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Soil Biology & Biochemistry 39 (2007) 1782–1793

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Exotic plant influences soil nematode communities through litter input

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Received 29 November 2006; received in revised form 3 February 2007; accepted 14 February 2007
Available online 15 March 2007

Abstract

The impact of exotic plant invasions on soil communities and nutrient cycling processes has received an increasing attention in recent years. To test whether the exotic plant invasions affect nematode communities through altering litter quality, we compared mass loss and nematode colonization during the stem litter decomposition of invasive *Spartina alterniflora* and native *Phragmites australis* in salt marshes of the Yangtze River estuary, China. Plastic drinking straws were synchronously used as controls. The addition of plant residues was found stimulating the growth of nematodes, particularly bacterial feeders on day 16 after burial. A top–down control of bacterivous nematodes by carnivores existed in nematode succession during the litter decomposition. With higher nitrogen content and lower C:N ratio, stem litter of the invasive *S. alterniflora* decayed faster and supported more abundant nematodes than the native *P. australis*. The greater nematode abundance in *S. alterniflora* was mainly due to two dominant genera of bacterial nematodes, namely *Diplolaimelloides* and *Diplolaimella*. Lower values of maturity index and structure index in *S. alterniflora* than in *P. australis* litter indicate that a more degraded food web condition resulted from the faster litter decay. A considerable difference in nematode community structures between two litter types only occurred in a certain period of the decomposition (from 8 to 32 days after burial), suggesting that the changes in faunal community structure are time dependent. In summary, this study confirmed the hypothesis that the invasion of *S. alterniflora* stimulates the growth of bacterial nematodes by producing higher quality of litter than the native *P. australis*. The results obtained here suggest that the invasion of exotic plant is likely to alter ecosystem functions indirectly through exerting its effect on soil decomposer communities such as nematodes.
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Keywords: Colonization; Decomposition; Litter quality; Succession; Wetland; *Spartina alterniflora*; *Phragmites australis*

1. Introduction

Invasions of exotic species have become a global problem and profoundly affect the invaded ecosystems in many different ways (Mooney and Drake, 1986; Vitousek et al., 1987, 1996; Ehrenfeld, 2003). The impact on soil communities and nutrient cycling processes is considered as an important ecological consequence of plant invasions and has received a growing attention (Ehrenfeld and Scott, 2001; Kourtev et al., 2002a; Ehrenfeld, 2003; Hawkes et al., 2005; Chen et al., 2005; Wolfe and Klironomos, 2005). Many studies have shown that exotic plant species alter the density, diversity or community structure of soil microorganisms and fauna, though the effects varied across sites or ecosystems (Belnap and Phillips, 2001; Yeates and Williams, 2001; Kourtev et al., 2002a; Ravit et al., 2003; Chen et al., 2007). It is suggested that the exotic plant species affect soil biota directly through root exudates during growing seasons or through litter inputs during plant material decay (Wardle et al., 2004). However, our understanding of how exotic plants influencing soil communities through litter input has been poor, only Kourtev et al. (2002b) have demonstrated that the difference in litter chemistry between exotic and native plant species is a strong determinant of enzyme activities in decomposing litter.

Among soil communities, microorganisms are the primary decomposers, but microfauna (especially protozoa and nematodes) which feed on microbes are important

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0038-0717/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2007.02.011

intermediaries in detrital food webs (Ingham et al., 1985; Ruess, 2003). These soil biota interact to affect the decomposition processes of detritus (Abrams and Mitchell, 1980; Pradhan et al., 1988; Alkemade et al., 1992a, b). Plant litter differing in the quality may favor different soil microorganisms (Conn and Dighton, 2000; Kourtev et al., 2002b; Aneja et al., 2006) and invertebrates (Bjørnlund and Christensen, 2005; Georgieva et al., 2005; Wardle et al., 2006), and consequently influence the interactions among soil biota and their effects on litter decomposition.

Spartina alterniflora and *Phragmites australis* are two invasive plants invading each other in many coastal salt marshes. *S. alterniflora* originated in the eastern coast of USA where it was invaded by a salt-tolerant genotype of *P. australis* (Rice et al., 2000; Chen, 2004). *S. alterniflora* was intentionally introduced to China in 1979 to promote sediment accretion and stabilize tidal flats in the coastal regions (Qin and Zhong, 1992). In many salt marshes in east coast of China, *S. alterniflora* rapidly spread and excluded the native plants like *P. australis* because of its great invading ability (Chen et al., 2004; Wang et al., 2006). Our previous study compared soil nematode communities under *S. alterniflora* and *P. australis* communities in the Yangtze River estuary (Chen et al., 2007). The abundance of bacterial-feeding nematodes was found to increase whereas the trophic diversity declined in the *S. alterniflora* marshes compared with those in the native *P. australis* marshes. Since the two plant species were reported to differ in their litter quality such as nitrogen and lignin concentrations (Windham, 2001; Gessner, 2000; Cheng et al., 2006), we hypothesized that the invasions of *S. alterniflora* influence nematode communities through producing litter with higher quality.

Using litter containers, we compared mass loss and nematode colonization during stem litter decomposition of invasive *S. alterniflora* and native *P. australis* in the marshes of the Yangtze River estuary, China. Our specific objectives were to answer questions: (1) if bacterial-feeding nematodes are more abundant in fast decomposing detritus, (2) if the nematode communities developed in two types of plant litter are different, and (3) if the nematode succession processes are different in two types of plant litter.

2. Material and methods

2.1. Site description

The study was conducted at the Wetland Experimental Station (31°31′013″ N, 121°58′297″ E) of Chongming Island, China. At the station, a native plant *P. australis* and an invasive plant *S. alterniflora* co-occur as dominant plants. The soil is a sandy clay loam with organic matter content of 0.97% and pH 7.3. During the period of study, soil water content varied between 54% and 100% due to tidal inundations and soil temperature varied between 19.7 and 31.5 °C.

2.2. Litter container preparation

Standing dead stems of *Phragmites australis* (hereafter *Phragmites*) and *Spartina alterniflora* (hereafter *Spartina*) were collected from Dongtan, Chongming Island in January 2005. All stems were gently washed, split vertically into two halves, and then cut into 2-cm-long pieces. All materials were oven dried to constant weight at 60 °C. Plastic drinking straws were also split vertically into two halves and then cut into fragments of 2 cm in length. These plastic pieces were treated as controls to test whether invertebrates colonize stem litter as refuges rather than food. The litter containers were small polyethylene tubes (48 mm in length, 36 mm in diameter) with 2 mm nylon meshes on both ends. Each litter container was packed with 8 g dry experimental materials (plant stem or plastic control litter).

2.3. Sampling design

Four 1×1 m plots, which were about 0.8 m apart from one other, were established at the experimental station as replicates. In each plot, equal numbers of containers with three types of litter (*Spartina, Phragmites* and control) were randomly buried on 20 May 2005. A total of 18 litter containers were buried in each plot. Each litter container was inserted into the soil to a depth of 5 cm after a hole was made by a similar size core. Three litter containers (one container per treatment) were retrieved from each plot on day 4, 8, 16, 32, 64 and 128 after burial. Thus, the experiment was a 6×3 (sampling dates $\times$ litter treatment) design with four replicates.

2.4. Sample processing

The entire contents from each retrieved container were mixed with water and the mud and nematodes were gently washed off the litter with a soft brush. The resultant mix was filtered through a 0.5 mm sieve placed over a 45 μm mesh sieve. The material retained on the 0.5 mm sieve was taken as the remains of the original litter, and its dry weight was measured after oven dried at 60 °C. The C and N concentration of the initial and remaining litter were measured with a NC Soil Analyzer (Flash EA 11121 Series, Thermo Finnigan, Italy). Nematodes retained on the 45 μm mesh sieve were fixed in 4% formaldehyde solution. After counting the total number of individuals, nematode specimens were slowly dehydrated in anhydrous glycerol, prepared on slides, and identified to genus. For samples in which nematode specimens were fewer than 100 individuals, all specimens were identified. For larger samples containing more than 100 nematode individuals, 100 randomly selected specimens were identified.

2.5. Nematode analyses

Nematodes were classified into five trophic functional groups (algal feeder, plant feeder, bacterial feeder, carnivore and omnivore) according to Yeates et al. (1993). There were no fungal-feeding nematode in all samples. Based on their life strategies, nematodes were designated a colonizer–persister (*c–p*) value ranging from 1 to 5 according to Bongers (1990) and Bongers and Bongers (1998). Nematodes with low *c–p* values have short generation time, high fecundity and feed continuously in enriched media, while nematodes with high *c–p* values have long generation time, large body size low fecundity and are sensitive to disturbance (Bongers and Bongers, 1998). Except for plant feeders, nematodes were further assigned into functional guilds integrating their feeding habits and *c–p* values, and the weightings of guilds along the structure and enrichment trajectories were determined according to Ferris et al. (2001). The structure trajectory is an indicator of the complexity of the soil food web. Food webs become structured when maturation, recovery from stress, and lack of perturbation is occurring (Ferris et al., 2001). The enrichment trajectory is an indicator of the level of primary enrichment of the food web. Food webs become enriched when nutrient resources are available due to disturbance, organism mortality, or shifting of environment into favorable conditions (Odum, 1985).

Several ecological indices were calculated to assess the nematode community. Shannon–Weaver diversity index (H') was calculated at the genus level. $H' = -\sum p_i \ln p_i$, where p_i is the proportion of individuals in the ith taxon. The maturity index (MI) was calculated according to Bongers (1990). $\mathrm{MI} = \sum v(i)f(i)$, where $v(i)$ is the *c–p* value of taxon i, $f(i)$ is the frequency of taxon i in a sample. The structure index (SI) and enrichment index (EI) were calculated according to Ferris et al. (2001). Structure index $(\mathrm{SI}) = 100 \times \sum k_s n_s / (\sum k_s n_s + \sum k_b n_b)$, Enrichment index $(\mathrm{EI}) = 100 \times \sum k_e n_e / (\sum k_e n_e + \sum k_b n_b)$, where k_b is the weighting assigned to the guild Ba_2 as shown in Table 2, n_b is the abundance of nematodes in the guild Ba_2 which indicates the basal characteristic of the food web; k_s is the weighting assigned to guilds Ba_3–Ba_5, Al_2–Al_3, Om_4–Om_5 and Ca_3–Ca_4, n_s is the abundance of nematodes in these guilds which represents a structure condition of the food web; k_e is the weighting assigned to the guild Ba_1, n_e is the abundance of nematodes in the guild Ba_1 which represents an enriched condition of the food web.

2.6. Statistical analyses

All data were presented on a dry weight basis. The daily decomposition rates were estimated according to an exponential decomposition model: $L_t = L_0 e^{-kt}$, where L_t is the litter mass at time t, L_0 is the litter mass at time 0, k is the exponent that characterizes the decomposition rate, and t is the time in days (Chapin et al., 2002). In this study, t referred to the time interval between two successive sampling dates.

Two-way ANOVA was carried out to analyze effects of treatment and sampling time on litter decomposition and nematodes. A Tukey HSD test was used if significant differences were detected among treatments on each sampling date. Significance levels were set to $P<0.05$.

Table 1
Percentage of weight of remaining day mass, carbon and nitrogen, C:N ratio and decomposition rate of *Spartina alterniflora* and *Phragmites australis* stems in litter containers

	% weigh remaining	Decomposition rate	% C remaining	% N remaining	C:N ratio
Spartian alterniflora					
Day 4	80.9 (0.8)[a]	0.053 (0.002)[a]	85.7 (0.5)[a]	76.0 (5.6)	138.0 (7.3)
Day 8	76.6 (1.3)[a]	0.014 (0.004)[a]	81.1 (0.8)[a]	76.0 (4.2)	129.8 (4.7)[a]
Day 16	73.9 (0.8)[a]	0.004 (0.003)	77.7 (0.8)[a]	80.0 (4.5)	118.7 (7.3)[a]
Day 32	70.0 (0.5)[a]	0.003 (0.000)	73.3 (0.7)[a]	76.1 (4.5)	118.0 (8.6)[a]
Day 64	66.6 (0.8)[a]	0.002 (0.000)	66.9 (0.6)[a]	96.1 (8.1)	85.5 (5.0)
Day 128	59.9 (0.3)[a]	0.002 (0.000)	61.4 (1.0)[a]	97.2 (5.2)[a]	77.3 (1.3)
Phragmites australis					
Day 4	98.7 (0.2)[b]	0.003 (0.001)[b]	99.7 (0.7)[b]	109.9 (13.5)	145.5 (13.8)
Day 8	97.9 (0.2)[b]	0.002 (0.001)[b]	98.5 (0.2)[b]	87.5 (5.2)	175.6 (1.7)[b]
Day 16	97.8 (0.1)[b]	0.000 (0.000)	99.2 (0.5)[b]	94.6 (4.3)	163.2 (4.4)[b]
Day 32	96.2 (0.3)[b]	0.001 (0.000)	98.7 (0.3)[b]	98.7 (3.7)	155.5 (3.5)[b]
Day 64	91.1 (0.4)[b]	0.002 (0.000)	94.5 (0.6)[b]	136.3 (20.2)	112.3 (10.2)
Day 128	85.0 (0.4)[b]	0.001 (0.000)	87.7 (0.3)[b]	171.8 (15.1)[b]	80.2 (3.0)
Two-way ANOVA (*P*-value)					
Plant	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Time	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Plant*Time	**0.000**	**0.000**	**0.000**	**0.021**	**0.009**

Shown are the means with SE in parentheses ($n = 4$). The decomposition rate is expressed as daily decomposition exponent k between two consecutive sampling days. Significant effects ($P<0.05$) are indicated in bold. Different superscript letters indicate significant differences between two plant species at each sampling time (Tukey HSD test, $P<0.05$).

Table 2
Mean nematode abundance (ind. g^{-1} dry weight of remaining litter) in *Spartina alterniflora* (SA), *Phragmites australis* (PA) and Control (C) litter containers on day 4, 8, 16, 32, 64 and 128 after burial

Nematode taxa	*c–p* value	Guild (weighting)	Day 4			Day 8			Day 16			Day 32			Day 64			Day 128		
			SA	PA	C	SA	PA	C	SA	PA	C	SA	PA	C	SA	PA	C	SA	PA	C
Bacterial feeders																				
Amphidelus	4	Ba_4 (3.2)																1	0.7	
Anoplostoma	2	Ba_2 (0.8)			<0.1		0.4	0.2			0.6	1	1.6	2.7	0.4	0.3	0.9	0.8		0.5
Daptonema	2	Ba_2 (0.8)	0.2	0.4	0.5	0.7	0.3	0.7					0.3		0.3		0.1		0.6	<0.1
Desmoscolex	4	Ba_4 (3.2)			<0.1	<0.1		0.1			<0.1		<0.1	0.5			1		0.2	0.6
Diplolaimella	2	Ba_2 (0.8)	1.3	0.4	0.5	2.2	1.9	0.1	1.7	22.8	1	42.9	7.6	0.4	34.4	12.2	0.4	66.7	54.4	0.1
Diplolaimelloides	2	Ba_2 (0.8)	4.6	3.6	0.5	23.9	3.1	<0.1	273.3	89.8	2.9	79.9	10.5	0.5	26.7	7.5	0.3	13.2	10.3	<0.1
Eucephalobus	2	Ba_2 (0.8)																	0.1	
Halalaimus	4	Ba_4 (3.2)												<0.1				0.4	0.1	
Haliplectus	3	Ba_3 (1.8)	<0.1			0.1		0.1		0.2		1.6	2.1	0.8	5.1	2.9	1.1	2	1.5	<0.1
Leptolaimus	2	Ba_2 (0.8)		<0.1										<0.1						
Mesorhabditis	1	Ba_1 (3.2)	0.1										<0.1		0.3	0.2				
Microlaimus	2	Ba_2 (0.8)		<0.1																
Panagrolaimus	1	Ba_1 (3.2)	<0.1			0.1														
Parodontophora	2	Ba_2 (0.8)	0.2	<0.1	<0.1	0.3	<0.1	0.5			<0.1			0.4	0.3	0.9	0.5			0.6
Plectus	2	Ba_2 (0.8)	<0.1																	
Rhabditis	1	Ba_1 (3.2)		<0.1						0.2			<0.1		0.2			0.2		
Rhabdontlaimus	1	Ba_1 (3.2)		<0.1																
Terschellingia	3	Ba_3 (1.8)				0.3	0.1	<0.1							0.2	0.4		4.6	8.1	0.2
Theristus	2	Ba_2 (0.8)																1.1	0.7	0.1
Algal feeders																				
Chromadorina	3	Al_3 (1.8)												<0.1						
Ethmolaimus	3	Al_3 (1.8)												<0.1						<0.1
Hypodontolaimus	3	Al_3 (1.8)	0.1	0.2	0.9	1.7	0.3	0.7						0.2		0.1			0.3	<0.1
Neochromadora	3	Al_3 (1.8)	0.2	0.2	0.5		0.6	<0.1		1.6	0.8	9.2	8.3	3.5	21	9.2	1.3	0.7		0.2
Paracanthonchus	2	Al_2 (0.8)	<0.1	<0.1	0.3		<0.1	0.1					<0.1	<0.1	0.9	0.6	0.2			
Polysigma	3	Al_3 (1.8)	0.1	<0.1	0.3	0.2	<0.1	<0.1				0.4		<0.1	1	0.2			0.2	
Ptycholaimellus	3	Al_3 (1.8)					0.2	<0.1			0.1			<0.1		0.3		0.6	0.1	0.2
Plant feeders																				
Lenonchium	4															0.1				
Tylenchus	2																	0.8	0.4	
Omnivores																				
Aporcelaimus	5	Om_5 (5.0)															<0.1			
Dorylaimus	4	Om_4 (3.2)				0.1			0.9		0.1	0.6	0.7	1.4		0.2	0.2			0.4
Carnivores																				
Oncholaimus	4	Ca_4 (3.2)			<0.1		0.4	<0.1			0.1	8	12.2	2.5	8.6	8.5	0.4	0.4	0.2	0.1
Sphaerolaimus	3	Ca_3 (1.8)		<0.1		0.1		0.2					0.6		0.3	<0.1	0.1		1.3	0.4
Tripyloides	3	Ca_3 (1.8)												<0.1			<0.1			

Table 3
Summary of two-way analysis of variance (ANOVA) to test the effects of treatments and time on total density, generic Shannon-Weaver diversity, maturity index and abundance of nematodes in different trophic groups

Variables	Error df	Treatment (2 df)		Time (5 df)		Treatment*time (10 df)	
		F	*P*	*F*	*P*	*F*	*P*
Total density	54	89.1	**0.000**	35.1	**0.000**	13.8	**0.000**
Shannon-Weaver diversity	54	49.3	**0.000**	18.5	**0.000**	1.5	0.183
Maturity index	54	64.1	**0.000**	25.7	**0.000**	4.1	**0.000**
Bacterial feeders	54	87.8	**0.000**	39.7	**0.000**	15.9	**0.000**
Algal feeders	54	1.7	0.188	3.7	**0.006**	1.2	0.330
Plant feeders	54	0.9	0.399	2.8	**0.027**	0.9	0.549
Omnivores	54	0.6	0.530	2.6	**0.034**	0.7	0.681
Carnivores	54	5.9	**0.005**	12.6	**0.000**	2.3	**0.026**

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

To meet assumptions of ANOVA, the proportional data were square-root transformed and the numeric data were log transformed prior to statistical analyses.

Multivariate analyses were undertaken with the Plymouth routines in multivariate ecological research (PRIMER) version 5.2 software package (Clarke and Warwick, 1994). Two-way crossed analysis of similarity (ANOSIM) was used to test treatment and time effects on the nematode community. One-way ANOSIM was further conducted to test treatment effects on nematode community structure at each sampling time. All pair-wise comparisons between different treatments or between different sampling times were based on Bray–Curtis similarities of log $(x+1)$ transformed nematode abundance data. Significance levels were set to $P<0.05$.

3. Results

3.1. Litter quality, mass loss and nutrient dynamics during decomposition

Spartina had higher initial nitrogen content (0.35%) in stems than *Phragmites* (0.28%), and hence lower C:N ratio (121.0) than *Phragmites* (157.8).

The litter mass loss and its decomposition rate varied significantly between plant species and among buried times (Table 1). The percentages of mass remaining of *Spartina* stems were significantly lower than *Phragmites* throughout the experiment. At the end of the experiment there were 40% mass lost in *Spartina* stems, and only 15% in *Phragmites*. The decomposition rate of *Spartina* litter

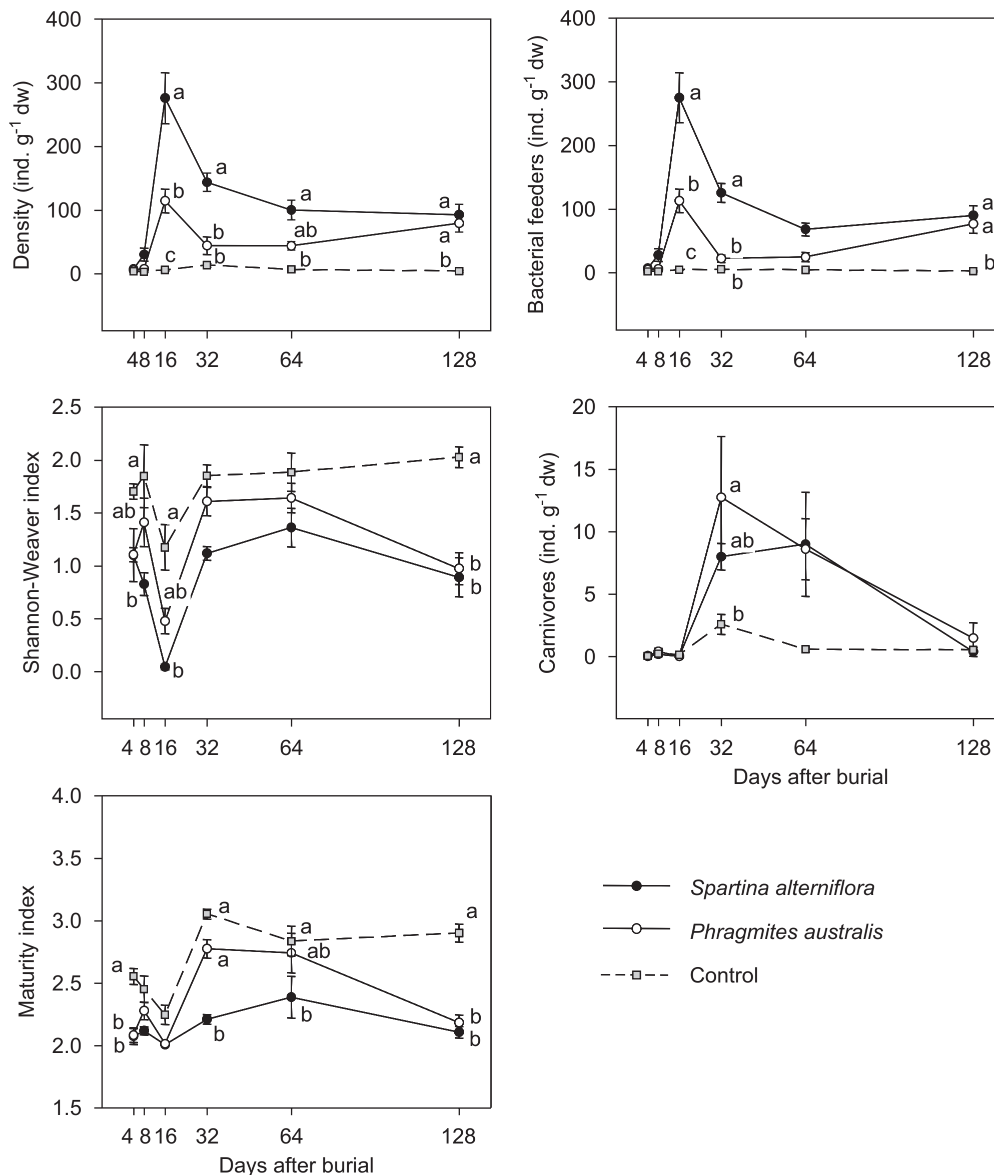

Fig. 1. The total abundance of nematode, the Shannon–Weaver diversity index, the maturity index, and the abundance of bacterial feeders and carnivores in *Spartina alterniflora*, *Phragmites australis* and control containers. Abundance data are expressed as ind. g^{-1} dry weight of remaining litter. Vertical bars indicate standard errors of the means ($n = 4$). Different letters (a, b, c) indicate significant differences among treatments at each sampling time ($P<0.05$).

during the first and second four days ($k = 0.053$ and 0.014 day^{-1}, respectively) was significantly higher than that of *Phragmites* litter ($k = 0.003$ and 0.002 day^{-1}, respectively).

The percentage of remaining carbon and nitrogen and the C:N ratio in litter varied significantly between plant species and among buried times (Table 1). Following the pattern of weight loss, the carbon loss of the *Spartina* litter was significantly greater than *Phragmites* throughout the experiment. Nitrogen was immobilized in *Phragmites* stem litter compared with a slight release from the *Spartina* litter at the end of the experiment. The C:N ratio of the remaining litter was significantly lower in *Spartina* than that in *Phragmites* at 8, 16 and 32 days after burial, but no significant difference between the two plant species were found thereafter.

3.2. Nematode populations and ecological indices

A total of 24, 27 and 23 nematode genera were found in *Spartina*, *Phragmites* and control during the entire experiment, respectively (Table 2). *Diplolaimelloides* and *Diplolaimella* dominated in both *Spartina* (*Diplolaimelloides* representing 66.84% and *Diplolaimella* 21.19% of the total abundance) and *Phragmites* litter (*Diplolaimelloides* representing 40.59% and *Diplolaimella* 35.96% of the total abundance). *Diplolaimelloides* peaked at days 16, while *Diplolaimella* peaked at the end of the experiment in both plant litter treatments. In the control litter, *Neochromadora*, *Anoplostoma* and *Diplolaimelloides* were dominant genera, contributing 17.87%, 13.47% and 12.23% to the total abundance, respectively.

Two-way ANOVA shows that the nematode density, diversity and maturity indices in the litter containers significantly differed among treatments and among burial time (Table 3). The total nematode abundance was the highest in *Spartina* litter at each stage of the experiment, followed by *Phragmites* and control (Fig. 1). The total nematode abundance remained low in control containers throughout the experiment. In both *Spartina* and *Phragmites* litter containers, total nematode numbers increased rapidly and peaked on day 16, on average, 275.9 and 114.5 ind./g dw, respectively. On day 16, 32, 64 and 128 after burial, significantly greater number of nematodes colonized on *Spartina* litter than the control. Significantly more nematodes were found in *Phragmites* litter than in the control only on day 16 and 128. Significantly higher

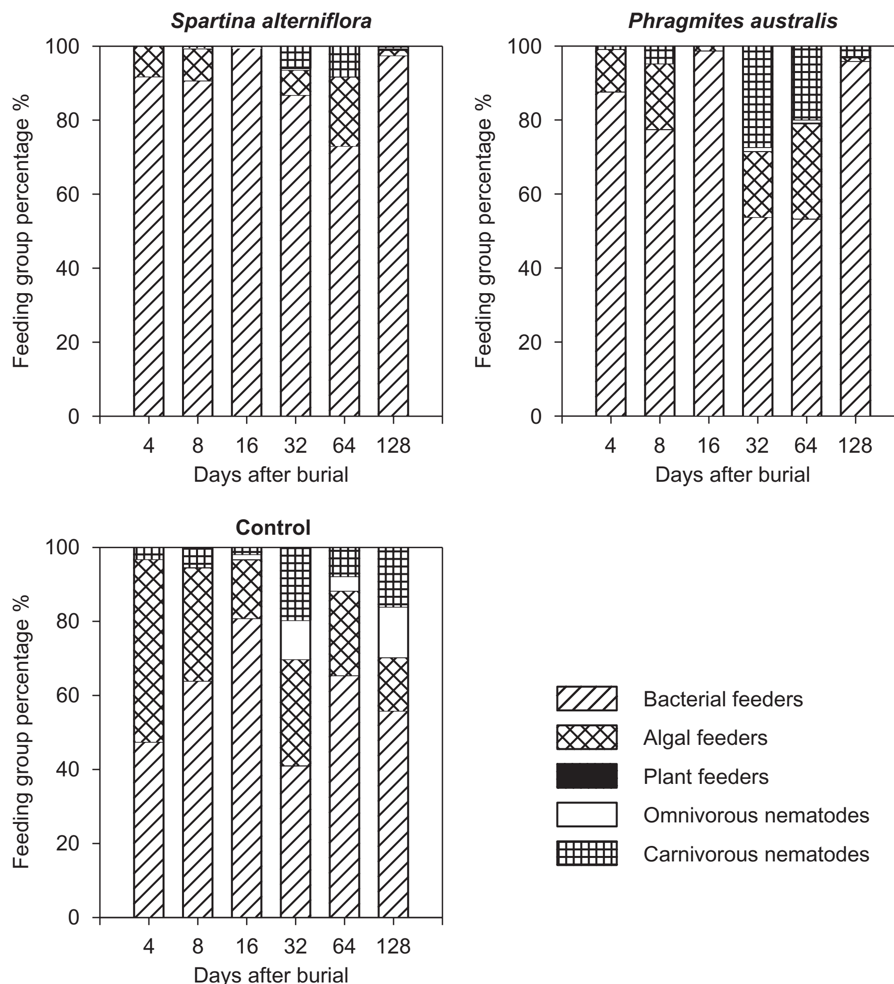

Fig. 2. Proportional composition of nematode feeding groups in *Spartina alterniflora*, *Phragmites australis* and control containers at each sampling time.

nematode densities were detected in decomposing *Spartina* than *Phragmites* on day 16 and 32, but no significant differences were found thereafter. At each stage of experiment, the value of Shannon–Weaver diversity index of nematode genera in control was higher than in the residues of both plants (Fig. 1). Nematode diversity in control containers was significantly higher than that in *Spartina* litter containers on day 8, 16 and 128, and than that in *Phragmites* litter containers only at the end of experiment. *Spartina* litter had generally lower nematode diversity than *Phragmites* litter, but the difference between the two plant treatments over the experimental period was not statistically significant. The value of nematode maturity index was consistently greater in control than in *Phragmites* and *Spartina* litter containers (Fig. 1). The control had significantly higher maturity index than *Spartina* on day 4, 32, 64, 128, and *Phragmites* on day 4 and 128. A significant difference in nematode maturity index between *Spartina* and *Phragmites* litter containers was only observed on day 32 after burial.

3.3. Nematode trophic groups and faunal profile analyses

The abundance of all nematode trophic groups in litter containers was changed significantly over time (Table 3). Significant effects of litter type and interaction between litter and buried time were observed only for bacterial feeders and carnivores. Bacterial feeders followed exactly the same pattern of the total nematodes, but there was no significant difference between *Spartina* and control on day 64 (Fig. 1). This indicates that most changes of nematode abundance were due to change in bacterivores. No significant difference in the abundance of algal feeding, plant feeding, omnivorous and carnivorous nematode was observed between *Spartina* and *Phragmites* litter, or between *Phragmites* and control throughout the experiment. Generally, there was no significant difference on the abundance of these four trophic groups between *Spartina* and control, except that the *Spartina* litter contained significantly more algal feeders and carnivores than the control on day 64 and 32. The carnivore abundance reached the maximum between day 32 and 64 in both *Spartina* and *Phragmites* litter containers.

The trophic composition of nematode in the three types of litter during the experiment was shown in Fig. 2. The proportional dominance of bacterial feeders was highest in the *Spartina* litter and lowest in the control. In both *Spartina* and *Phragmites* litter containers, the percentage of bacterial-feeding nematodes reached the highest on days 16 and 128, but for carnivores on day 32–64. The percentages of plant feeders were quite low in all the treatments. No fungal feeders were found in this study.

Faunal profiles of nematode were constructed for diagnosing the food web for each type of litter (Fig. 3). Comparatively, controls had the most structured food webs at each sampling time, followed by *Phragmites* and *Spartina*. For *Phragmites* and *Spartina* treatments, the food web tended to be more structured on day 32 and 64 after burial. In control containers, a more structured food web occurred at late stages of experiment (from day 32 to 128)

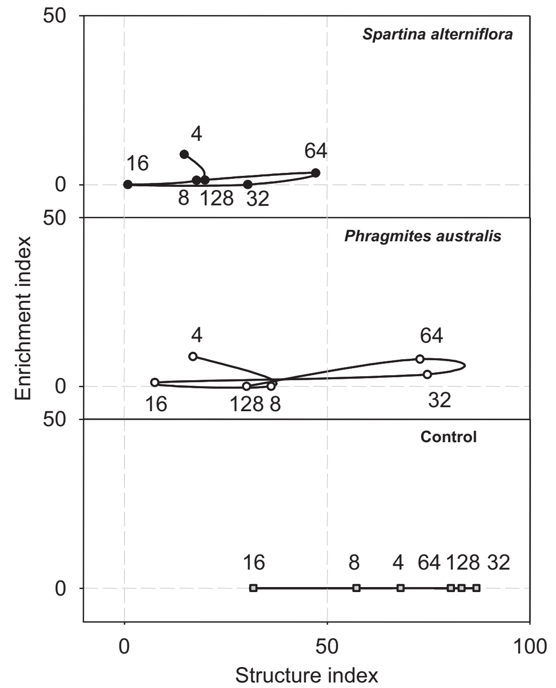

Fig. 3. Faunal profile representing the structure and enrichment conditions of soil food web indicated by nematode in *Spartina alterniflora*, *Phragmites australis* and control containers. Numbers represent samples taken on day 4, 8, 16, 32, 64 and 128 after burial.

Table 4
Two-way crossed ANOSIM for testing the effects of treatment and time on nematode communities, and the pair-wise differences in nematode communities between treatments (SA: *Spartina alterniflora*; PA: *Phragmites australis*; C: Control) and between sampling times

	Global test R	Pairwise test R	P
Treatment	0.595		**0.001**
SA and PA		0.255	**0.002**
SA and C		0.887	**0.001**
PA and C		0.818	**0.001**
Time	0.769		**0.001**
Days 4 and 8		0.316	**0.001**
Days 4 and 16		0.764	**0.001**
Days 4 and 32		0.910	**0.001**
Days 4 and 64		0.882	**0.001**
Days 4 and 128		0.913	**0.001**
Days 8 and 16		0.872	**0.001**
Days 8 and 32		0.861	**0.001**
Days 8 and 64		0.858	**0.001**
Days 8 and 128		0.868	**0.001**
Days 16 and 32		0.948	**0.001**
Days 16 and 64		0.892	**0.001**
Days 16 and 128		0.854	**0.001**
Days 32 and 64		0.163	**0.041**
Days 32 and 128		0.920	**0.001**
Days 64 and 128		0.753	**0.001**

Significant effects $P < 0.05$ are indicated in bold.

Table 5
One-way ANOSIM for testing the treatment effects on nematode communities, and the pair-wise differences in nematode communities between treatments (SA: *Spartina alterniflora*; PA: *Phragmites australis*; C: Control) on day 4, 8, 16, 32, 64 and 128 after burial

Days after burial	Global test		Pair-wise test					
			SA and PA		SA and C		PA and C	
	R	*P*	*R*	*P*	*R*	*P*	*R*	*P*
Day 4	0.292	**0.014**	0.042	0.457	0.427	0.057	0.417	**0.029**
Day 8	0.780	**0.001**	0.406	**0.029**	1.000	**0.029**	0.917	**0.029**
Day 16	0.743	**0.002**	0.448	0.086	1.000	**0.029**	1.000	**0.029**
Day 32	0.653	**0.001**	0.521	**0.029**	0.927	**0.029**	0.802	**0.029**
Day 64	0.551	**0.001**	0.146	0.171	0.969	**0.029**	0.771	**0.029**
Day 128	0.549	**0.008**	-0.031	0.657	1.000	**0.029**	1.000	**0.029**

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

than that at the early stages (first 16 days). The faunal profiles revealed that the enrichment index was not necessarily associated with litter type and sampling time.

3.4. Nematode community structure

Two-way crossed ANOSIM revealed significant effects of treatment (Global test $R = 0.595$, $P = 0.001$) and time (Global test $R = 0.769$, $P = 0.001$) on nematode communities (Table 4). The dissimilarities in nematode communities between pair of treatments or between pair of sampling times were all significant ($P<0.05$). One-way ANOSIM revealed significant treatment effects on nematode communities at all sampling times (Table 5). At each sampling time, the dissimilarities in nematode communities between *Spartina* and control, and between *Phragmites* and control were significant ($P<0.05$) or marginally significant ($P = 0.057$ between *Spartina* and control on day 4). The dissimilarities in nematode communities between *Spartina* and *Phragmites* were only significant on day 8 and 32, and marginally significant on day 16 ($P = 0.086$).

4. Discussion

4.1. Effects of plant residue addition on nematode succession

The addition of plant residues was found to stimulate the growth of nematodes, particularly bacterial feeders. On day 16 after burial, the total nematode abundance in decomposing plant litter reached as high as 19.6–47.3 times of that in the control. Bacteria have great ability to colonize detritus-enriched habitats (Wasilewska et al., 1981; Wasilewake, 1992), which can explain why a great number of bacterial-feeding nematodes were found in decomposing litter containers. The generic diversity of nematode was reduced by the addition of plant residue throughout the experiment, indicating that a few genera become dominant in decomposing litter. Compared with control, the lower nematode maturity index and structure index in decomposing plant detritus indicate enriched conditions and enhanced nutrient availabilities. In sum, the addition of plant residue led to the changes in nematode communities, including an increase in nematode abundance, the decreases in taxonomic diversity, maturity index and structure index, and the alterations of community structure, all of which coincided with many earlier studies (McSorley and Frederick, 1999; Zhou, 2001; Ferris and Matute, 2003; Wang, et al., 2004).

Wang et al. (2004) have concluded, based on their experiments sampled at 2-week intervals, that nematode abundance reaches the peak at 14 ± 14 days after burial. The explanation for that they offer is that this duration of time coincides well with the quick decomposition of plant residues with relatively low C:N ratio, such as sunn hemp. In the present study, we found that the nematode abundance peaked at 16 days after burial, suggesting that the conclusion of Wang et al. (2004) may be applicable to plant residues with C:N ratio higher than 120. A quick increase of nematode abundance around 2 or 3 weeks after residue application has also been recorded by other workers (Santos et al., 1981; Gee and Somerfield, 1997; Fu et al., 2000). We agree with Fu et al. (2000) that this increase in nematode number may be due to the reproduction of bacterial-feeding nematodes within the plant litter containers, because the abundance of all nematode genera remained low in control throughout experiment. In this study, most genera of bacterial-feeding nematodes colonized plant litter during the first 8 days. It is suggested that the preferential migration of nematodes as pointed out by Griffiths and Caul (1993) may be essential at the early stage of the colonization experiment, but their reproduction may play a more important role at the later stages.

Previous studies in terrestrial ecosystems have found that nematode communities always started with enrichment-opportunists with a *c–p* value of 1 and a short life cycle, and subsequently dominated by general-opportunists with a *c–p* value of 2 and a long life cycle (Ettema and Bongers, 1993; Ferris and Matute, 2003; Wang et al., 2004; Bjørnlund and Christensen, 2005). This is envisaged as a typical pattern of succession in terrestrial ecosystems. In this study, however, the early rapid increase in bacterivore abundance was due to the presence of *Diplolaimelloides*

and *Diplolaimella,* which belong to the *c–p* group 2. Even though some nematodes with *c–p* value of 1 (e.g. *Mesorhabditis* and *Panagrolaimus*) colonized the plant litter during the first 4 days, they were rare at later stages of decomposition. Our findings agree with the conclusions drawn from other studies (Lorenzen, 1969; Hopper, 1970; Hopper et al., 1973; Alkemade et al., 1994; Zhou, 2001) that the detrital systems of marsh vegetation or temperate mangroves are dominated by two closely related genera, namely *Diplolaimelloides* and *Diplolaimella*. In our study, *Diplolaimelloides* attained its highest population density at early stages, while *Diplolaimella* abundance gradually overwhelmed the former at late stages of experiment. The temporal separation of the two genera suggested that the inter-genera competition occurred in the nematode succession during litter decomposition. At the end of experiment (day 128), *Terchellingia* with a *c–p* value of 3 became a third dominant genus, and accounted for a substantial portion of the abundance of bacterial-feeding nematodes. Thus, a shift of bacterial-feeding nematode genera occurred in plant litter containers, suggesting that microbial communities might have developed in response to chemical changes of residues at different phases of decomposition, and different nematode taxa that are associated with specific microbial communities may flourish as time lapses.

Previous studies in terrestrial ecosystems have found that the substrate in the organic matter decomposition changes with time from readily decomposable compounds to a proportionally greater recalcitrant fraction during decomposition (Chapin et al., 2002). Substrate is initially colonized by bacteria, whereas at later stages fungi gain more importance. This pattern of succession is reflected by the nematode community with a succession of bacterial feeders followed by fungal feeders (Freckman, 1988; Wang et al., 2004). However, in our study no fungal feeders were detected in all litter containers. This result is consistent with our previous field investigations (Wu et al., 2002; Chen et al., 2007) that the fugal feeders was an infrequent group (no more than 10% of the total nematodes) in the marshes of Chongming island. Neher et al. (2005) have compared nematode community composition among wetland, forest and agricultural ecosystems and found that the percentages of fungivores were least in wetland soil. Therefore, we speculated that the high water content of wetland soil might be a reason for the low abundance of fungivores. Moreover, the enrichment index kept low in all types of litter containers throughout the experiment because of the absence of fungal feeders and the low abundance of bacterial-feeding enrichment opportunists. It suggested that the enrichment index (EI) was not effective and provided litter information in analyzing nematode successional trends in wetland ecosystems with high water content.

Top–down control effects during litter decomposition have been reported previously (Santos et al., 1981; Ettema and Bongers, 1993; Lenz and Eisenbeis, 1998; Laakso and Setälä, 1999; Wang et al., 2004; Bjørnlund and Christensen, 2005). In this study, a predator-controlled process also probably existed during the succession of nematode trophic groups. Abundance of bacterial-feeding nematodes in plant litter containers peaked on day 16, followed by an increase in carnivore abundance between 32 and 64 days after burial. Abundance of bacterial feeders decreased between 32 and 64 days, suggesting that the carnivores might have preyed on part of the bacterial feeders. This conclusion is based on the fact that as the carnivore abundance declined 128 days after burial, the population of bacterial-feeding nematodes eventually recovered.

The majority of nematode genera colonizing plant litter occurred in the control, and most genera had similar densities in both plant litter and the control. This suggests that most nematode taxa responded to plant litter as habitats rather than food resources. Based on a finding that only five out of 59 nematode species are closely correlated with the leaf decomposition of *Spartina anglica*, Alkemade et al. (1993) have also concluded that most nematode species colonize the decomposing material as a living space.

4.2. Effects of plant litter type on decomposition processes and nematode communities

Many previous studies have found that plant species differ tremendously in litter quality they have produced (Vestergaard et al., 2001; Wardle et al., 2006), and that the decomposition rate is positively related to nitrogen concentration of litter (Taylor et al., 1989; Smith and Bradford, 2003). In our study, *Spartina* has higher initial nitrogen content and lower C:N ratio in its stems than *Phragmites*, and *Spartina* litter decomposed faster than *Phragmites*. This result is consistent with Windham (2001) who has found that *Spartina patens* (another species of genus *Spartina*) litter has lower C:N ratio and decomposes faster than *Phragmites* litter. The difference in decomposition rate between two plant litter types was observed mainly at the early stage of decomposition. In the first sampling after burial, *Spartina* litter decomposed much faster than *Phragmites* litter. Being consistent with Gessner (2000), we found that the *Phragmites* stem litter immobilized nitrogen at the end of the experiment, but the *Spartina* stem litter tended to release nitrogen as time lapsed. This suggested that the invasion of exotic *Spartina* could contribute to nutrient enrichment in the soil through supplying litter of higher quality.

Within a site, resource quality may be the most important factor affecting abundance of soil organisms (Blair et al., 1990). Previous studies have found that invertebrates are more abundant in fast decomposing litter than slow one (e.g. Blair et al., 1990; Goodfriend et al., 1998; Angradi et al., 2001; Barajas-Guzman and Alvarez-Sanchez, 2003). In terms of nematodes, Bjørnlund and Christensen (2005) have shown that nematode abundance is much higher in ash litter (C:N = 20) across all samplings than beech litter (C:N = 40). Vestergaard et al. (2001) have

reported that maize leaves (C:N = 20) support higher nematode densities than barley straw (C:N = 190). In this study, a higher nematode abundance was associated with the faster decomposing *Spartina* litter than the slower decomposing *Phragmites* litter, with significant differences occurring on day 16 and 32 after burial. The higher nematode abundance in *Spartina* than in *Phragmites* litter was mainly due to the presence of bacterivores, whereas the abundance of other trophic groups did not differ significantly between two litter types at all sampling times. Since the growth of bacterial-feeding nematodes requires a high bacterial biomass (Ingham et al., 1985; Griffiths et al., 1992; Georgieva et al., 2005), the higher bacterial-feeding nematode abundance may indicate a higher bacterial production associated with the faster decomposing *Spartina* litter. The results of this study support our previous investigation (Chen et al., 2007) that marshes dominated by *Spartina* are inhabited by a greater number of bacterivorous nematodes than the *Phragmites* marshes. It is therefore reasonable to assume that *Spartina* invasion increased the number of bacterivorous nematodes in soil through producing litter of higher quality than the native *Phragmite*. Ferris and Matute (2003) have found that a litter with a lower C:N ratio is more rapidly occupied by bacterivorous nematodes than litters with higher C:N ratios. However, our study revealed a similar fluctuation pattern of nematode abundances between two litter types.

Wardle et al. (2006) pointed out that there is no clear effect of litter quality on faunal diversity, and that high quality litter does not consistently support different levels of faunal diversity than low quality litter. Our study indicates a lower nematode generic diversity in *Spartina* than *Phragmites* litter containers, but the difference was not significant over the whole experiment. The lower values of maturity index and structure index in *Spartina* than *Phragmites* litter containers indicate a more degraded food web structure resulting from the faster litter decay.

It has been well documented that the varying litter quality is likely to cause changes in microbial communities (Conn and Dighton, 2000; Kourtev et al., 2002b; Mille-Lindblom et al., 2006; Aneja et al., 2006). In relation to soil fauna, Wardle et al (2006) have found that different litter types favor different faunal components, while Angradi et al. (2001) have found little effect of litter type on invertebrate composition. Georgieva et al. (2005) have pointed out that the composition of nematode has a clear relationship to initial resource quality. Our study indicates that a considerable difference in the structure of nematode community between two litter types only occurred at certain times of litter decomposition (from 8 to 32 days after burial). Our results suggest that the changes of faunal community structure caused by different litter types may be time-dependent, which could be the reason for discrepancies among previous studies.

Litter quality, through affecting the abundance, composition and activities of decomposer community, is the major factor controlling the rates of organic matter decomposition and nutrient release (Wardle and Lavelle, 1997; Blair et al., 1990). Mayer et al. (2005) have found that invasive grasses cause shifts in macrodetritivous communities, which in turn results in the changes in ecosystem functions such as decomposition. Our study confirmed the hypothesis that the invasion of *Spartina* may yield a greater number of bacterial nematodes by producing litter of higher quality than the native *Phragmites*. Many studies have proved that bacterial nematodes can stimulate bacterial growth and accelerate nutrient cycling (Ingham et al., 1985; Griffiths, 1994; Griffiths et al., 1999). The two dominant genera of bacterial nematodes in this study, namely *Diplolaimelloides* and *Diplolaimella*, have been studied extensively in terms of their roles in the detrital systems (Alkemade et al., 1992a, b; De Mesel et al., 2003, 2004). They are believed to play important roles in enhancing detritus decomposition by stimulating bacterial growth (Warwick, 1987; Alkemade et al., 1993). Therefore, we suggest that the invasion of *Spartina* into the Yangtze River estuary may eventually alter ecosystem functioning (e.g. enhancing decomposition rate) partly by stimulating the growth of bacterial-feeding nematodes. This influence of soil fauna on ecosystem functioning through indirect effects obviously needs further investigations.

Acknowledgments

We would like to thank Bin Zhao, Haiqiang Guo and Yongjian Gu for field sampling, Lifeng Jiang and Ronghao Peng for chemical analysis, and Ciyu Song and Xiaohong Wang for nematode sorting. This study was supported by NSFC funds (30570299 and 30370285), Science and Technology Department of Shanghai (04DZ19301 and 04QMX1405) and Ministry of Education (NCET-04-0360, 105063).

References

Abrams, B.I., Mitchell, M.J., 1980. Role of nematode–bacterial interactions in heterotrophic systems with emphasis on sewage sludge decomposition. Oikos 35, 404–410.

Alkemade, R., Wielemaker, A., de Jong, S.A., Sandee, A.J.J., 1992a. Experimental evidence for role of bioturbation by the marine nematode *Diplolaimella dievengatensis* in stimulation the mineralization of *Spartina anglica* detritus. Marine Ecology-Progress Series 90, 149–155.

Alkemade, R., Wielemaker, A., Hemminga, M.A., 1992b. Stimulation of decomposition of *Spartina anglica* leaves by the bacterivorous marine nematode *Diplolaimelloides bruciei* (Monhysteridae). Journal of Experimental Marine Biology and Ecology 159, 267–278.

Alkemade, R., Wielemaker, A., Hemminga, M.A., 1993. Correlation between nematode abundance and decomposition rate of *Spartina anglica* leaves. Marine Ecology-Progress Series 99, 293–300.

Alkemade, R., Wielemaker, A., Herman, P.M.J., Hemminga, M.A., 1994. Population dynamics of *Diplolaimelloides bruciei*, a nematode associated with the salt marsh plant *Spartina anglica*. Marine Ecology-Progress Series 105, 277–284.

Aneja, M.K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J.C., Schloter, M., 2006. Microbial colonization of beech and spruce litter—influence of decomposition site and plant litter

species on the diversity of microbial community. Microbial Ecology 52, 127–135.

Angradi, T.R., Hagan, S.M., Able, K.W., 2001. Vegetation type and the intertidal macroinvertebrate fauna of a brackish marsh: *Phragmites* vs. *Spartina*. Wetlands 21, 75–92.

Barajas-Guzman, G., Alvarez-Sanchez, J., 2003. The relationships between litter fauna and rates of litter decomposition in a tropical rain forest. Applied Soil Ecology 24, 91–100.

Belnap, J., Phillips, S.L., 2001. Soil biota in an ungrazed grassland: response to annual grass *(Bromus tectorum)* invasion. Ecological Applications 11, 1261–1275.

Bjørnlund, L., Christensen, S., 2005. How does litter quality and site heterogeneity interact on decomposer food webs of a semi-natural forest? Soil Biology & Biochemistry 37, 203–213.

Blair, J.M., Parmelee, R.W., Beare, M.H., 1990. Decay rates, nitrogen fluxes and decomposer communities in single and mixed species foliar litter. Ecology 71, 1976–1985.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Applied Soil Ecology 10, 239–251.

Chapin, F.S., Matson, P.A., Mooney, H.A., 2002. Principles of Terrestrial Ecosystem Ecology. Springer, New York, 436pp.

Chen, H., Li, B., Hu, J., Chen, J., Wu, J., 2007. Benthic nematode communities in the Yangtze River estuary as influenced by *Spartina alterniflora* invasions. Marine Ecology-Progress Series, in press.

Chen, H., Li, Y., Li, B., Chen, J., Wu, J., 2005. Impacts of exotic plant invasions on soil biodiversity and ecosystem processes. Biodiversity Science 13, 555–565.

Chen, Z., 2004. Ecological impacts of introduced *Spartina alterniflora* invasions in the coastal ecosystems of Chongming Dongtan, the Yangtze River estuary. Ph.D. Thesis, Fudan University, Shanghai.

Chen, Z., Li, B., Chen, J., 2004. Ecological consequences and management of *Spartina* spp. invasions in coastal ecosystems. Biodiversity Science 12, 280–289.

Cheng, X., Luo, Y., Chen, J., Lin, G., Chen, J., Li, B., 2006. Short-term C_4 plant *Spartina alterniflora* invasions change the soil carbon in C_3 plant-dominated tidal wetlands on a growing estuarine island. Soil Biology & Biochemistry 38, 3380–3386.

Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Plymouth.

Conn, C., Dighton, J., 2000. Litter quality influences on decomposition, ectomycorrhizal community structure and mycorrhizal root surface acid phosphatase activity. Soil Biology & Biochemistry 32, 489–496.

De Mesel, I., Derycke, S., Swings, J., Vincx, M., Moens, T., 2003. Influence of bacterivorous nematodes on the decomposition of cordgrass. Journal of Experimental Marine Biology and Ecology 296, 227–242.

De Mesel, I., Derycke, S., Moens, T., Van der Gucht, K., Vincx, M., Swings, J., 2004. Top–down impact of bacterivorous nematodes on the bacterial community structure: a microcosm study. Environmental Microbiology 6, 733–744.

Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6, 503–523.

Ehrenfeld, J.G., Scott, N., 2001. Invasive species and the soil: effects on organisms and ecosystem processes. Ecological Application 11, 1259–1260.

Ettema, C.H., Bongers, T., 1993. Characterization of nematode colonization and succession in disturbed soil using the maturity index. Biology and Fertility of Soils 16, 79–85.

Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. Applied Soil Ecology 23, 93–110.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied Soil Ecology 18, 13–29.

Freckman, D.W., 1988. Bacterivorous nematodes and organic matter decomposition. Agriculture Ecosystems and Environment 24, 195–218.

Fu, S.L., Coleman, D.C., Hendrix, P.F., Crossley, D.A., 2000. Responses of trophic groups of soil nematodes to residue application under conventional tillage and no-till regimes. Soil Biology & Biochemistry 32, 1731–1741.

Gee, J.M., Somerfield, P.J., 1997. Do mangrove diversity and leaf litter decay promote meiofaunal diversity? Journal of Experimental Marine Biology and Ecology 218, 13–33.

Georgieva, S., Christensen, S., Stevnbak, K., 2005. Nematode succession and microfauna-microorganism interactions during root residue decomposition. Soil Biology & Biochemistry 37, 1763–1774.

Gessner, M.O., 2000. Breakdown and nutrient dynamics of submerged *Phragmites* shoots in the littoral zone of a temperate hardwater lake. Aquatic Botany 66, 9–20.

Goodfriend, W.L., Olsen, M.W., Frye, R.J., 1998. Decomposition of seawater-irrigated halophytes: implications for potential carbon storage. Plant and Soil 202, 214–250.

Griffiths, B., Welschen, R., van Arendonk, J.J.C.M., Lambers, H., 1992. The effect of nitrate-nitrogen supply on bacteria and bacterial-feeding fauna in the rhizosphere of different grass species. Oecologia 91, 253–259.

Griffiths, B.S., 1994. Microbial-feeding nematodes and protozoa in soil: their effects on microbial activity and nitrogen mineralization in decomposing hotspots and the rhizosphere. Plant and Soil 164, 25–33.

Griffiths, B.S., Caul, S., 1993. Migration of bacterial-feeding nematodes, but not protozoa, to decomposing grass residues. Biology and Fertility of Soils 15, 201–207.

Griffiths, B.S., Bonkowski, M., Dobson, G., Caul, S., 1999. Changes in soil microbial community structure in the presence of microbial-feeding nematodes and protozoa. Pedobiologia 43, 297–304.

Hawkes, C.V., Wren, I.F., Herman, D.J., Firestone, M.K., 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecology Letters 8, 976–985.

Hopper, B.E., 1970. *Diplolaimelloides bruciei*: n. sp. (*Monhysteridae*: Nematoda), prevalent in marsh grass, *Spartina alterniflora* Loisel. Canadian Journal of Zoology 48, 573–575.

Hopper, B.E., Fell, J.W., Cefalu, R.C., 1973. Effect of temperature on life cycles of nematodes associated with the mangrove (*Rhizophora mangle*) detrital system. Marine Biology 23, 293–296.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of bacteria, fungi, and their nematode grazers: effect on nutrient cycling and plant growth. Ecological Monographs 55, 119–140.

Kourtev, P.S., Ehrenfeld, J.G., Haggblom, M., 2002a. Exotic plant species alter the microbial community structure and function in the soil. Ecology 83, 3152–3166.

Kourtev, P.S., Ehrenfeld, J.G., Huang, W.Z., 2002b. Enzyme activities during litter decomposition of two exotic and two native plant species in hardwood forests of New Jersey. Soil Biology & Biochemistry 34, 1207–1218.

Laakso, J., Setälä, H., 1999. Population- and ecosystem-level effects of predation on microbial-feeding nematodes. Oecologia 120, 279–286.

Lenz, R., Eisenbeis, G., 1998. The vertical distribution of decomposition activity and of litter-colonizing nematodes in soils under different tillage. Pedobiologia 42, 193–204.

Lorenzen, S., 1969. Freilebende meeresnematoden aus dem Schlickwatt und den Salzwieesen der Nordseekuste. Veröffentlichung des Institus für Meeresforschung, Bremerhaven 11, 195–238.

Mayer, P.M., Tunnell, S.J., Engle, D.M., Jorgensen, E.E., Nunn, P., 2005. Invasive grass alters litter decomposition by influencing macrodetritivores. Ecosystems 8, 200–209.

McSorley, R., Frederick, J.J., 1999. Nematode population fluctuations during decomposition of specific organic amendments. Journal of Nematology 31, 37–44.

Mille-Lindblom, C., Fischer, H., Tranvik, L.J., 2006. Litter-associated bacteria and fungi—a comparison of biomass and communities across lakes and plant species. Freshwater Biology 51, 730–741.

Mooney, H.A., Drake, J.A., 1986. Ecology of Biological Invasions of North America and Hawaii. Springer, New York, 321pp.

Neher, D.A., Wu, J., Barbercheck, M.E., Anas, O., 2005. Ecosystem type affects interpretation of soil nematode community measures. Applied Soil Ecology 30, 47–64.

Odum, E.P., 1985. Trends in expected in stressed ecosystems. Bioscience 35, 419–422.

Pradhan, G.B., Senapati, B.K., Dash, M.C., 1988. Relationship of soil nematode populations to carbon: nitrogen in tropical habitats and their role in the laboratory decomposition of litter amendments. Revue D Ecologia ET De Biologie Du Sol 25, 59–76.

Qin, P., Zhong, C.X., 1992. Applied Studies on *Spartina*. Ocean Press.

Ravit, B., Ehrenfeld, J.G., Haggblom, M.M., 2003. A comparison of sediment microbial communities associated with *Phragmites australis* and *Spartina alterniflora* in two brackish wetlands of New Jersey. Estuaries 26, 465–474.

Rice, D., Rooth, J., Stevenson, J.C., 2000. Colonization and expansion of *Phragmites australis* in upper Chesapeake Bay tidal marshes. Wetlands 20, 280–299.

Ruess, L., 2003. Nematode soil faunal analysis of decomposition pathways in different ecosystems. Nematology 5, 179–181.

Santos, P.F., Philips, J., Whitford, W.G., 1981. The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62, 664–669.

Smith, V.C., Bradford, M.A., 2003. Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. Applied Soil Ecology 24, 197–203.

Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70, 97–104.

Vestergaard, P., Rønn, R., Christensen, S., 2001. Reduced particle size of plant material does not stimulate decomposition, but affects the microbivorous microfauna. Soil Biology & Biochemistry 33, 1805–1810.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., Matson, P.A., 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238, 802–804.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change. American Scientist 84, 218–228.

Wang, K.H., McSorley, R., Marshall, A.J., Gallaher, R.N., 2004. Nematode community changes associated with decomposition of *Crotalaria juncea* amendment in litterbags. Applied Soil Ecology 27, 31–45.

Wang, Q., An, S., Ma, Z., Zhao, B., Chen, J., Li, B., 2006. Invasive *Spartina alterniflora*: biology, ecology and management. Acta Phytotaxonomica Sinica 44, 559–588.

Wardle, D.A., Lavelle, P., 1997. Linkages between soil biota, plant litter quality and decomposition. In: Giller, K.E., Cadisch, G. (Eds.), Driven by Nature-Plant Litter Quality and Decomposition. CAB International, Wallingford, pp. 107–120.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633.

Wardle, D.A., Yeates, G.W., Barker, G.M., Bonner, K.I., 2006. The influence of plant litter diversity on decomposer abundance and diversity. Soil Biology & Biochemistry 38, 1052–1062.

Warwick, R.M., 1987. Meiofauna: their role in marine detrital systems. Detritus and microbial ecology in aquaculture. In: ICLARM Conference Proceedings, vol. 14, pp. 282–295.

Wasilewake, L., 1992. Participation of soil nematodes in grass litter decomposition under diverse biocenotic conditions of meadows. Ekologia Polske 40, 75–100.

Wasilewska, L., Paplinska, E., Zielinski, J., 1981. The role of nematodes in decomposition of plant material in a rye field. Pedobiologia 21, 182–191.

Windham, L., 2001. Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in brackish tidal marshes of New Jersey, USA. Wetlands 21, 179–188.

Wolfe, B.E., Klironomos, J.N., 2005. Breaking new ground: soil communities and exotic plant invasion. Bioscience 55, 477–487.

Wu, J., Fu, C., Chen, S., Chen, J., 2002. Soil faunal response to land use: effect of estuarine tideland reclamation on nematode communities. Applied Soil Ecology 21, 131–147.

Yeates, G.W., Williams, P.A., 2001. Influence of three invasive weeds and site factors on soil microfauna in New Zealand. Pedobiologia 45, 367–383.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habitats in soil nematode families and genera-an outline for soil ecologists. Journal of Nematology 25, 315–331.

Zhou, H., 2001. Effects of leaf litter addition on meiofaunal colonization of azoic sediments in a subtropical mangrove in Hong Kong. Journal of Experimental Marine Biology and Ecology 256, 99–121.