have direct consequences on consumers in the food chain (Dawson and Schrama 2016). The living root input of invasive *S. alterniflora* decreased the ratio of bacteria to fungi PLFAs in the microbial community (Figure 1) and supported 36.30% fewer nematodes in total than that of native *P. australis* (Figure 2), suggesting a lack of available nutrients in the rhizosphere soil after *S. alterniflora* invasion.

The living root-derived resource of a specific plant species can greatly influence most soil biotic groups (Albers and others 2006; Pollierer and others 2007; Eissfeller and others 2013). Our study demonstrated that the differences of living root input between invasive *S. alterniflora* and native *P. australis* strongly affected soil nematodes at both low (plant-feeding nematodes) and high trophic

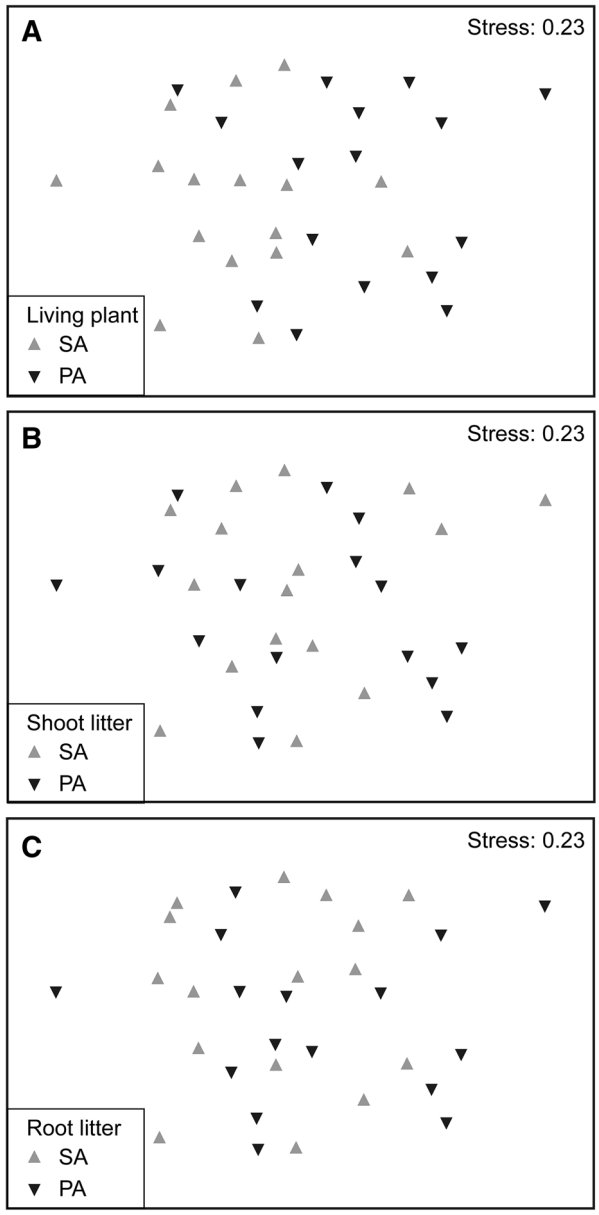

Figure 4. Non-metric multidimensional scaling ordination of nematode communities affected by living plant identity (**A**), shoot litter identity (**B**) or root litter identity (**C**). SA = *Spartina alterniflora*, PA = *Phragmites australis*.

level positions (omnivorous nematodes), and the structure and the function of nematode community. The identity of living roots may have direct effects on the performance of plant-feeding soil organisms during growing seasons (Yeates 1999). Our study found that plant-feeding nematodes were 627% less abundant in the presence of living roots of invasive *S. alterniflora* compared with those of native *P. australis*; though the shoot and root biomass (in the soil depth of 0–10 cm) of *S. alterniflora* was 300 and 100% greater than those of

P. australis, respectively (Figure 2). These findings support the enemy release hypothesis of plant invasion (van der Putten and others 2005; Morriën and others 2012). Less plant-feeding nematodes may ''release'' *S. alterniflora* from root herbivory pressures in the non-native ranges compared with native *P. australis*, which facilitates growth of *S. alterniflora*. The living roots of *S. alterniflora* had a lower N content than that in *P. australis* roots in the Yangtze estuary (Liao and others 2008). Therefore, we speculate that the living roots of *S. alterniflora* may be less palatable for root-feeding animals than those of *P. australis*. Whether the difference in root palatability between invasive and native plants alters the soil community structure and feedback to plant growth in other systems needs more investigation.

Invasion of *S. alterniflora* resulted in a food web with fewer omnivores and lower trophic diversity compared to native *P. australis*. This result agrees with another study that the invasion of *S. alterniflora* leads to a simplified soil food web when it replaces a *P. australis* community (Chen and others 2007b). Our study further suggested that this is presumably because of changes in living root identity. Living root identity impacts allocation of resources to the rhizosphere through root exudation and soil fauna at high trophic levels through a bottom-up cascading effect (Cheng and others 1996). The smaller structure and functional footprint of nematodes under invasive *S. alterniflora* than native *P. australis* also suggested a lower available carbon resource in the rhizosphere of *S. alterniflora* which supported a simpler and less stable food web than that of *P. australis*. Although our study did not analyze root exudates of *S. alterniflora* and *P. australis* directly, the results implied that differences in quality and/or quantity of resource input from living roots between invasive and native plants had a major effect on soil food web structure and function.

Our study found that *S. alterniflora*, as an invasive, had a considerable effect on native soil fauna and simplified the structure of the food web. However, in North America, where *S. alterniflora* is native and *P. australis* is invasive, the revere species effect was observed. The abundance, richness and diversity of arthropods increased in a *S. alterniflora* marsh after removal of *P. australis* (Gratton and Denno 2005). This indicates that the invasive status of these plants in their respective locations is more important to community assembly than the taxonomic species identity of the plant itself. After being introduced to China, *S. alterniflora* experienced a rapid evolutionary change in morphology, growth rate, biomass allocation and phenotypic plasticity (Qing and others 2011). Specifically, invasive populations of *S. alterniflora* became more vigorous with a greater total biomass and greater photosynthetic rate than native populations (Qing and others 2011). Therefore, *S. alterniflora* had the potential to change the quantity or quality of the resource input into the soil and affect soil biota in the ecosystems that it is invading.

The Influence of Root Litter Identity

In addition to root exudates from living roots, the quantity, quality and timing of litter production also change after plant invasion (Wolfe and Klironomos 2005). The quantity of litter was held constant in this study, so any observed differences in the soil food web between *S. alterniflora* and *P. australis* litter additions are attributed to contrasting quality of litter between these two plant species. Litter quality is one of the most important factors affecting soil biota, as soil fauna are more abundant when litter decomposes faster (Wardle and others 2004). As expected from its relatively low C/N ratio, the litter of the native plant *P. australis* decayed faster than invasive *S. alterniflora* litter. The root litter input of native *P. australis* supported 34% more bacteria-feeding nematodes than that of invasive *S. alterniflora* (Figure 2), which supports the hypothesis that litter quality of invasive plants is an important factor affecting detritivores (Ehrenfeld 2010).

In our study, different soil food web components responded differently to living and dead belowground carbon input. The identity of root litter exerted influences on the soil food web mainly via biota involved in decomposition processes (that is, bacterial-feeding nematodes) by bottom-up effects through bacteria. In contrast, living roots influenced other trophic groups (plant-feeding and omnivorous nematodes). Moreover, the identities of dead (root litter) and living roots had interactive effects on the fungal PLFAs, abundance of predaceous nematodes and structure and functional footprints of nematodes. This suggests that the identity of dead and living roots should be considered simultaneously when we interpret the mechanisms of how invasive plants affect ecosystem processes.

Root litter is suggested to play a major role in organic matter dynamics of ecosystems because it represents a large part of the total annual plant litter production from a global estimate (Freschet and others 2013). Some experimental studies have emphasized the greater importance of root litter

decomposition for the soil carbon budget than leaf litter decomposition (Bird and Torn 2006; Hansson and others 2010). Together with the present study, we suggest that the role of root litter identity of invasive plants in determining soil biota and ecosystem nutrient dynamics may be underestimated.

The Influence of Shoot Litter Identity

Invasive plant species alter nutrient release from decomposing leaf litter by changing soil microbe activities and the abundance of detritivores within the food web (Reinhart and VandeVoort 2006; Bastow and others 2008). Therefore, the aboveground parts of plant residues deserve greater emphasis. Surprisingly, our study indicates that shoot litter identity had a weaker impact on the structure and function of soil microbiota, only with a greater effect size on bacterial PLFAs compared with living root or root litter identity (Table 3). This is in contrast to the study by Eisenhauer and Reich (2012), in which shoot litter identity, rather than root litter identity, had greater effects on decomposers. Litter not only provides a resource to soil biota, but also alters habitat structure and conditions (Osler and others 2006; Keith and others 2009). Soil animals may treat shoot litter as habitat rather than as a food resource (Osler and others 2006). The resource-mediated effects of shoot litter identity were weak for the soil community in another 1-year experiment (Keith and others 2009). Perhaps, duration of experiments is another possible explanation for apparently weak impacts of shoot litter identity, which is supported by a previous experiment that found that stem litter of *S. alterniflora* supported a greater abundance of bacterial-feeding nematodes only in a short-term decomposition period (that is, 16 and 32 days) than that of *P. australis*, but the difference became less thereafter and was not significant after 64 and 128 days of decomposition (Chen and others 2007a). The decomposition process of the present study lasted for three months. Together with the previous and present studies, we conclude that the resource-mediated effects of root litter identity may surpass shoot litter identity in influencing soil organisms after three months or longer. Moreover, the relatively small difference in shoot litter C/N ratio between *S. alterniflora* and *P. australis* (53.71 vs. 39.29) in contrast to the differences in their root litter C/N ratio (63.66 vs. 34.03), which indicated a smaller litter quality difference of shoot litter than that of root litter, may also explain the weak influence of shoot litter identity on soil food web. Another possible reason is that the factors controlling the decomposition dynamics of shoot and root litter may differ. For instance, Zhao and others (2014) found that the decomposition of shoot litter is mainly affected by initial nutrient content and C component, whereas root decomposition is determined primarily by the protected compounds in litter.

Conclusions

The differences in structure and function of soil microbiota between this pair of co-occurring invasive *S. alterniflora* and native *P. australis* plant species are attributed mainly to the difference in their belowground resource input (living root-derived and root litter) rather than aboveground resource input (shoot litter). Thus, we recommend that the belowground resource input needs to receive more attention when considering the mechanisms of how invasive plants affect ecosystem processes. Furthermore, our study provides a case to illuminate that the difference of living root-derived resource input between invasive and native plants is greater than the effect of dead plant residue inputs. Whether the impact of living roots is common for invasive plants begs further research.

This study demonstrates that different components of the soil microbiota rely differentially on living root- and litter-derived resource inputs. Species identity of shoot and root litter affects bacteria and bacteria-feeding nematodes, which are mainly involved in decomposition, whereas that of living root affects the abundance of plant-feeding and omnivorous nematodes. Exotic *S. alterniflora* performs better than native *P. australis* in the field and appears to simplify soil food web structure, and greatly affect soil food web functions. This suggests that invasive plants that differ from native species in the pathways of resource input to the ecosystem can influence unique components of the soil food web and have different ecological consequences.

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Compliance with Ethical Standards

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

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