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Effects of *Spartina alterniflora* invasion on benthic nematode communities in the Yangtze Estuary

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ABSTRACT: Invasions of exotic plant species in estuaries have occurred worldwide, and may profoundly affect native biodiversity and estuarine ecosystem functioning. To assess the effect of plant invasions on benthic meiofauna, we compared the nematode communities in marshes dominated, respectively, by invasive *Spartina alterniflora* and native *Scirpus mariqueter* and *Phragmites australis* at 3 local sites over 2 seasons in the Yangtze River estuary, PR China. *S. alterniflora* stands had generally lower nematode trophic diversity than the stands of the 2 native plants, suggesting that the exotic plant led to a simplified benthic food web. The relative abundance of bacterial-feeding nematodes tended to increase in *S. alterniflora* marshes compared to *P. australis* marshes. The increased bacterial-feeding nematodes in *S. alterniflora* stands are likely to reflect the altered decomposition processes, rates and pathways, which may, in turn, modify belowground nutrient cycling of the estuarine ecosystems. The dissimilarity in nematode community structure between *S. alterniflora* and *S. mariqueter* marshes was smaller than that between *S. alterniflora* and *P. australis* marshes, and the dissimilarity between *Spartina*-invaded and native marshes was even smaller than between the 2 native plant marshes. It is suggested that the detection of the ecological consequences of plant invasions depends on which native plant species is considered. Site effects were generally detected in the comparison of sediment properties and nematodes among 3 plant marshes. Sediment water content, electrical conductivity, bacterial biomass and litter biomass were identified as the most important factors in the shaping of the nematode communities.

KEY WORDS: Community structure · Cordgrass · C_3 plant · C_4 plant · Diversity · Exotic plant · Nematodes · Wetlands

INTRODUCTION

Estuaries are widely recognized as an important ecosystem type for a wide range of marine communities, and play major roles in conserving biodiversity (Levin et al. 2001). However, they are undergoing rapid environmental changes caused by anthropogenic activities, including eutrophication, non-nutrient pollutants, overfishing, habitat alteration, global climate, and species invasions (Levin et al. 1996, Jackson et al. 2001). Compared with other ecosystems, estuaries have become one of the most heavily invaded ecosystems in the world (Cohen & Carlton 1998, Grosholz 2002). Invasions of exotic plant species in the estuaries have occurred worldwide (Ruiz et al. 1997), and may profoundly affect native biodiversity and estuarine ecosystem functioning (Posey 1988, Posey et al. 1993, Talley & Levin 2001, Cheng et al. 2006).

Cordgrasses (plants in the genus *Spartina* Schreb.) are successful invaders in coastal wetlands and have spread across the globe (Chen et al. 2004, Levin et al. 2006). *S. alterniflora* has caused considerable evolutionary and ecological consequences to global estuaries (Wang et al. 2006). It originated on the east and gulf coasts of the USA and spread to many coastal and estuarine regions of the world, including tidal marshes on the west coast of North America, as well as in Australia, France, The Netherlands, UK, New Zealand and China (Kriwoken & Hedge 2000, Neira et al. 2005). Many previous studies have reported that

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Spartina invasions influence benthic communities when compared with unvegetated mudflats (Zipperer 1996, O'Connell 2002, Neira et al. 2005), and several studies have compared benthic macrofaunal communities of the invasive *Spartina* and those of native vegetated marshes (Hedge & Kriwoken 2000, Chen et al. 2005, Neira et al. 2005), and yielded inconsistent results. In Little Swanport estuary, Tasmania, Hedge & Kriwoken (2000) found that species richness and total abundance of macrofauna in invasive *S. anglica* and native saltmarshes do not differ significantly. Chen et al. (2005) reported that the replacement of *Scirpus mariqueter* by *S. alterniflora* results in reduced macroinvertebrate density and species diversity in salt marshes of Chongming Island in the Yangtze River estuary, China. Neira et al. (2005) found higher macrofaunal species richness in *Spartina* hybrid-invaded patches relative to native *Salicornia* marshes in San Francisco Bay, USA, but no differences in total macrofaunal density were found. These studies suggest that the responses of benthic macrofauna to *Spartina* spp. invasions are quite variable, depending on the vegetation type and invaded sites (Neira et al. 2005). However, knowledge is lacking about the impacts of *Spartina* invasions on benthic meiofaunal communities such as nematodes.

In the present study, we compared the benthic nematode communities of *Spartina alterniflora*-invaded marshes and 2 native plant marshes (*Scirpus mariqueter* and *Phragmites australis*) at 3 local sites over 2 seasons in the Yangtze River estuary, China. *S. alterniflora* was intentionally introduced into the Yangtze River estuary to promote sediment accretion and growth of salt marshes in the late 1980s, as it has a number of biological traits promoting that goal, including fast growth, dense rhizomal network, and great biomass. This species spread to most of the wetlands in the Yangtze River estuary and is now excluding native plant species by forming dense monocultures.

Nematodes were selected to evaluate the effects of plant invasion in this study, because they have close relationships with vegetations (Ingham et al. 1985, Yeates 1999). In addition, they are the most abundant metazoan taxon, comprising 60 to 90% of the total fauna in estuarine sediments (Coull 1999). They play a central role in the detrital food web (Moore & de Ruiter 1991) and are assumed to function as regulators of decomposition and mineralization processes (Coleman 1985). Thus, nematode communities can provide unique insights into many aspects of ecosystem processes and have been increasingly used as bioindicators of ecosystem functioning (Ritz & Trudgill 1999, Wu et al. 2002). In the present study, we analyzed the density, diversity, community structure, and trophic composition of benthic nematodes, and related the various sediment properties and vegetation characteristics to nematode communities. The specific objectives of the study were: (1) to compare the nematode communities between the invasive *Spartina alterniflora* and the native plant marshes and (2) to increase our limited knowledge of the effects of plant invasions on benthic nematodes in estuarine ecosystems.

MATERIALS AND METHODS

Study sites. The study was carried out in the tidal marshes of the Yangtze River estuary, PR China. Tidal marshes from 3 sites in the estuary were chosen for study: Dongtan of Chongming Island, Jiuduansha Islands, and Nanhui (Fig. 1). At these sites, *Scirpus mariqueter* (hereafter *Scirpus*) and *Phragmites australis* (hereafter *Phragmites*) were the most common marsh plant species; both are C_3 plants and native to the Yangtze River estuary. *Scirpus* occurs in middle and high marshes, and *Phragmites* in high marshes (Gao & Zhang 2006). Since the tidal marshes in the study area are now heavily infested with introduced C_4 plant *Spartina alterniflora* (hereafter *Spartina*), the 2 native plant species are rapidly being replaced by this exotic plant. *Spartina* expands its range mainly by colonizing the high marsh zones, but also by extending to the middle marshes.

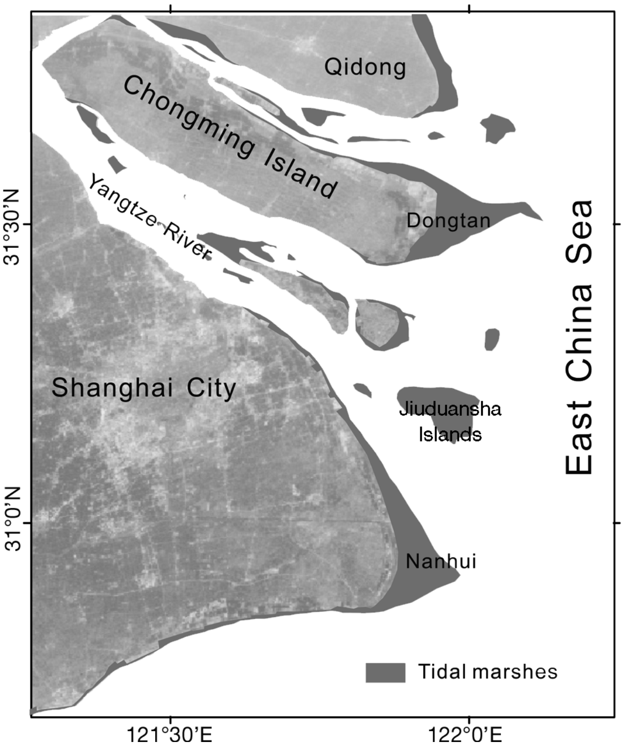

Fig. 1. Location of 3 sampling sites (Dongtan, Jiuduansha, and Nanhui) in the Yangtze River estuary, PR China

In Dongtan marshes, small *Spartina* patches were first found in 1995. *Spartina* was intentionally introduced to Jiuduansha in 1997, to attract shorebirds away from flightpaths in and out of Pudong Airport. Both Dongtan and Jiuduansha are national nature reserves. Comparatively, Nanhui received more disturbance than the other 2 sites. In Nanhui marshes, *Spartina* was first transplanted to promote sediment accretion in the late 1980s. At each study site, 3 meadows at more-or-less similar tidal elevations were selected for sampling in the tidal marshes dominated by *Spartina*, *Scirpus*, and *Phragmites*, respectively. A global positioning system (GPS) was used to ensure the consistency of sampling location in different sampling seasons.

Sampling design and environmental conditions. Samplings were carried out in March and August 2004. Sediment samples were collected using a modified O'Connor split corer (3.2 cm diameter, 10 cm depth). In each meadow, 4 transects of 20 m in length parallel to the coastline were established with a random starting point. Ten sediment cores taken at 2 m intervals along each transect were bulked into a single composite sample to reduce variance associated with the aggregated spatial pattern of benthic nematodes. Thus, 4 composite samples were obtained at each meadow as 4 independent replicates. Each of the composite sediment samples was well homogenized by hand and then split into 4 parts: 150 g of sediment were fixed in 4% formalin for nematode community analysis, 50 g of sediment were used for measurement of bacterial biomass, 100 g were dried to constant weight at 80°C to determine water content, and the rest of each sub-sample was air-dried and analyzed for physical and chemical properties, including organic matter, pH, electrical conductivity, total nitrogen, total phosphorus (measured at the Institute of Soil Science, Chinese Academy of Sciences), and sediment grain composition (measured at the Cold and Arid Environmental and Engineering Research Institute, Chinese Academy of Sciences). The biomass of sedimentary bacteria was determined by counting bacteria stained with fluoroscein isothiocyanate (FITC) by direct microscopic observation (Babiuk & Paul 1970). Standing shoots of plants were harvested in two 25 × 25 cm quadrats along each transect, for the determination of shoot biomass. Surface litter within the quadrat was also collected for the determination of litter biomass. There were no standing shoots of *Scirpus* in March and no surface litter of *Scirpus* in August.

Nematodes. Nematodes were extracted by flotation in Ludox TM in the laboratory (Griffiths et al. 1990). After counting the total numbers of nematodes under a dissecting microscope, about 100 nematode specimens per sample were randomly selected and identified to genus level in glycerol mounts.

Nematodes were assigned to 6 trophic groups (algal feeder, plant feeder, bacterial feeder, fungal feeder, carnivore, and omnivore) according to Yeates et al. (1993). Several ecological indices were calculated to assess the nematode community. The Shannon-Wiener diversity index (H') was calculated at the genus level. The trophic diversity index (TD) was calculated based on the trophic group ratios.

Statistical analysis. The effects of plant type, site, and sampling time on nematodes, sediment properties, and plant characteristics were examined using a 3-way factorial ANOVA. Least-square-difference (LSD) tests were used after the 3-way ANOVA to detect for the differences in environmental variables, nematode genus number, density, Shannon-Wiener diversity index, trophic diversity index, and feeding group proportions between the marshes dominated by different plant species at each site in March and August, respectively. To meet the assumptions of ANOVA, the proportional data were arcsine-square-root transformed and the numeric data were log transformed prior to statistical analyses when necessary. All analyses were executed using the statistical package Statistica (Version 6.0, StatSoft).

All multivariate analyses were undertaken using the PRIMER (Version 5.2) software package (Clarke & Warwick 1994). Using a ranked similarity matrix based on Bray-Curtis similarity measures of $\log(x + 1)$ transformed nematode genera data, an ordination plot was produced by non-metric multidimensional scaling (MDS). The 2-way crossed analysis of similarity (ANOSIM) (Clarke & Warwick 1994) was used to test vegetation and site effects on the nematode community. The BIO-ENV procedure (Clarke & Ainsworth 1993) was used to identify the environmental variables that best explained variation in nematode communities at the genus level and the functional group level, respectively. BIO-ENV uses Spearman's rank correlation between the resulting ranked similarity matrices of nematofauna and correlation-based PCA (principal component analysis) of the normalized environmental variables.

RESULTS

The magnitude or directions of differences in most sediment conditions between *Spartina* and 2 native plant marshes varied among the 3 sites and between 2 sampling seasons (Table 1). Most sediment properties were significantly different between *Spartina* and the 2 native plant marshes, except at Jiuduansha in August (Table 1). In March, *Spartina* generally had greater shoot biomass, but lower litter biomass than both *Phragmites* and *Scirpus*, and the magnitude of the

Table 1. Sediment properties and plant characteristics of *Spartina alterniflora* (SA) and 2 native plant marshes (SM: *Scirpus mariqueter*; PA: *Phragmites australis*) at 3 study sites measured in March and August 2004. Shown are the mean values with SE in parentheses (n = 4). Different superscripted letters (a,b,c) indicate significant differences between plant species at each sampling site ($p < 0.05$). EC: electrical conductivity

	Dongtan			Jiuduansha			Nanhui		
	SA	SM	PA	SA	SM	PA	SA	SM	PA
March 2004									
Sand (%)	15.9 (1.7)^{a}	63.0 (2.9)^{b}	43.3 (1.7)^{c}	33.8 (8.3)^{a}	44.7 (5.8)^{a}	63.6 (10.2)^{b}	37.4 (8.9)^{a}	16.0 (0.6)^{b}	57.0 (6.5)^{c}
Silt (%)	78.3 (2.2)^{a}	32.6 (2.7)^{b}	50.8 (1.8)^{c}	59.9 (8.2)^{a}	52.3 (4.5)^{a}	31.2 (10.4)^{b}	57.7 (8.8)^{a}	79.9 (0.7)^{b}	38.1 (6.4)^{c}
Clay (%)	5.8 (0.5)	4.4 (0.5)	5.9 (0.5)	6.2 (0.5)^{a}	3.0 (1.8)^{b}	5.2 (0.5)^{a}	4.9 (0.2)	4.1 (0.3)	4.9 (0.5)
pH	8.0 (0.01)^{a}	8.2 (0.04)^{b}	8.0 (0.01)^{a}	7.9 (0.05)^{a}	8.1 (0.05)^{b}	8.2 (0.06)^{b}	8.0 (0.07)^{a}	8.1 (0.05)^{a}	8.4 (0.08)^{b}
Water content (%)	91.5 (2.5)^{a}	37.9 (2.0)^{b}	51.9 (0.4)^{c}	74.6 (10.5)^{a}	53.8 (2.6)^{b}	39.0 (3.4)^{c}	61.1 (8.4)^{a}	98.4 (4.2)^{b}	45.5 (4.4)^{c}
EC (mS cm^{-1})	5.42 (0.14)^{a}	2.86 (0.20)^{b}	3.89 (0.12)^{c}	2.94 (0.32)^{a}	2.59 (0.10)^{a}	1.34 (0.21)^{b}	3.49 (0.37)^{a}	2.28 (0.09)^{b}	0.95 (0.11)^{c}
Organic matter (mg g^{-1})	21.5 (0.99)^{a}	8.0 (0.95)^{b}	14.5 (0.18)^{c}	17.0 (2.23)^{a}	13.9 (0.67)^{ab}	11.1(2.06)^{b}	13.9 (2.03)	18.0 (0.46)	19.1 (3.46)
Total nitrogen (mg g^{-1})	1.20 (0.05)^{a}	0.42 (0.05)^{b}	0.82 (0.01)^{c}	0.95 (0.11)^{a}	0.79 (0.05)^{a}	0.59 (0.13)^{b}	0.75 (0.11)^{a}	1.17 (0.02)^{b}	0.94 (0.15)^{ab}
Total phosphorus (mg g)	0.84 (0.02)^{a}	0.63 (0.01)^{b}	0.73 (0.01)^{c}	0.75 (0.02)	0.72 (0.02)	0.70 (0.03)	0.67 (0.02)^{a}	0.78 (0.01)^{b}	0.70 (0.01)^{a}
Bacterial biomass (µg g^{-1})	432 (23)^{a}	230 (10)^{b}	276 (43)^{b}	333 (40)^{a}	212 (16)^{b}	207 (8)^{b}	386 (24)^{a}	570 (87)^{b}	230 (9)^{c}
Shoot biomass (g m^{-2})	2243 (189)^{a}	0 (0)^{b}	966 (160)^{c}	2244 (84)^{a}	0 (0)^{b}	956 (92)^{c}	1486 (192)^{a}	0 (0)^{b}	1311 (204)^{a}
Litter biomass (g m^{-2})	41 (6)^{a}	148 (37)^{b}	135 (13)^{b}	93 (16)	101 (27)	108 (25)	25 (9)^{a}	55 (12)^{a}	334 (24)^{b}
August 2004									
Sand (%)	22.9 (3.6)^{a}	64.0 (2.7)^{b}	28.5 (1.6)^{a}	37.4 (8.5)	44.5 (6.2)	50.5 (8.3)	39.5 (8.9)^{a}	19.4 (1.8)^{b}	22.7 (2.9)^{ab}
Silt (%)	72.1 (3.5)^{a}	32.6 (2.5)^{b}	66.6 (1.9)^{a}	58.2 (8.4)	52.0 (6.5)	45.4 (8.4)	55.9 (9.0)^{a}	75.5 (1.8)^{b}	71.8 (3.6)^{ab}
Clay (%)	5.0 (0.2)	3.4 (0.2)	4.9 (0.4)	4.3 (0.3)	3.5 (0.4)	4.1 (0.2)	4.7 (0.1)	5.1 (0.2)	5.6 (0.8)
pH	8.0 (0.03)^{a}	8.2 (0.03)^{b}	8.1 (0.01)^{ab}	8.0 (0.05)	8.0 (0.05)	8.1 (0.06)	8.1 (0.03)^{a}	8.1 (0.02)^{a}	7.9 (0.03)^{b}
Water content (%)	77.0 (3.3)^{a}	37.4 (0.6)^{b}	43.0 (0.4)^{b}	60.3 (7.4)^{a}	47.5 (2.1)^{ab}	41.6 (2.9)^{b}	52.7 (6.5)^{a}	119.7 (2.4)^{b}	67.7 (5.9)^{c}
EC (mS cm^{-1})	4.82 (0.30)^{a}	1.88 (0.12)^{b}	3.82 (0.07)^{c}	1.64 (0.18)^{a}	2.10 (0.13)^{b}	1.57 (0.06)^{a}	3.92 (0.40)	4.35 (0.17)	3.84 (0.18)
Organic matter (mg g^{-1})	21.2 (1.35)^{a}	9.0 (0.41)^{b}	16.5 (0.25)^{a}	17.4 (2.05)	14.3 (0.96)	15.0 (1.70)	13.9 (1.48)^{a}	18.0 (0.45)^{a}	29.6 (4.14)^{b}
Total nitrogen (mg g^{-1})	1.11 (0.06)^{a}	0.45 (0.02)^{b}	0.91 (0.02)^{a}	0.87 (0.10)	0.77 (0.07)	0.76 (0.11)	0.70 (0.10)^{a}	1.14 (0.03)^{b}	1.46 (0.16)^{b}
Total phosphorus (mg g^{-1})	0.85 (0.03)^{a}	0.64 (0.00)^{b}	0.82 (0.01)^{a}	0.74 (0.01)	0.71 (0.01)	0.76 (0.06)	0.68 (0.01)^{a}	0.83 (0.02)^{b}	0.81 (0.02)^{b}
Bacterial biomass (µg g^{-1})	399 (27)^{a}	141 (9)^{b}	204 (24)^{c}	310 (49)	258 (10)	350 (56)	152 (16)^{a}	297 (21)^{b}	201 (32)^{a}
Shoot biomass (g m^{-2})	2575 (531)^{a}	564 (18)^{b}	1878 (141)^{a}	2881 (266)^{a}	497 (78)^{b}	2058 (377)^{c}	1346 (219)^{a}	335 (45)^{b}	2095 (162)^{c}
Litter biomass (g m^{-2})	58 (33)^{a}	0 (0)^{b}	17 (2)^{a}	87 (35)^{a}	0 (0)^{b}	142 (32)^{c}	1.8 (1.1)^{a}	0 (0)^{b}	112 (22)^{c}

differences varied across sites. In August, *Spartina* had greater shoot and litter biomass than *Scirpus*, but the differences in shoot and litter biomass between *Spartina* and *Phragmites* were not consistent at different sites. A 3-way ANOVA shows that all parameters for sediment properties and plant characteristics significantly differed among 3 marsh types (Table 2). Except for the percent clay content, all other parameters were significantly affected both by an interactive effect between time and plant and by an interactive effect between site and plant (Table 2).

A total of 59 nematode genera were identified in our study, more than half of which were bacterial feeders (Table 3). Nematode generic richness, density, values of H', and TD indices were significantly affected by the plant species (Table 4), and were also significantly affected by an interactive effect between site and plant. All feeding groups were affected by plant type, except for algal feeders (Table 4). The interactions between plant type and site were significant for all nematode feeding groups (Table 4).

No significant difference was observed in nematode genus number between *Spartina*-invaded and *Phragmites* marshes at any site in the 2 sampling seasons (Fig. 2a). At Dongtan and Jiuduansha, the differences in genus number between *Spartina* and *Scirpus* marshes varied with seasons. At Nanhui, *Spartina*-invaded marshes had lower nematode genus number than *Scirpus* marshes in both seasons. Total nematode density was significantly higher in *Spartina*-invaded marshes than in the 2 native plant marshes at Dongtan, but not at Jiuduansha and Nanhui (Fig. 2b). No significant differences in Shannon-Wiener diversity index were found between *Spartina*-invaded and *Phragmites* marshes, except at Jiuduansha in August (Fig. 2c). *Scirpus* marshes had significantly lower Shannon-Wiener diversity than *Spartina*-invaded marshes at Nanhui in both seasons. At Dongtan and Jiuduansha, the differences in Shannon-Wiener diversity between *Spartina*

Table 2. Summary of 3-way ANOVA testing the effects of plant species (*Spartina alterniflora*, *Scirpus mariqueter*, *Phragmites australis*), site, and sampling time on sediment properties and plant characteristics. Shown are *F*-values with significance levels in parentheses (significant differences $p < 0.05$ are indicated in bold)

Variable	Error df	Plant type (2 df)	Site (2 df)	Time (1 df)	Plant × Site (4 df)	Plant × Time (2 df)	Site × Time (2 df)	Plant × Site × Time (4 df)
Sand	54	**8.73 (<0.001)**	**8.80 (<0.001)**	2.96 (0.091)	**17.94 (<0.001)**	**8.24 (<0.001)**	0.69 (0.505)	0.76 (0.558)
Silt	54	**8.02 (<0.001)**	**8.02 (<0.001)**	3.67 (0.061)	**16.94 (<0.001)**	**8.14 (<0.001)**	0.42 (0.662)	0.69 (0.599)
Clay	54	**7.58 (0.001)**	2.40 (0.101)	0.19 (0.668)	1.76 (0.150)	1.96 (0.151)	1.10 (0.342)	1.33 (0.272)
pH	54	**13.63 (<0.001)**	1.74 (0.185)	0.96 (0.331)	**5.22 (0.001)**	**10.75 (0.000)**	**5.73 (0.006)**	**9.68 (<0.001)**
Water content	54	**30.18 (<0.001)**	**25.52 (<0.001)**	0.26 (0.611)	**43.83 (<0.001)**	**4.45 (0.016)**	**5.19 (0.009)**	1.82 (0.139)
Electrical conductivity	54	**50.63 (<0.001)**	**93.03 (<0.001)**	**9.42 (0.003)**	**31.46 (<0.001)**	**33.88 (< 0.001)**	**68.39 (< 0.001)**	**7.98 (<0.001)**
Organic matter	54	**11.90 (<0.001)**	**8.81 (<0.001)**	**5.88 (0.019)**	**21.32 (<0.001)**	**3.28 (0.045)**	0.21 (0.814)	0.63 (0.640)
Total nitrogen	54	**6.24 (0.004)**	**10.84 (<0.001)**	1.89 (0.175)	**27.53 (<0.001)**	**4.30 (0.018)**	0.27 (0.766)	0.59 (0.672)
Total phosphorus	54	**6.31 (0.003)**	1.49 (0.235)	**10.22 (0.002)**	**33.22 (<0.001)**	**7.14 (0.002)**	1.66 (0.199)	0.13 (0.971)
Microbial biomass	54	**12.26 (<0.001)**	0.49 (0.615)	**19.89 (<0.001)**	**22.90 (<0.001)**	**5.53 (0.007)**	**20.98 (< 0.001)**	**3.36 (0.016)**
Shoot biomass	54	**2477 (<0.001)**	**5.16 (0.009)**	**1486 (<0.001)**	**6.41 (<0.001)**	**1067 (<0.001)**	3.18 (0.050)	0.40 (0.808)
Litter biomass	54	**134.35 (<0.001)**	**13.40 (<0.001)**	**305.80 (<0.001)**	**27.00 (<0.001)**	**98.53 (<0.001)**	**6.70 (0.003)**	**9.44 (<0.001)**

and *Scirpus* marshes varied with seasons. *Spartina*-invaded marshes had lower nematode trophic diversity than *Phragmites* marshes in all comparisons, with significant differences occurring at Dongtan in August, at Jiuduansha in March, and at Nanhui in both seasons (Fig. 2d). *Spartina* marshes had significantly lower nematode trophic diversity than *Scirpus* marshes at Dongtan in both seasons and at Jiuduansha in March, while no significant differences were observed in other cases.

The dominant trophic groups were bacterial feeders and algal feeders for all types of marshes (Fig. 3). Percentages of algal feeders (Fig. 3a) exhibited significant differences among plant species at Dongtan and Nanhui, while inconsistent differences between *Spartina* and the 2 native marshes were observed across sites and seasons. In most comparisons, the relative abundance of plant feeders (Fig. 3b) and fungal feeders (Fig. 3c) in *Spartina* marshes was generally similar to that in *Scirpus* marshes, but lower than that in *Phragmites* marshes. In terms of the bacterial feeders (Fig. 3d), *Spartina* marshes tended to have more bacterial feeders than *Phragmites* marshes at all sites and in both seasons, with significant differences occurring at Dongtan and Jiuduansha in both seasons and at Nanhui in March. *Spartina* marshes also had more bacterial feeders than *Scirpus* marshes, except at Nanhui in August. The percentages of carnivores (Fig. 3e) and omnivores (Fig. 3f) exhibited inconsistent trends among different types of vegetation across sites and between seasons.

Two-way crossed ANOSIM revealed highly significant plant (Global test: $R = 0.748$, $p = 0.001$) and site effects (Global test: $R = 0.830$, $p = 0.001$) on nematode communities (Table 5). The dissimilarities in nematode communities were smaller between *Spartina* and *Scirpus* marshes (ANOSIM, pairwise test: $R = 0.679$, $p = 0.001$) than between *Spartina* and *Phragmites* marshes (ANOSIM, pairwise test: $R = 0.790$, $p = 0.001$). The non-metric MDS analyses show that all plots for *Spartina* were completely separated from those for *Phragmites* marshes, but partly overlapped with those for *Scirpus* marshes (Fig. 4). The greatest dissimilarities of nematode communities among pairs of plants were found between 2 naturally vegetated marshes (ANOSIM, pairwise test: $R = 0.852$, $p = 0.001$). The nematode community dissimilarity among pairs of sites was the smallest between Dongtan and Jiuduansha (ANOSIM, pairwise test: $R = 0.731$, $p = 0.001$).

BIO-ENV analysis was conducted at both the genus level and the functional group level (Table 6). The correlation coefficients of the best single environmental variable and combinational variables were generally low (coefficients < 0.25). Water content, electrical conductivity, bacterial biomass, and litter biomass were correlated with nematode composition in the analysis

Table 3. Benthic nematodes in *Spartina alterniflora* (SA) and 2 native marshes (SM: *Scirpus mariqueter*; PA: *Phragmites australis*) sampled in March and August 2004. Shown are the mean values (expressed as individuals per 10 g dry sediment) with SE in parentheses (n = 12)

Nematode taxa	March			August		
	SA	SM	PA	SA	SM	PA
Algal feeders						
Chromadorina	1.0 (0.6)	0.7 (0.7)	1.5 (0.9)	0.7 (0.5)	0.3 (0.3)	0.1 (0.1)
Chromadorita	12.0 (6.0)	1.3 (0.5)	0.4 (0.4)			
Ethmolaimus	30.0 (15.4)			24.4 (10.7)		
Hypodontolaimus	17.7 (6.9)	34.0 (13.1)	17.1 (7.1)	8.7 (2.9)	21.5 (6.4)	25.8 (10.3)
Neochromadora	6.0 (2.8)	1.5 (0.8)	5.6 (2.5)	5.9 (4.0)	0.3 (0.3)	1.0 (0.5)
Paracanthonchus	3.2 (1.2)	5.5 (2.2)	4.5 (1.7)	1.7 (1.3)	0.9 (0.8)	0.6 (0.2)
Polysigma	17.9 (3.3)	135.6 (45.7)	3.5 (1.4)	14.1 (4.0)	27.6 (7.8)	4.0 (1.4)
Prochromadora	0.4 (0.2)	0.8 (0.7)	1.5 (0.9)	0.4 (0.3)		0.1 (0.1)
Ptycholaimellus	2.3 (1.1)	2.7 (2.0)	5.5 (2.6)	3.8 (1.7)	0.4 (0.3)	9.5 (3.8)
Plant feeders						
Dolichodorus	0.6 (0.3)	0.0 (0.0)	8.0 (1.9)	0.7 (0.4)	0.1 (0.1)	35.6 (8.6)
Helicotylenchus			2.0 (1.6)			0.3 (0.3)
Hirschmanniella			0.2 (0.2)		2.9 (1.0)	0.9 (0.7)
Hoplolaimidae[a]	0.3 (0.3)		0.7 (0.7)			3.0 (1.5)
Lenonchium	1.5 (1.0)	0.4 (0.3)	0.9 (0.5)	1.1 (0.5)	10.7 (4.0)	0.4 (0.2)
Bacterial feeders						
Alaimus			1.1 (1.1)			0.1 (0.1)
Amphidelus	0.3 (0.3)	0.05 (0.05)	1.7 (0.6)	0.8 (0.8)		1.5 (0.5)
Anoplostoma	12.5 (2.1)	22.9 (4.3)	17.4 (2.9)	9.0 (2.4)	12.4 (3.3)	5.2 (0.9)
Antomicron	0.5 (0.3)					
Calligyras			0.1 (0.1)			
Campylaimus	0.7 (0.6)	0.2 (0.2)	0.1 (0.1)			
Cobbia	15.6 (10.1)				14.6 (7.2)	
Daptonema	23.8 (4.0)	33.9 (9.6)	4.1 (1.4)	14.6 (6.2)	98.9 (43.3)	2.7 (1.8)
Deontolaimus	0.2 (0.2)		0.6 (0.6)			0.4 (0.4)
Desmoscolex	25.5 (5.2)	7.7 (4.7)	7.9 (2.6)	4.0 (1.2)	3.7 (1.9)	1.2 (0.5)
Diplolaimella	15.4 (4.0)	17.2 (4.9)	9.6 (2.3)	12.8 (5.7)	12.6 (4.9)	3.4 (0.8)
Diplolaimelloides	0.8 (0.5)	2.4 (1.5)	1.9 (0.9)	0.4 (0.2)	1.5 (0.7)	0.6 (0.4)
Eucephalobus			0.2 (0.2)	0.03 (0.03)		0.9 (0.6)
Eumorpholaimus	18.5 (5.9)	0.6 (0.4)	1.2 (0.8)	17.1 (9.1)		
Halalaimus	21.2 (3.6)	10.7 (3.2)	7.3 (1.5)	8.3 (2.4)	0.8 (0.4)	3.8 (1.4)
Haliplectus	8.0 (4.0)	0.1 (0.1)	27.0 (6.7)	19.0 (12.7)	0.1 (0.1)	28.1 (9.5)
Leptolaimus	22.8 (9.7)	2.9 (1.2)	0.1 (0.1)	11.4 (6.1)	1.7 (0.8)	0.04 (0.04)
Leptosomatum	0.1 (0.1)					
Linhomoeus	0.5 (0.5)			4.8 (3.0)		
Metalinhomoeus	5.7 (2.0)	11.4 (5.0)	2.4 (1.7)	6.5 (2.3)	8.7 (4.0)	0.5 (0.4)
Microlaimus	4.4 (2.4)	11.3 (3.4)	0.4 (0.4)	1.8 (0.8)	1.1 (0.7)	
Monhystera		0.7 (0.4)	4.3 (1.7)			0.1 (0.1)
Mononchoides		0.2 (0.2)	0.1 (0.1)			0.1 (0.1)
Oxystomina	1.3 (1.0)	1.7 (0.8)	0.3 (0.2)	2.2 (1.3)	0.9 (0.5)	0.4 (0.2)
Parodontophora	28.0 (6.8)	36.5 (8.5)	10.1 (2.8)	31.9 (7.5)	78.1 (24.2)	10.7 (4.2)
Rhabditidae[a]	0.3 (0.3)	0.1 (0.1)				0.1 (0.1)
Rhabditis		0.4 (0.4)	0.3 (0.2)	0.6 (0.4)	0.1 (0.1)	0.6 (0.3)
Terschellingia	40.1 (16.0)	24.6 (11.5)	6.0 (2.7)	31.7 (12.6)	2.2 (2.1)	27.1 (16.3)
Theristus	18.7 (5.4)	70.0 (29.6)	0.1 (0.1)	7.5 (2.4)	59.6 (25.7)	0.4 (0.4)
Wieseria				0.2 (0.2)		0.2 (0.1)
Fungal feeders						
Tylenchidae 1[a]		0.6 (0.6)	21.4 (6.0)	0.03 (0.03)	0.2 (0.2)	11.6 (3.4)
Tylenchidae 2[a]	0.1 (0.1)	9.2 (3.9)	16.3 (11.9)		0.1 (0.1)	5.8 (2.3)
Tylencholaimus			15.7 (9.2)			2.6 (1.8)
Carnivorous nematodes						
Adoncholaimus				2.0 (1.1)		
Belbolla	0.2 (0.2)					
Calytronema						0.4 (0.2)
Nygolaimus	0.2 (0.2)	1.6 (1.2)	1.7 (1.6)	0.2 (0.1)	1.3 (0.8)	1.4 (0.9)
Oncholaimus	0.3 (0.3)		0.5 (0.3)	0.4 (0.2)		0.3 (0.3)
Sphaerolaimus	3.1 (1.0)	8.7 (4.0)	0.7 (0.3)	5.8 (1.2)	2.3 (0.7)	3.6 (1.6)
Tripyloides	15.5 (7.0)	9.7 (3.0)	0.1 (0.1)	0.9 (0.6)	2.6 (0.9)	0.1 (0.1)
Viscosia	6.1 (3.7)	5.6 (2.5)	1.1 (0.7)	1.7 (0.8)	8.9 (4.9)	0.7 (0.7)
Omnivorous nematodes						
Dorylaimidae[a]	0.1 (0.1)		2.4 (1.8)	0.2 (0.1)	1.1 (0.6)	1.9 (1.0)
Dorylaimoides			3.2 (2.2)			2.1 (1.3)
Dorylaimus	2.9 (1.0)	6.2 (2.1)	7.4 (2.5)	3.4 (1.4)	3.4 (1.0)	5.4 (3.1)
Eudorylaimus						0.3 (0.2)

[a] Contains 1 genus

Table 4. Summary of 3-way ANOVA testing the effects of plant type (*Spartina alterniflora*, *Scirpus mariqueter*, *Phragmites australis*), site, and sampling time on nematode genus number, density, diversity indices, and trophic group proportions. Shown are *F*-values with significance levels in parentheses (significant differences $p < 0.05$ are indicated in bold). *H'*: Shannon-Wiener diversity index; TD: trophic diversity index; feeding habits of nematodes are abbreviated as: Al, algal feeders; Pl, plant feeders; Ba, bacterial feeders; Fu, fungal feeder; Ca, carnivorous nematodes; Om, omnivorous nematodes

Variable	Error df	Plant type (2 df)	Site (2 df)	Time (1 df)	Plant × Site (4 df)	Plant × Time (2 df)	Site × Time (2 df)	Plant × Site × Time (4 df)
Genus number	54	**4.07 (0.023)**	**4.76 (0.012)**	2.84 (0.098)	**6.99 (<0.001)**	1.55 (0.222)	0.28 (0.758)	0.45 (0.769)
Density	54	**8.16 (<0.001)**	**83.61 (<0.001)**	**13.91 (<0.001)**	**16.76 (<0.001)**	0.57 (0.568)	1.36 (0.265)	2.00 (0.107)
H'	54	**4.60 (0.014)**	2.91 (0.063)	**16.76 (<0.001)**	**7.07 (<0.001)**	0.86 (0.428)	0.29 (0.749)	1.64 (0.179)
TD	54	**28.21 (<0.001)**	**5.46 (0.007)**	3.46 (0.068)	**6.36 (<0.001)**	1.75 (0.183)	**10.24 (<0.001)**	2.00 (0.108)
Al (%)	54	2.00 (0.145)	0.01 (0.990)	0.08 (0.780)	**6.88 (<0.001)**	**3.39 (0.041)**	3.08 (0.054)	2.49 (0.054)
Pl (%)	54	**61.31 (<0.001)**	**15.92 (<0.001)**	**56.30 (<0.001)**	**3.28 (0.018)**	**11.54 (<0.001)**	**4.68 (0.013)**	1.06 (0.385)
Ba (%)	54	**35.32 (<0.001)**	**9.61 (<0.001)**	**4.63 (0.036)**	**10.10 (<0.001)**	**6.67 (0.003)**	**20.10 (<0.001)**	**4.52 (0.003)**
Fu (%)	54	**73.77 (<0.001)**	**3.33 (0.043)**	**5.49 (0.023)**	**5.18 (0.001)**	2.08 (0.135)	1.92 (0.157)	**6.33 (<0.001)**
Ca (%)	54	**11.91 (<0.001)**	1.02 (0.366)	2.06 (0.157)	**5.06 (0.002)**	1.25 (0.294)	1.31 (0.277)	**4.78 (0.002)**
Om (%)	54	**6.34 (0.003)**	0.00 (0.998)	1.44 (0.235)	**8.08 (<0.001)**	2.10 (0.133)	**4.67 (0.013)**	1.57 (0.196)

both at the genus level and the functional group level. The silt percentage of the sediment was only correlated with the nematode community at the functional group level. When the analysis was restricted to the single best variable, water content was the most influential variable.

DISCUSSION

Nematode communities as affected by plant species

In the present study, we found no significant differences in nematode generic richness or in Shannon-Wiener diversity between *Spartina*-invaded and *Phragmites* marshes. This is consistent with the study of Yuhas et al. (2005), in which *Spartina* and *Phragmites* marshes were found to support similar taxon richness of benthic fauna (both macrofauna and meiofauna). However, our results are inconsistent with those of Angradi et al. (2001), who found that the taxon richness of macroinvertebrates is greater in *Spartina* marshes than in *Phragmites*-invaded marshes in southern New Jersey. Gratton & Denno (2005) found that the changes in arthropod trophic structure after the replacement of *Spartina* by *Phragmites* are mainly caused by the changes in detritivores, herbivores, and carnivores. In this study, *Spartina*-invaded marshes generally had lower nematode trophic diversity than *Phragmites* marshes, with bacterivores tending to be more common. The nematode community structure was found to be distinctly different in *Spartina* versus *Phragmites* marshes, as revealed by MDS and ANOSIM analyses. Such differences in community composition have also been found for microbial communities (Ravit et al. 2003) and arthropod communities (Gratton & Denno 2005) on salt marshes in New Jersey, where *Phragmites* is an invader. Therefore, it can be speculated that the invasion of *Spartina* and *Phragmites* into each other affects both aboveground and belowground ecosystem processes.

Few studies have compared faunal communities between *Spartina* and *Scirpus*. One recent study, conducted at Dongtan of Chongming Island, shows that the macroinvertebrate species richness and diversity tends to be lower in the *Spartina* community than in the *Scirpus* community (Chen et al. 2005). This pattern was not observed for nematode generic richness and diversity. Chen et al. (2005) found that invasions of *Spartina* into the *Scirpus* community alter the trophic group structure of macroinvertebrates. However, the differences in nematode trophic group proportions between *Spartina* and *Scirpus* marshes gen-

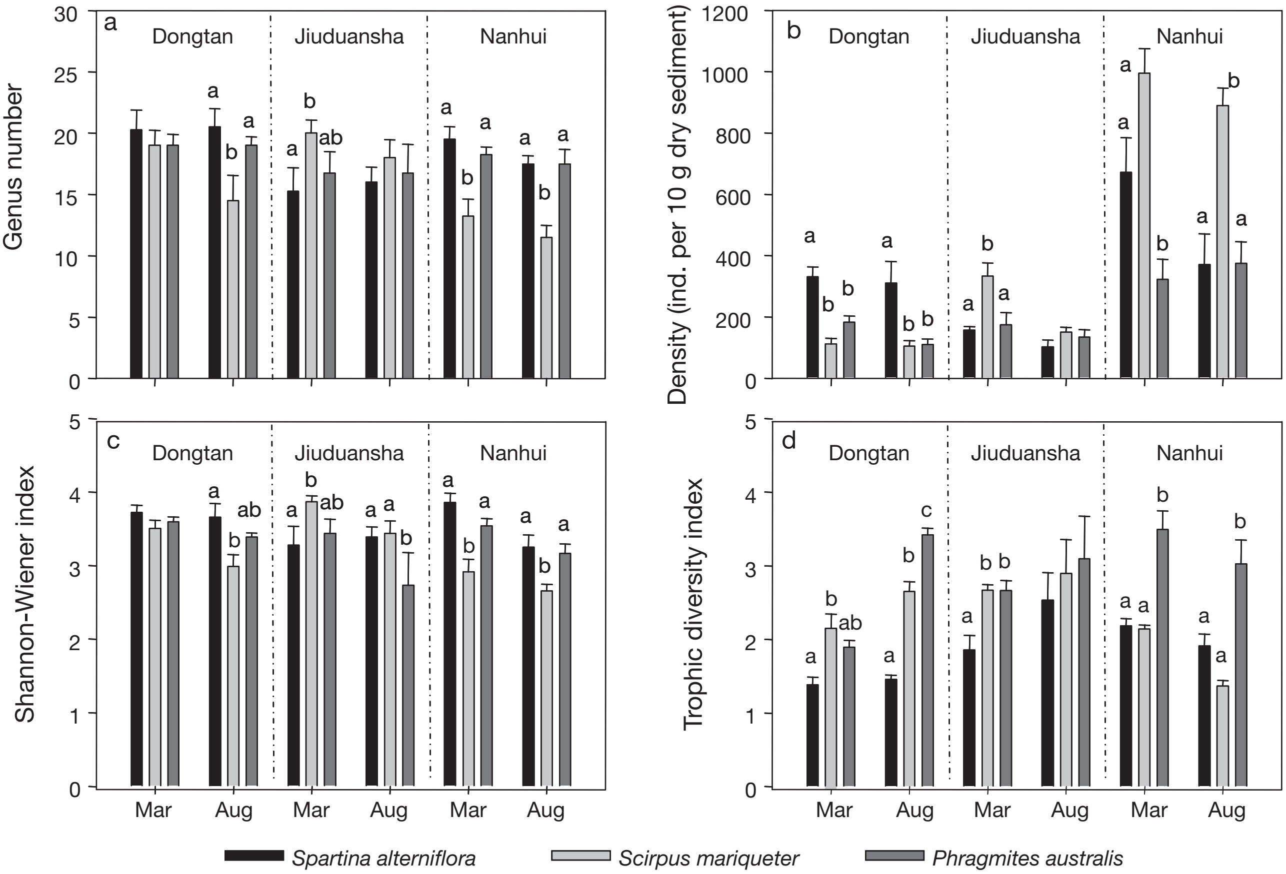

Fig. 2. (a) Nematode genus number, (b) nematode density, (c) Shannon-Wiener diversity index, and (d) trophic diversity index in the 3 marshes dominated respectively by *Spartina alterniflora*, *Scirpus mariqueter*, and *Phragmites australis* at 3 sites in March and August 2004. Error bars indicate standard error of the mean (n = 4). Different letters above bars (a,b,c) indicate significant differences between plant species at each sampling site and in each season ($p < 0.05$)

Table 5. Two-way crossed ANOSIM for testing the vegetation and site effects on nematode communities, and the differences in nematode communities between plants and between sampling sites. SA: *Spartina alterniflora*; SM: *Scirpus mariqueter*; PA: *Phragmites australis*

	Global test *R*	Pairwise test *R*	Significance level (%)
Plants	0.748		0.1
SA and SM		0.679	0.1
SA and PA		0.790	0.1
SM and PA		0.852	0.1
Sites	0.830		0.1
Dongtan and Jiuduansha		0.731	0.1
Dongtan and Nanhui		0.915	0.1
Jiuduansha and Nanhui		0.856	0.1

erally varied across sites and between seasons. Therefore, this study did not reveal an apparent difference in nematode taxon richness, diversity, or trophic composition between *Spartina* and *Scirpus* marshes.

Table 6. Results from BIO-ENV analysis of nematode communities (at the genus level and the functional group level) and environmental variables. The best combination of environment variables includes all variables marked with 'y' and the single best variable is indicated by 'X'. Correlation coefficients are given for the best combination of environmental variables and for the best single environmental variable

	Genus level	Functional group level
Combination	0.165	0.242
Single	0.159	0.161
Sand		
Silt		y
Clay		
pH		
Water content	X, y	X, y
Electrical conductivity	y	y
Organic matter		
Total nitrogen		
Total phosphorus		
Bacterial biomass	y	y
Shoot biomass		
Litter biomass	y	y

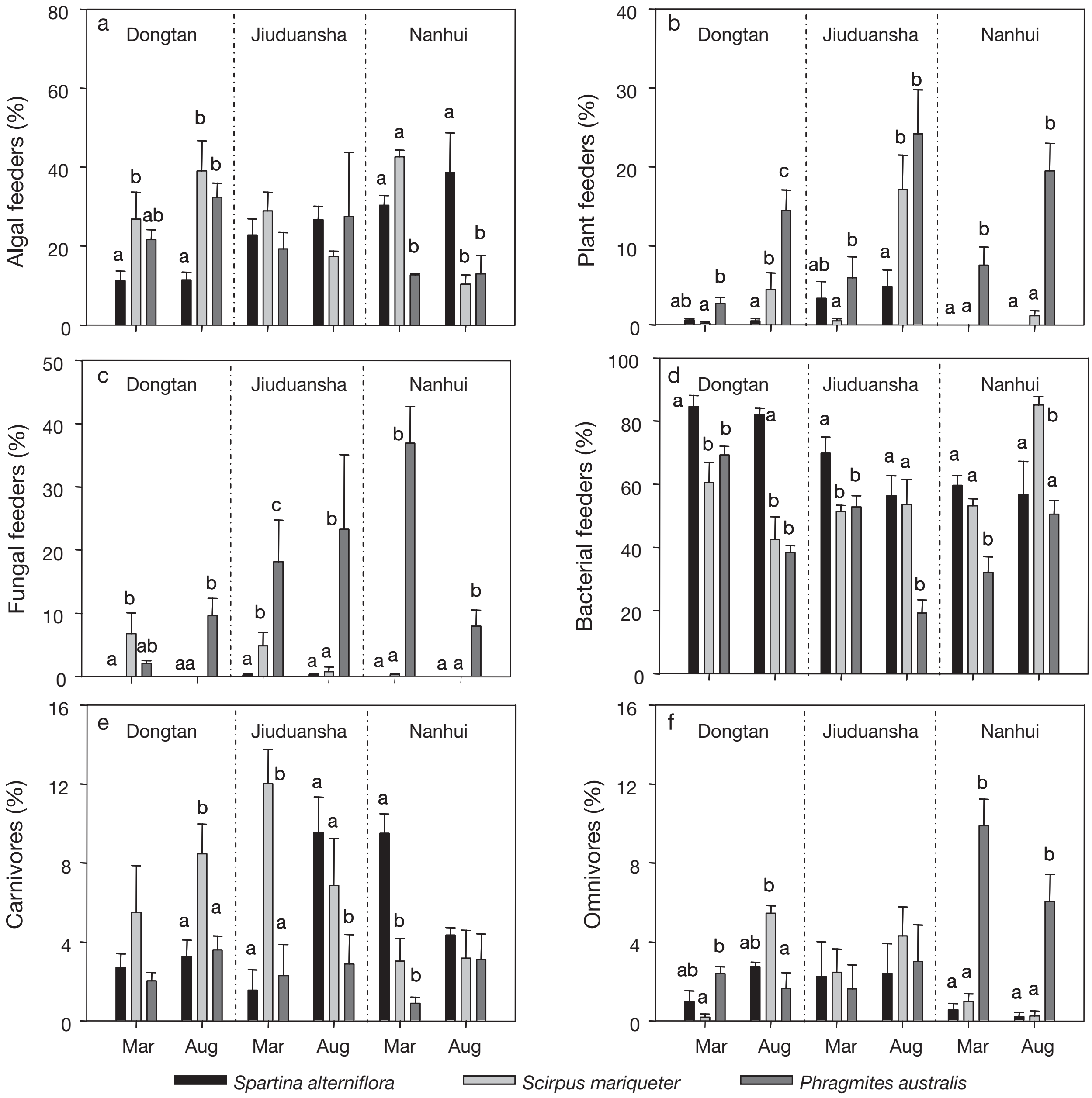

Fig. 3. Proportions of nematode feeding groups in the 3 marshes dominated, respectively, by *Spartina alterniflora*, *Scirpus mariqueter*, and *Phragmites australis* at 3 sites in March and August 2004: (a) algal feeders, (b) plant feeders, (c) fungal feeders, (d) bacterial feeders, (e) carnivores, and (f) omnivores. Error bars indicate standard error of the mean (n = 4). Different letters above bars (a,b,c) indicate significant differences between plant species at each sampling site and in each season ($p < 0.05$)

Comparatively, the dissimilarity in the nematode community structure between *Spartina* and *Phargmites* marshes was greater than that between *Spartina* and *Scirpus* marshes, and the dissimilarity between *Spartina*-invaded and native marshes was even smaller than that between the 2 native plant marshes. In fact, the effects of *Spartina* invasions on nematode communities depended on which native plant species were considered. A similar result has been reported from a terrestrial system invaded by *Bromus*. Belnap & Phillips (2001) found that the soil biota in plots from *Hilaria* to *Bromus* generally respond to the *Bromus* invasion in an opposite manner compared with plots from *Stipa* to *Bromus*. Therefore, it is important to consider native plants when the ecological consequences of plant invasions are assessed.

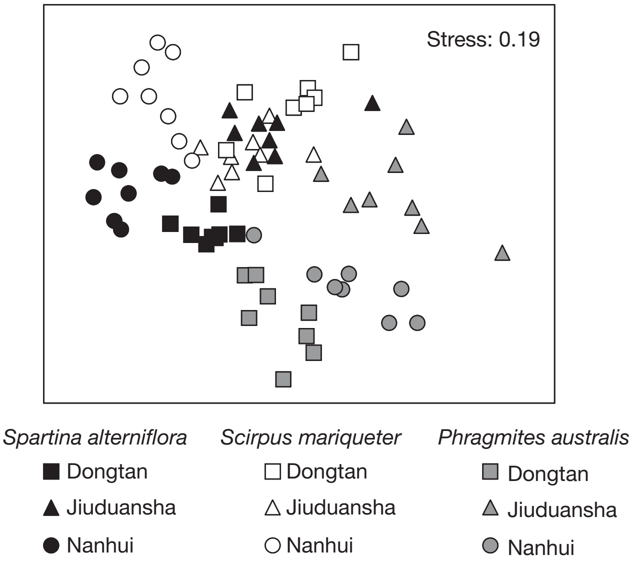

Fig. 4. Non-metric multidimensional scaling ordination of nematode communities in the 3 marshes dominated, respectively, by *Spartina alterniflora*, *Scirpus mariqueter*, and *Phragmites australis* at 3 sites. All replicate samples are included for analysis

Effects of *Spartina alterniflora* invasions across sites

Based on differences in morphology, physiology, and phenology, it has been documented that the replacement of extant marsh vegetation by exotic vascular plants may be expected to alter physical and chemical sediment properties (Talley & Levin 2001). In the present study, the directions and magnitudes of the differences in sediment properties between *Spartina* and 2 native plant marshes were not consistent among different sites. Our data suggest that the impacts of *Spartina* invasion on sediment conditions in estuarine marshes of the Yangtze River are site specific and are driven by both plant invasion and natural environmental variation.

In the present study, the invasive *Spartina* generally had greater live shoot biomass than both *Scirpus* and *Phragmites* at all sites. Previous studies have indicated that, in the home regions of *Spartina*, the aboveground vegetation biomass of *Spartina* is smaller than that of *Phragmites* (Angradi et al. 2001, Osgood et al. 2003). The present study implies that the exotic plants grow better in the introduced range than in their natural range.

In terms of the impacts of invasive plants on animal communities, site effects have been documented previously. Hanson et al. (2002) found that *Phragmites* invasion impacts fishes in some habitats, but not others. Posey et al. (2003) demonstrated that the effect of macrophyte type is smaller than that of location in controlling macrofaunal distributions. Robertson & Weis (2005) also found apparent between-site variations in their study. Yeates & Williams (2001) investigated the influence of invasive weeds on nematode communities in New Zealand and pointed out that site is an important factor determining the impact of the invasive plant on nematodes. In this study, prominent site effects were also found in the relationship between nematodes and vegetation types, especially in the comparison of abundance, generic richness, diversity, and most feeding group proportions between *Spartina* and *Scirpus* marshes. However, patterns of nematode generic richness and diversity were generally similar between *Spartina* and *Phragmites* marshes at all the sites, and *Spartina*-invaded marshes had generally lower trophic diversity, a higher proportion of bacterial feeders, but a lower proportion of fungal feeders than *Phragmites* marshes. Therefore, the contribution of site effects varied with different extant plant species. Ravit et al. (2003) reported that the differences in microbial populations between plant species depend on the disturbance level of different sites. In this study, the nematode community dissimilarity among pairs of sites was the smallest between Dongtan and Jiuduansha. This is probably because Nanhui was more disturbed than the other sites. In addition to the disturbance level, the histories of plant invasion at different sites may also influence the site effects.

Although several studies have documented the roles of seasonality in the evaluation of invasive plant effects on fauna (Angradi et al. 2001, Talley & Levin 2001, Osgood et al. 2003), our present study revealed that seasonal variation has less effect on nematode communities than sites and plant species.

Underlying mechanisms and trophic implications

There were significant physiological and morphological differences between *Spartina* and the 2 native plants, such as photosynthesis pathways (C_4 vs. C_3) and salt tolerance (*Spartina* can excrete salts using its salt glands). The differences in these attributes are expected to change belowground biological communities and their composition (Wardle et al. 2004, Zedler & Kercher 2004), including nematodes. However, the present study revealed that the dissimilarity in nematode community structure between 2 C_3 plants (*Phragmites* and *Scirpus*) was greater than that between C_3 and C_4 plants (native plants and *Spartina*). This suggests that the plant attributes, such as photosynthesis pathways, may not be as important as expected in structuring belowground communities.

Two mechanisms have been proposed to explain how plant identity affects belowground biodiversity. First, different plant species may differ in their abilities to control resources available to organisms, through altering biotic and abiotic soil properties (Levin & Talley 2000, Talley & Levin 2001, Neira et al. 2005). Second, different plant species with different suites of traits may return organic matter of differing qualities or quantities to the soil (Díaz et al. 2004). In the present study, sediment water content, electrical conductivity, bacterial biomass, and litter biomass were identified as the most influential factors in shaping nematode communities, suggesting that both mechanisms might coexist in structuring nematode communities in the Yangtze River estuary. Wardle (2006) hypothesized that plant species drive soil organisms through litter production rather than through rhizosphere exudation. Although the rhizosphere characteristics were not investigated, our study did determine that litter production was more important than live plant biomass in affecting nematode communities. However, in the present study, the correlations between the environmental variables measured and the nematode communities were generally low at both the genus level and the functional group level. This suggests that other characteristics may also play important roles in structuring nematode communities.

In the current study, *Spartina* marshes had generally lower trophic diversity of nematodes than both *Scirpus* and *Phragmites* marshes, suggesting that the benthic food web became simpler after the invasion of *Spartina*. The relative abundance of bacterial-feeding nematodes tended to increase, but fungal feeders tended to decrease in *Spartina* compared with *Phragmites* communities. Since the abundance of different trophic groups of nematodes may reflect the presence of their food resource, the changes in the relative abundance of bacterial-feeding and fungal-feeding nematodes may be related to increased bacterial activity and suppressed fungal activity in *Spartina* marshes. These changes in *Spartina* marshes are likely to alter the decomposition processes, rates, and pathways, which may, in turn, modify belowground nutrient cycling of the estuarine wetlands. Ingham et al. (1985) found that bacterial-feeding nematodes can excrete NH_4^+-N, which may accelerate plant uptake and growth. Therefore, the trophic changes of nematodes may be expected to affect plant growth and the further expansion of invasive plants like *Spartina*.

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