Exotic plant influences soil nematode communities through litter input

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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 bacterivorous 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.

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...
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; Anjea 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′01″ N, 121°58′29″ 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 × 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 45 μm 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, enrichment of the food web. Food webs become enriched trajectory is an indicator of the level of primary enrichment of the food web; $k_s$ is the weighting assigned to the guild Ba2 as shown in Table 2, $n_s$ is the abundance of nematodes in the guild Ba2 which indicates the basal characteristic of the food web; $k_c$ is the weighting assigned to the guild Ba1, $n_c$ is the abundance of nematodes in the guild Ba1 which represents a structured condition of the food web; $c–p$ values, and their life strategies, nematodes were designated a colonizer–persister ($c–p$) value ranging from 1 to 5 according to Bongers (1990). MI = $\sum t(i)f(i)$, where $t(i)$ 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 (SI) = $100 \times \sum k_n$, where $k_n$ is the weighting assigned to the guild Ba2 as shown in Table 2. $n_s$ is the abundance of nematodes in the guild Ba2 which indicates the basal characteristic of the food web; $k_s$ is the weighting assigned to guilds Ba3–Ba5, Al2–Al3, Om4–Om5 and Ca3–Ca4, $n_s$ is the abundance of nematodes in these guilds which represents a structured condition of the food web; $k_c$ is the weighting assigned to the guild Ba1, $n_c$ is the abundance of nematodes in the guild Ba1 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

<table>
<thead>
<tr>
<th>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</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spartina alterniflora</strong></td>
</tr>
<tr>
<td>% weigh remaining   Dec. rate</td>
</tr>
<tr>
<td>Day 4              80.9 (0.8)$^a$ 0.053 (0.002)$^a$</td>
</tr>
<tr>
<td>Day 8              76.6 (1.3)$^a$ 0.014 (0.004)$^a$</td>
</tr>
<tr>
<td>Day 16             73.9 (0.8)$^a$ 0.004 (0.003)$^a$</td>
</tr>
<tr>
<td>Day 32             70.0 (0.5)$^b$ 0.003 (0.000)$^b$</td>
</tr>
<tr>
<td>Day 64             66.6 (0.8)$^a$ 0.002 (0.000)$^a$</td>
</tr>
<tr>
<td>Day 128            59.9 (0.3)$^a$ 0.002 (0.000)$^a$</td>
</tr>
</tbody>
</table>

| **Phragmites australis**                                    |
| % weigh remaining   Dec. rate | % C remaining | % N remaining | C:N ratio |
| 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)$^b$ | 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)$^b$ | 98.7 (0.3)$^b$ | 98.7 (4.7) | 155.3 (5.5)$^b$ |
| Day 64             91.1 (0.4)$^b$ 0.002 (0.000)$^b$ | 94.5 (0.6)$^b$ | 136.3 (20.2) | 112.3 (10.2) |
| Day 128            85.0 (0.4)$^b$ 0.001 (0.000)$^b$ | 87.7 (0.3)$^b$ | 171.8 (15.1)$^b$ | 80.2 (3.0) |

Two-way ANOVA (P-value): Plant: 0.000, Time: 0.000, Plant*Time: 0.000

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

<table>
<thead>
<tr>
<th>Nematode taxa</th>
<th>c-p value</th>
<th>Guild (weighting)</th>
<th>Day 4</th>
<th>Day 8</th>
<th>Day 16</th>
<th>Day 32</th>
<th>Day 64</th>
<th>Day 128</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>SA</td>
<td>PA</td>
<td>C</td>
<td>SA</td>
<td>PA</td>
<td>C</td>
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<tr>
<td><strong>Bacterial feeders</strong></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td><em>Amphidelus</em></td>
<td>4</td>
<td>Ba₄ (3.2)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td><em>Anoplostoma</em></td>
<td>2</td>
<td>Ba₂ (0.8)</td>
<td>&lt;0.1</td>
<td>0.4</td>
<td>0.2</td>
<td>0.6</td>
<td>1.1</td>
<td>1.6</td>
</tr>
<tr>
<td><em>Daptonema</em></td>
<td>2</td>
<td>Ba₂ (0.8)</td>
<td>0.2</td>
<td>0.4</td>
<td>0.5</td>
<td>0.7</td>
<td>0.3</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Desmoscolex</em></td>
<td>4</td>
<td>Ba₄ (3.2)</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.1</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.5</td>
</tr>
<tr>
<td><em>Diplolaimella</em></td>
<td>2</td>
<td>Ba₃ (0.8)</td>
<td>1.3</td>
<td>0.4</td>
<td>0.5</td>
<td>2.2</td>
<td>2.1</td>
<td>2.2</td>
</tr>
<tr>
<td><em>Diploscolomeloides</em></td>
<td>2</td>
<td>Ba₂ (0.8)</td>
<td>4.6</td>
<td>3.6</td>
<td>0.5</td>
<td>23.9</td>
<td>3.1</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td><em>Eucephalobus</em></td>
<td>2</td>
<td>Ba₂ (0.8)</td>
<td></td>
<td></td>
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<tr>
<td><strong>Algal feeders</strong></td>
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</tr>
<tr>
<td><em>Chromadorina</em></td>
<td>3</td>
<td>Al₃ (1.8)</td>
<td></td>
<td></td>
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<tr>
<td><em>Ethmolaimus</em></td>
<td>3</td>
<td>Al₃ (1.8)</td>
<td></td>
<td></td>
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<tr>
<td><em>Hypodontolaimus</em></td>
<td>3</td>
<td>Al₃ (1.8)</td>
<td>0.1</td>
<td>0.2</td>
<td>0.9</td>
<td>1.7</td>
<td>0.3</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Neochromadora</em></td>
<td>3</td>
<td>Al₃ (1.8)</td>
<td>0.2</td>
<td>0.2</td>
<td>0.5</td>
<td>0.6</td>
<td>&lt;0.1</td>
<td>1.6</td>
</tr>
<tr>
<td><em>Paracanthonchus</em></td>
<td>2</td>
<td>Al₃ (0.8)</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.3</td>
<td>&lt;0.1</td>
<td>0.5</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td><em>Polyssigma</em></td>
<td>3</td>
<td>Al₃ (1.8)</td>
<td>0.1</td>
<td>&lt;0.1</td>
<td>0.3</td>
<td>0.2</td>
<td>&lt;0.1</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Psycholaimellus</em></td>
<td>3</td>
<td>Al₃ (1.8)</td>
<td>0.2</td>
<td>&lt;0.1</td>
<td>0.1</td>
<td>&lt;0.1</td>
<td>0.3</td>
<td>0.6</td>
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<tr>
<td><strong>Plant feeders</strong></td>
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<tr>
<td><em>Lenonchium</em></td>
<td>4</td>
<td></td>
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<tr>
<td><em>Tylenchus</em></td>
<td>2</td>
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<tr>
<td><strong>Omnivores</strong></td>
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<tr>
<td><em>Aporcelaimus</em></td>
<td>5</td>
<td>Om₅ (5.0)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Dorylaimus</em></td>
<td>4</td>
<td>Om₄ (3.2)</td>
<td>0.1</td>
<td>0.9</td>
<td>0.1</td>
<td>0.6</td>
<td>0.7</td>
<td>1.4</td>
</tr>
<tr>
<td><strong>Carnivores</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Oncholaimus</em></td>
<td>4</td>
<td>Ca₄ (3.2)</td>
<td>&lt;0.1</td>
<td>0.4</td>
<td>&lt;0.1</td>
<td>0.1</td>
<td>8.2</td>
<td>12.2</td>
</tr>
<tr>
<td><em>Spaeroalaimus</em></td>
<td>3</td>
<td>Ca₃ (1.8)</td>
<td>&lt;0.1</td>
<td>0.1</td>
<td>0.2</td>
<td>0.6</td>
<td>0.3</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td><em>Tripyloides</em></td>
<td>3</td>
<td>Ca₃ (1.8)</td>
<td></td>
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</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Variables</th>
<th>Error df</th>
<th>Treatment (2 df)</th>
<th>Time (5 df)</th>
<th>Treatment*time (10 df)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>Total density</td>
<td>54</td>
<td>89.1</td>
<td>0.000</td>
<td>35.1</td>
</tr>
<tr>
<td>Shannon-Weaver diversity</td>
<td>54</td>
<td>49.3</td>
<td>0.000</td>
<td>18.5</td>
</tr>
<tr>
<td>Maturity index</td>
<td>54</td>
<td>64.1</td>
<td>0.000</td>
<td>25.7</td>
</tr>
<tr>
<td>Bacterial feeders</td>
<td>54</td>
<td>87.8</td>
<td>0.000</td>
<td>39.7</td>
</tr>
<tr>
<td>Algal feeders</td>
<td>54</td>
<td>1.7</td>
<td>0.188</td>
<td>3.7</td>
</tr>
<tr>
<td>Plant feeders</td>
<td>54</td>
<td>0.9</td>
<td>0.399</td>
<td>2.8</td>
</tr>
<tr>
<td>Omnivores</td>
<td>54</td>
<td>0.6</td>
<td>0.530</td>
<td>2.6</td>
</tr>
<tr>
<td>Carnivores</td>
<td>54</td>
<td>5.9</td>
<td>0.005</td>
<td>12.6</td>
</tr>
</tbody>
</table>

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

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* \((Diplolaimelloides \text{ representing } 66.84\% \text{ and } Diplolaimella \text{ 21.19}\% \text{ of the total \text{abundance}})\) and *Phragmites* litter \((Diplolaimelloides \text{ representing } 40.59\% \text{ and } Diplolaimella \text{ 35.96}\% \text{ of the total \text{abundance}})\). *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.](image-url)
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).
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 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 abundance 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; Bjornlund 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 calcitrant 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 fungal 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; Björnlund 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, Bjornlund 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 Phragmites. 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 macrodetritivorous 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.

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