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ORIGINAL PAPER

Effects of saltmarsh invasion by *Spartina alterniflora* on arthropod community structure and diets

**Yu-Tong Wu · Cheng-Huan Wang ·
Xiao-Dong Zhang · Bin Zhao · Li-Fen Jiang ·
Jia-Kuan Chen · Bo Li**

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Abstract Invasive plants strongly affect physical and biotic environments of native ecosystems. Insects and other arthropods as one of the major components of many ecosystems are very sensitive to subtle changes in abiotic and biotic environments. We examined the effects of exotic *Spartina alterniflora* invasion on community structure and diets of arthropods in a saltmarsh previously dominated by native *Phragmites australis* in Yangtze River estuary through net sweeping and plant harvesting methods and stable isotope analysis. Our results showed that diversity indices were not significantly different between exotic and native plant communities, but the total abundance of insects estimated through plant harvesting method was found to be lower in *Spartina* monoculture than that in *Phragmites* monoculture. Community structure of insects in *Spartina* monoculture was dissimilar to that in *Phragmites* monoculture and *Phragmites*–*Spartina* mixture. Moreover, stable carbon isotope patterns of arthropods were significantly different between *Phragmites* and *Spartina* monocultures. Although some native arthropods (perhaps generalists) shifted their diets, many native taxa did prefer *Phragmites* to *Spartina* even in *Spartina* monoculture. *Spartina* invasions resulted in reduced abundances of some arthropds, and increased dominance of others feeding preferably on *Spartina*. This study provides evidence that invasive plants can change the community structure and diets of native arthropods, which will eventually alter the arthropod food web, and affect the integrity and functioning of native ecosystems within a nature reserve that has been set aside for conserving the native biodiversity and maintaining the ecosystem integrity. In this sense, *Spartina* invasions in the Yangtze River estuary need to be managed appropriately.

Keywords Diet · Insect community structure · *Phragmites australis* · Saltmarsh · *Spartina alterniflora* · Yangtze River estuary

Introduction

Invasive plants seriously threaten native biotic communities and modify physical environments of the invaded systems (Chambers et al. 1999; Lodge et al. 2006; Levine 2008). They may competitively exclude native plants on which native animals (e.g. insects, benthos, birds) may depend (Benoit and Askins 1999; Gratton and Denno 2005), which may in turn influence the structure and functioning of native ecosystems (Vitousek et al. 1997; McKinney and Lockwood 1999; Dukes and Mooney 2004).

Y.-T. Wu · C.-H. Wang · X.-D. Zhang ·
B. Zhao · L.-F. Jiang · J.-K. Chen · B. Li (✉)
Coastal Ecosystems Research Station of Yangtze River
Estuary, Ministry of Education Key Laboratory for
Biodiversity Science and Ecological Engineering,
Institute of Biodiversity Science, Fudan University,
Shanghai 200433, China
e-mail: bool@fudan.edu.cn

Insects are exceptionally diverse, and one of the major components of many ecosystems, which control key ecosystem processes, in particular, the transformation of plant materials to animal materials during primary consumption (Speight et al. 1999). Insects are also sensitive to the changes in both abiotic and biotic environments, so they can be envisaged as useful indicators of subtle environmental changes (Schowalter 2000). Plants are primary producers of ecosystems and provide consumers with both food and habitats. Therefore, any shift in species composition of plant communities may alter the resource availability and habitat properties for native consumers, and hence have profound influence on local fauna, particularly insects or arthropods in general (e.g., Tallamy 2004; Gratton and Denno 2005, 2006). In particular, invasions by exotic plants disrupt the ecological interactions between organisms at different trophic levels (Dukes and Mooney 2004), and thus affect the native arthropod communities (Carroll et al. 1997; Levine et al. 2003; Gratton and Denno 2005).

Many studies have examined the effects of invasive plants on native arthropod biodiversity, and the conclusions drawn from different studies appear to be mixed, depending on the study systems (e.g. Olckers and Hulley 1991; Agrawal and Kotanen 2003; Frenzel and Brandl 2003; Herrera and Dudley 2003; Gratton and Denno 2005, 2006). Moreover, most of the studies available have been conducted in typical terrestrial ecosystems. Although plant invasions are accelerating in many estuaries like San Francisco Bay (Cohen and Carlton 1998) and Yangtze River estuary (Li et al. 2008), few studies have been conducted to examine how arthropod communities in the estuarine wetlands respond to plant invasions. We here report a case study examining the effects of *Spartina alterniflora* (hereafter *Spartina*) invasions on arthropod communities in a saltmarsh in the Yangtze River estuary, China.

The Yangtze River estuary is an important ecoregion that has large area of estuarine wetlands, of which Dongtan on Chongming Island was recognized as the Wetland of International Importance, at which a nature reserve—Chongming Dongtan National Nature Reserve was established in 2005. However, Dongtan wetland set aside for conserving the native biodiversity and the ecosystem integrity is heavily infested with invasive exotic plant, *Spartina*, which is devaluing the wetland.

For the purposes of erosion control, soil amelioration and dike protection, *Spartina* was intentionally introduced from three sites in North America (North Carolina, Georgia and Florida) to China in 1979 (An et al. 2007). *Spartina* has a number of biological traits (e.g. fast growth, well-developed belowground structures, high salt tolerance, great reproductive capacity through both clonal growth and sexual reproduction), making it a suitable species for ecological restoration (Hinkle and Mitsch 2005). For this reason, it was widely introduced to the east coast of China (Chung 2006), and is widely distributed along the east coast of China, from Tianjin to Baihai in Guangxi (Wang et al. 2006a). The coverage of *Spartina* in China was approximately 260 ha in six counties by 1985 (Chung 1989) and increased to more than 112,000 ha by 2000 (An et al. 2007).

Spartina was first found in 1995 in Dongtan wetland on Chongming Island in the Yangtze River estuary, and is believed to have arrived there though natural dispersal by water flow from Qidong, Jiangsu Province. For rapid sediment accretion in mudflats in the estuary, *Spartina* was intentionally introduced to Dongtan wetland twice, in 2001 and 2003, leading to a rapid range expansion in the estuary. While the introductions of *Spartina* to the estuary have effectively promoted sedimentation, native plants in the Yangtze River estuary, such as *Scirpus mariqueter* (hereafter *Scirpus*; Chen et al. 2004) and *Phragmites australis* (hereafter *Phragmites*; Wang et al. 2006b) were rapidly replaced by the exotic plant as *Spartina* is much more competitive than the natives. The changes in physical environments caused by *Spartina* invasions have also contributed to such rapid species replacement. *Spartina* now occupies 49.5% of vegetated area at Dongtan, Chongming Island, and it has thus become the most abundant plant species in the saltmarshes just over 10 years since its first occurrence in the estuary (Wang 2007).

The relacement of the native plants by *Spartina* has profound effects on the native ecosystems in the Yangtze River estuary (see an overview by Li et al. 2008). Previous studies have examined the effects of *Spartina* invasions on biodiversity including native plants (Chen et al. 2004; Wang et al. 2006b), rhizosphere bacteria (Wang et al. 2007), benthos (Chen et al. 2005; Chen et al. 2007) and fish (Quan et al. 2007) and carbon and nitrogen processes in the estuary (Liao et al. 2007, 2008). Nevertheless, there is a lack of the data on how insects and other arthropods, as one of the major components of many ecosystems, are affected by *Spartina* invasions, which precludes us from making a convincing conclusion as to whether or not *Spartina* should be extirpated in the Yangtze River estuary. The major aim of the present study was to offer such information. In so doing, this study used net sweeping and plant harvesting methods to estimate the diversity of insects, and the natural abundances of stable isotopes to infer the reliance of arthropods on native *Phragmites* and exotic *Spartina* in terms of diet. The questions we asked are: (1) What effects do *Spartina* invasions have on the diversity of marsh insects in the Yangtze River estuary? (2) Can such effects be explained by the changes in arthropods' diet caused by the replacement of *Phragmites* by *Spartina*?

Materials and methods

Study sites

This study was conducted in Dongtan Wetland of International Importance on Chongming Island/Chongming Dongtan National Nature Reserve (31°25′–31°38′ N, 121°50′–122°05′ E) in Yangtze River estuary, China. The wetland consists three parts, Dongwangsha, Buyugang and Tuanjiesha (Fig. 1). Its annual precipitation is 1,022 mm; and mean temperature is 15.3°C, with monthly maximum of 27.5°C in July and minimum of 2.9°C in January. Total area of the vegetation varies from year to year due to rapid sedimentation, and was 3,822.57 hm^2 in 2005. There are few native vascular plant species in the saltmarshes, and the dominant native species are *Phragmites* and *Scirpus*, both of which are C_3 plants. An exotic C_4 grass, *Spartina*, has invaded the saltmarshes since the mid 1990s, and has now become the most dominant plant species in Dongtan wetland. Native plant *Phragmites* is patchily distributed in the north and northeast of the island, and a large area of pure *Phragmites* stand unaffected by *Spartina* is restricted to Tuanjiesha, which is in the south of the island. Over the study area, *Phragmites* and *Spartina* form either monocultures or their mixtures, which exist in mosaics (Wang 2007).

Insect community structure

Sampling

To examine the effects of *Spartina* invasions on community structure of native insects in the saltmarshes, we sampled insects in three different habitat

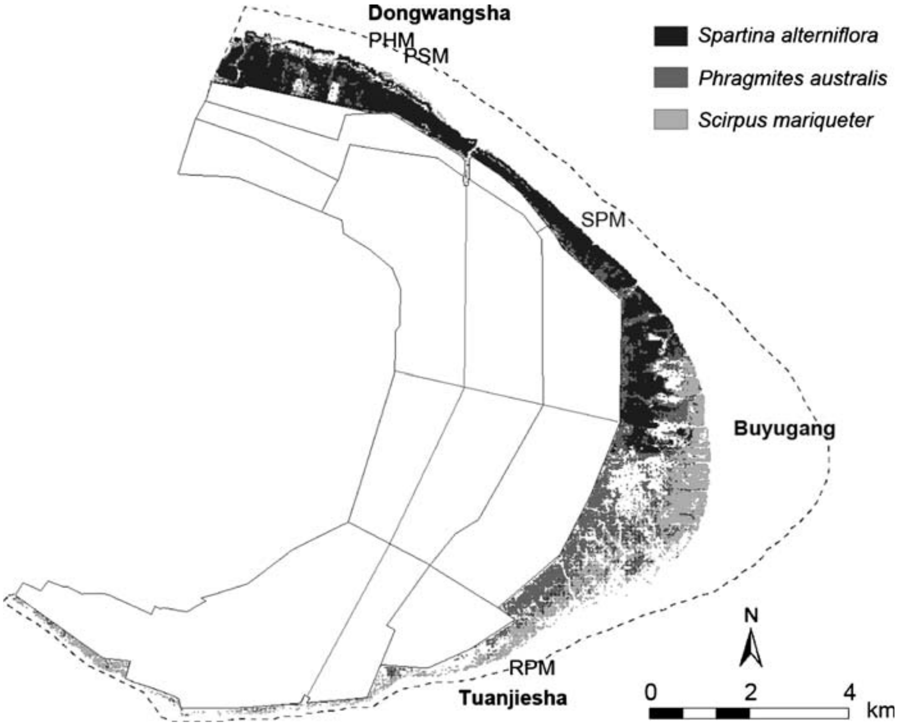

Fig. 1 Spatial distribution of plant communities in intertidal zones at Chongming Dongtan, in the Yangtze River estuary in 2005 (Wang 2007). Abbreviations of different plant communities are defined as PHM: *Phragmites* monoculture; PSM: *Phragmites–Spartina* mixture; SPM: *Spartina* monoculture; and RPM: reference *Phragmites* monoculture

types (i.e., three types of plant communities): (1) *Phragmites* monoculture (in the north of Dongtan wetland, N 31°34.770′, E 121°54.077′); (2) *Phragmites–Spartina* mixture in which *Phragmites* was slightly taller than *Spartina* (in the north of Dongtan wetland, N 31°34.999′, E 121°54.392′); and (3) *Spartina* monoculture (in the northeast of Dongtan wetland, N 31°32.365′, E 121°58.082′). To make the results comparable among plant communities, all the three habitats were located between Dongwangsha and Buyugang (Fig. 1) in the north of Dongtan wetland, which were adjacent to each other. *Phragmites–Spartina* mixture represented a transitional type that *Spartina* was invading *Phragmites* community. Five plots (10 m × 10 m) in each habitat were randomly chosen as replicates. Those plots were at least 20 m away from each other to ensure sampling to be independent.

Because insects tend to move from one habitat to another, the changes of endophagous insects are more reliable to reflect alterations of plant communities than ectophagous insects (Bernay and Chapman 1994). In order to make our insect sampling effective, we employed both net sweeping (35-cm-diameter net) and plant harvesting methods, as practiced in a similar study system by Gratton and Denno (2005). With the net sweeping method, 200 sweeps were taken within each plot. In so doing, each plot was divided into four parallel transects which were apart at least 2 m from each other. We took 50 sweeps on each transect. Net contents of four 50-sweep samples were emptied into a sealable plastic bag and were combined to give a single sample for a plot. The same person sampled all sampling plots in order to avoid the differences in sampling effort caused by different persons. We used plant harvesting method to collect internal or concealed feeding insects. We randomly positioned five 0.25 m × 0.25 m quadrats in each plot, and harvested the aboveground parts of plants for each quadrat. All the materials were put into sealable plastic bags and were transported to the laboratory for inspection. Plant stems were dissected with a clipper, and all internally feeding insects were collected and counted. The insects of five quadrats were then combined to give a single sample. All insects were stored in refrigerator at −20°C till being processed. If the insects collected were larvae, they were fed in Petri dishes at room temperature until they were identifiable.

Because summer is the season of the greatest abundance and diversity of insects and other arthropods, sampling in the saltmarshes is suggested to be performed between June and September (Davis and Gray 1966; Gao et al. 2006). To make our single-season sampling meaningful, samples were collected from 28th June to 3rd July and from 18th to 22nd August, 2006 during the growing season of *Phragmites* and *Spartina*. Sampling time was between 10 AM and 3 PM on sunny days. The August sampling was supplementary to the June sampling. All insects were identified to family level or morphospecies, and their numbers were counted. Because of technical difficulties, spiders were not included in the analysis. The classification of insects followed *Insect Morphology Taxonomy* (Xin et al. 1985), *Taxonomy of Insect Larva* (Zhong 1990) and *Insect Taxonomy* (Zheng and Gui 1999).

Statistical analysis

Species/taxon richness (d), Simpson's index ($1-\lambda$) and species density (Ds) were obtained from the collected data, whose changes were used to assess the effects of *Spartina* invasions on insect communities. Simpson's index ($1-\lambda$) measures the probability that two individuals randomly selected from a sample belong to different species (or taxon). The value of the index ranges from 0 to 1. Thus, the greater the value, the greater the sample diversity. These indices are calculated by:

$$d = (S-1)/\log(N);$$

$$1-\lambda = 1-\sum_{i=1}^{s} P_i^2;$$

$$Ds = N/\mathrm{A}$$

where S is the total number of species per sampled plot, N is the total number of individuals per sampled plot, P_i is the ratio of individuals of ith species in total individuals for a sampled plot, A is the area of a sampled plot.

One-way ANOVA was used to examine diversity index (species richness and Simpson's index) of insect communities and total density among habitats. Levene's test was used to verify homogeneity of variance (diversity index and total density), among the sampled plots for each habitat type. The Tukey HSD tests were used to conduct the follow-up tests. If the variances were not homoscedastic, the data were then log transformed to meet the assumptions for statistics prior to analysis. Non-metric multidimensional scaling (MDS) was used to examine the similarities of insect communities among the three plant communities. All analyses were performed through using either STATISTICA 6.0 or PRIMER 5 (Clarke and Warwick 1994).

Arthropods' diets

Sampling

Unlike the analysis of insect community structure, the samples of dietary analysis included spiders as top predators. For this reason, arthropod rather than insect is used in this section. The samples used for the above analysis of the community structure were also used for dietary analysis of arthropods using stable isotopes, which can ensure dietary analysis to be comparable to that of arthropod community structure. In order to make the comparisons more convincing, we also sampled arthropods from pure *Phragmites* stand at Tuanjiesha (see Fig. 1) which is here defined as reference *Phragmites* monoculture in further description, where *Phragmites* grew well isolated from *Spartina*, and thus should not have been affected by *Spartina* as the effects of *Spartina* are spatially local. The sampling procedure was the same as that used for insect community structure. In addition to herbivorous and predacious insects, spiders, as arthropod top predators in the saltmarsh, were also collected in our study.

Stable isotope analysis

Stable isotopes are the different forms of a given chemical element that have different atomic masses, but do not decay radioactively. They are increasingly used to reveal the trophic relationships between the biotic components of ecosystems based on energy flows. The stable isotopes of carbon include ^{13}C and ^{12}C (expressed as δ^{13}C), which are relatively conserved as 'carbon' is transferred from resources (e.g. plants or prey) to consumers (e.g., herbivores or predators) through a food web (Gratton and Denno 2006). For this reason, the C isotope signatures exhibit little or no difference between trophic levels, and can be used to determine the sources of production for consumers (Vander Zanden et al. 1999). In contrast, stable isotopes of N have two forms (^{15}N and ^{14}N, expressed as δ^{15}N), whose signatures become enriched by 3–4‰ between two consecutive trophic levels (Vander Zanden et al. 1999). Therefore, δ^{15}N can be used to determine the consumer trophic position in a food web. In our study system, the dominant plants included a C_3 plant (native *Phragmites*) and a C_4 plant (exotic *Spartina*), which have distinctive δ^{13}C isotope signatures due to their different photosynthetic pathways (Gratton and Denno 2006), allowing us to identify the food sources of the marsh arthropods through comparing their δ^{13}C signatures with those of basal resources.

In order to meet the requirements for minimum amount of materials in stable isotope analysis (0.5–1.0 mg dry mass per sample), we only selected a limited number of taxa (8–16 species, see Table 4) that had enough materials for such analysis. Since body sizes vary among the taxa, varying numbers of individuals were used for different taxa in the analysis, i.e., 20–100 individuals for smaller taxa, 5 individuals for larger taxa. Leaf tissues of *Phragmites* or *Spartina* for isotope analysis were collected from 10 randomly selected plants from each sampled plot, immersed and rinsed with deionized water before use. Soil samples were collected on the soil surface in each habitat by soil core of 3 cm in diameter and 5 cm in depth (sampling depth), and also immersed and rinsed with deionized water, and then passed through a 0.15 mm sieve. All samples (including arthropods, plants and soil) were dried at 55°C for 48 h, and then ground to fine powder using mortar and pestle.

Carbon and nitrogen stable isotope ratios were analyzed on an isotope ratio mass spectrometer (Thermo Finnigen, Delta-Plus, Flash, EA, 1112 Series, USA) in the Stable Isotope Laboratory for Ecological and Environment Research, Institute of Botany, the Chinese Academy of Sciences, China. Urea and glycine were analyzed as accuracy and precision standards for isotopic ratios. Ratios of ^{13}C/^{12}C and ^{15}N/^{14}N are expressed in δ notation as ‰, which are consistent with international standards (Vienna Pee Dee Belemnite for carbon, and atmospheric for nitrogen). δ is calculated by the formula:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N, R is the ratio of ^{13}C/^{12}C or ^{15}N/^{14}N. The analytical precisions of these measurements were 0.2‰ for δ^{13}C and 0.3‰ for δ^{15}N, respectively. We calculated the mean values of δ^{13}C and δ^{15}N for plants, soil and each taxon of arthropods selected.

To get an in-depth result, a two-source mixing model was used to quantify the contributions of food sources to arthropods' diets. Mean δ^{13}C values of two primary producers, insect consumers, and predator spiders were used in this equation. Isotopically feasible combination of source contributions summing to 100%, sources were aggregated into two groups, i.e. C_3 vascular plant (*Phragmites australis*), C_4 vascular plant (*Spartina alterniflora*). The respective percentage contributions from C_3 plant and C_4 plant are given by the following equations:

$$p_3 = \frac{\delta^{13}C_{\text{insect}} - \delta^{13}C_4}{\delta^{13}C_3 - \delta^{13}C_4} \times 100\%$$

$$p_4 = 1 - P_3$$

where P_3 and P_4 are respective percentage contributions of C_3 and C_4 plants; and $\delta^{13}C_3$ and$\delta^{13}C_4$ are respective stable isotope values of C_3 and C_4 plants.

Table 1 Insect composition of different taxon levels in the three plant communities through net sweeping and plant harvesting methods

Plant community type	Order	Family	Species	Individuals
Phragmites monoculture	11	73	119	3,550
Phragmites–Spartina mixture	12	72	118	4,274
Spartina monoculture	11	60	98	2,136

Results

Insect communities as affected by invasive *Spartina*

In total, 9960 individuals of insects were found from three plant communities, which belonged to 11 orders, 111 families and 212 species, respectively (Table 1, Appendix I). Both family and species numbers were the highest in *Phragmites–Spartina* mixture, and the lowest in *Spartina* monoculture. Diversity indices including species richness ($F_{2,12} = 3.12$, $P = 0.08$), Simpson's index ($F_{2,12} = 1.55$, $P = 0.25$) and the total density of insects ($F_{2,12} = 1.74$, $P = 0.22$) by net sweeping method were not significantly different among the three plant communities (Table 2, Fig. 2). However, both species richness ($F_{2,12} = 5.15$ $P < 0.05$) and the total density of insects ($F_{2,12} = 14.58$ $P < 0.01$) estimated by the plant harvesting method were significantly different among the three plant communities although Simpson's index was similar among the plant communities ($F_{2,12} = 0.72$ $P = 0.51$) (Table 2, Fig. 2). Only the total density of insects was found to be significantly different among the plant communities ($F_{2,12} = 13.76$ $P < 0.01$) when the collections by net sweeping and plant harvesting methods were combined (Table 2).

Table 2 Results of one-way ANOVA for comparison of diversity indices of insect communities by net sweeping method and plant harvesting method in the three plant communities

Collecting method	Variables	SS	Degree of freedom	MS	F	*P*
Net-sweeping	Species richness	3.92	2, 12	1.96	3.12	0.08
	Simpson's index	0.03	2, 12	0.02	1.55	0.25
	Total density	0.14	2, 12	0.07	1.74	0.22
Plant-harvesting	Species richness	4.18	2, 12	2.09	5.15	<0.05
	Simpson's index	0.10	2, 12	0.05	0.72	0.51
	Total density	6.45	2, 12	3.22	14.58	<0.01
Both net sweeping and plant harvesting	Species richness	2.66	2, 12	1.33	1.95	0.18
	Simpson's index	0.07	2, 12	0.04	2.21	0.15
	Total density	6.43	2, 12	3.22	13.76	<0.01

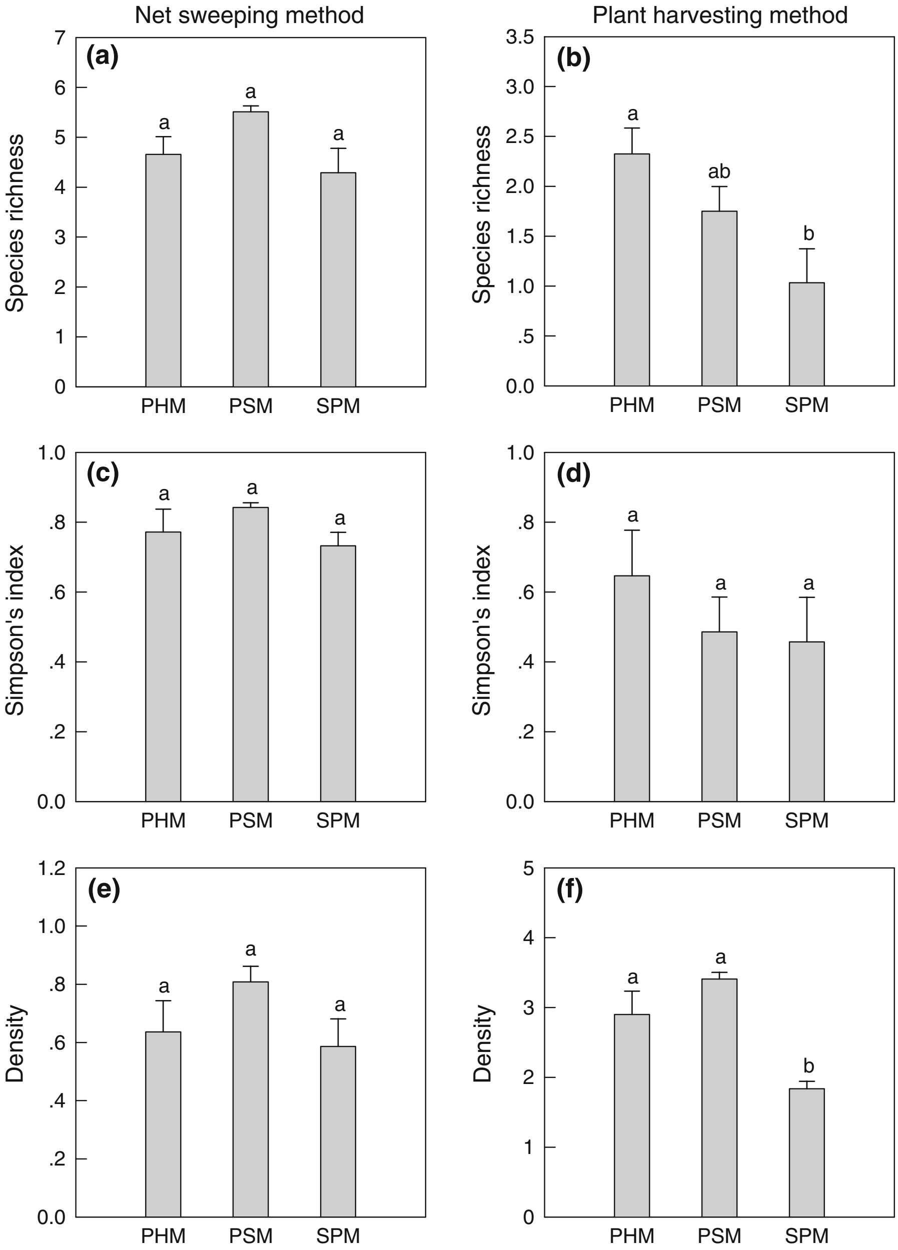

Fig. 2 Comparisons of insect communities collected from different plant communities through net sweeping (**a**, **c**, **e**) and plant harvesting methods (**b**, **d**, **f**). (**a**) and (**b**) Insect species richness; (**c**) and (**d**) Simpson's index; and (**e**) and (**f**) total density of insects. The means (±standard errors) are presented for all the variables in the figure. PHM: *Phragmites* monoculture, PSM: *Phragmites–Spartina* mixture, SPM: *Spartina* monoculture. The same lower case letters indicate no significant difference among the plant communities, and the different letters significant differences ($P < 0.05$)

Similarity of insect communities inhabiting different plant communities

Insect communities inhabiting the three plant communities could be separated clearly by MDS ordination (Fig. 3, stress: 0.09). Results show that insect community in *Phragmites* monoculture was similar to that in *Phragmites–Spartina* mixture, implying that insect community in the mixture might be more affected by *Phragmites* than by *Spartin*a. The insect community in *Spartina* monoculture appeared to be different from that in both *Phragmites* monoculture and *Phragmites–Spartina* mixture (Fig. 3).

Dietary partition through stable isotope analysis

Native *Phragmites* and exotic *Spartina* are respectively C_3 and C_4 plants. The $\delta^{13}C$ values were –14.18‰ (±1.52‰) and −25.38‰ (±1.33‰)

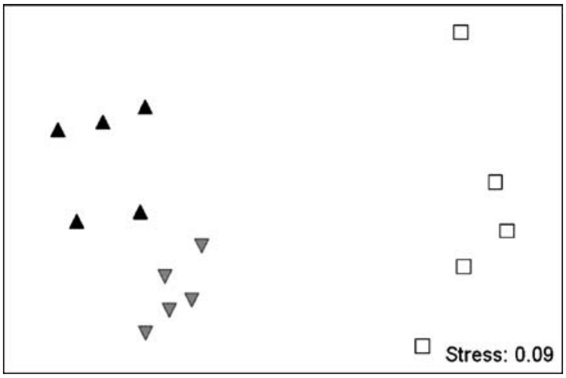

Fig. 3 Non-metric multidimensional scaling (MDS) ordination of insect communities for all the sampling plots, based on the data collected by both net sweeping and plant harvesting methods. ▲: *Phragmites* monoculture; ▼: *Phragmites–Spartina* mixture; □: *Spartina* monoculture

respectively for *Spartina* and *Phragmites*. The δ^{15}N value of *Phragmites* was 5.58‰ (±1.16‰), being similar to that of *Spartina* (4.83‰±1.08‰). Soil δ^{13}C value was −11.35‰ (±1.73‰); and soil δ^{15}N value was 2.41‰ (±0.80‰) (Fig. 4).

Stable isotope patterns of arthropods in reference *Phragemites* monoculture were significantly different from those in other three plant communities (Fig. 4). The δ^{13}C and δ^{15}N values of most arthropod taxa were slightly lower in reference *Phragmites* monoculture than in other plant communities. The δ^{15}N values of arthropods were higher in *Phragmites* monoculture and *Phragmites–Spartina* mixture than those in reference *Phragmites* and *Spartina* monocultures. Our results suggest that several taxa, including the generalist grasshoppers Tettigoniidae and Gryllidae, flies Tachinidae and Tachinidae, tended to select *Spartina* as their diet. However, some taxa, such as Coccinellidae and Ichneumonidae, still selected *Phragmites* as their diet. In general, the δ^{15}N values of arthropods showed a slightly decreasing trend when *Spartina* invaded the *Phragmites* community. It is suggested that the food web in *Phragmites* monoculture and *Phragmites–Spartina*

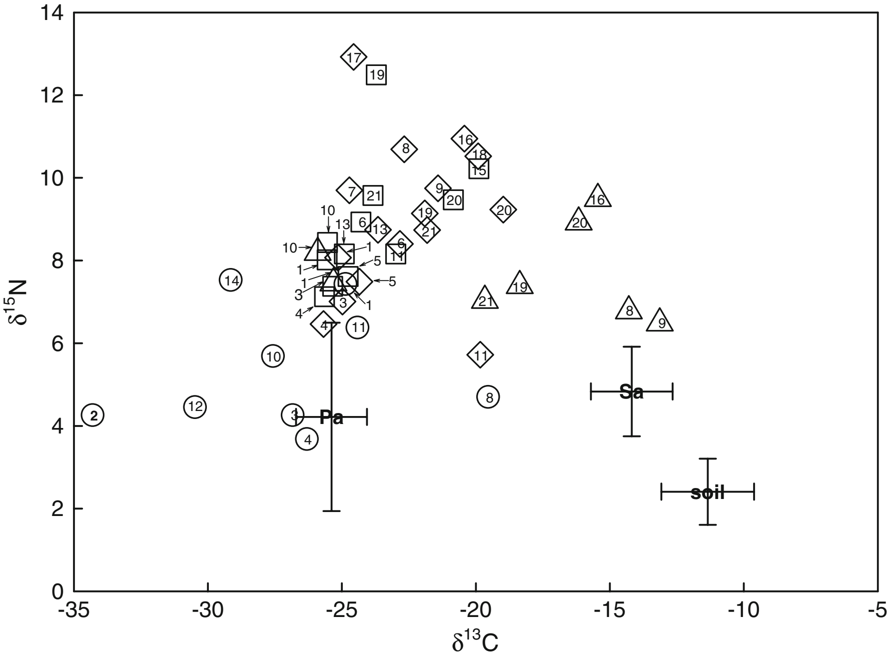

Fig. 4 Distribution of δ^{13}C andδ^{15}N isotopes for the major arthropod groups in four plant communities, collected by both net sweeping and plant harvesting methods. Base resources: **Soil**, soil; **Pa**, *Phragmites*; **Sa**, *Spartina*. Different symbols represent insect communities in different habitat types, i.e., ○: reference *Phragmites* monoculture; □**:** *Phragmites* monoculture; ◇**:** *Phragmites–Spartina* mixture; Δ**:** *Spartina* monoculture. 1: Coccinellidae; 2: Pedilidae; 3: Delphacidae; 4: Coccidae; 5: Lygaeidae; 6: Ichneumonidae; 7: Formicidae; 8: Tettigoniidae; 9: Gryllidae; 10: Caenagriidae; 11: Chrysopidae; 12: Leptophlebiidae; 13: Labiduridae; 14: Simuliidae; 15: Sarcophagidae; 16: Tachinidae; 17: Coenomyiidae; 18: Lauxaniidae; 19: Phoridae; 20: Pallopteridaec; 21: Spiders

Table 3 The mean distances between arthropods in a given habitat and the local dominant plant species/soil, calculated from the isotopic values given in Fig. 4

community	Reference *Phragmites* monoculture		*Phragmites* monoculture		*Spartina–Phragmites* mixture		*Spartina* monoculture		Total	
	mean	se	mean	se	mean	se	mean	se	mean	se
Number of arthropod groups	9	–	12	–	16	–	8	–	21	–
Within group distance	5.43	0.51	2.88	0.22	3.59	0.16	6.01	0.69	5.75	0.25
Distance from *Phragmites*	3.96	0.83	5.01	0.54	5.79	0.51	8.35	1.25	5.88	0.54
Distance from *Spartina*	12.96	1.38	10.69	0.42	9.66	0.49	5.97	1.37	10.44	0.82
Distance from soil	16.06	1.35	14.25	0.40	13.24	0.49	9.33	1.43	13.93	0.78

mixture was more complex than that in reference *Phragmites* and *Spartina* monocultures.

Surprisingly, spiders as the top arthropod predator did not have the highest δ^{15}N value; and the δ^{15}N values for the spiders were quite low, and varied among the plant communities except for reference *Phragmites* monoculture. The δ^{13}C values of the spiders were lower than those of other taxa. In contrast, the δ^{15}N values of some parasitic flies like Tachinidae and Saprophage like Lauxaniidae were higher than those of the spiders.

In order to better demonstrate the patterns given in Fig. 4, the mean distances between arthropods in a given habitat and the local dominant plant species/soil were calculated from the data given in Fig. 4 using the isotopic values, and presented in Table 3. Table 3 shows that arthropods were closer to *Phragmites* than *Spartina* and soil in relation to trophic relationship although those from *Spartina* monoculture were more similar to *Spartina* than others.

Phragmites and *Spartina*'s contributions to diets of arthropods

Although both *Phragmites* and *Spartina* were consumed by insects in the saltmarsh, their relative contributions to diets of insects and their predator spiders varied considerably among the arthropod taxa (Table 4). In reference *Phragmites* monoculture, insects mainly fed on *Phragmites* except for grasshopper (Tettigonidae). In *Phragmites* monocultures, there are members of a food web in which the dominant primary producer was *Phragmites*. The contributions of *Phragmites* to the diets of Diptera, Hymenoptera Ichneumonidae, Dermaptera Labiduridae and Neuroptera Chrysopidae in *Phragmites–Sparitina* mixture were lower than those in *Phragmites* monoculture. In *Spartina* monoculture, *Spartina* was the main food source for Diptera and the only food source for Orthoptera insects. Coleoptera insects just fed on *Phragmites* even in *Spartina* monoculture.

Discussion

Effects of *Spartina* invasion on insect community structure

Spartina is a global plant invader in coastal wetlands that can modify the abiotic and biotic environments through so-called ecosystem engineering processes (Crooks 2002). Our results obtained here show that *Spartina* invasion in saltmarshes altered native insect assemblages in the estuarine wetlands in the Yangtze River mouth. Although species richness, diversity and density of insects in *Phragmites–Spartina* mixture and *Spartina* monoculture obtained through using net sweeping method were not significantly different from those in *Phragmites* monoculture (Fig. 2), the number and structure of the native insect communities were considerably altered in response to *Spartina* invasion (Table 1, Fig. 3). It is highly likely that *Spartina* can modify physical environments of the wetlands (Lindsay and French 2006), and alters the quality of detritus and litter (Vince et al. 1981; Chen et al. 2007).

In this study, we sampled insects through using both net sweeping and plant harvesting methods, which are the two most appropriate ones. Other methods like color traps, sugar traps and pitfall traps are also available (Sutherland 2003), but could not be used in our study system that is greatly affected by tides. We found that the lowest

Table 4 The relative contributions of *Phragmites* (Pa) and *Spartina* (Sa) to diets of arthropods in different plant communities, expressed as %

Taxon	Feeding habit	Reference *Phragmites* monoculture		*Phragmites* monoculture		*Phragmites–Spartina* mixture		*Spartina* monoculture	
		Pa	Sa	Pa	Sa	Pa	Sa	Pa	Sa
Coleoptera									
Coccinellidae	MF	95 (C)	5 (C)	100 (C)	0	98 (C)	2 (C)	99 (S)	1 (S)
Pedilidae	MF	100 (C)	0						
Homoptera									
Coccidae	PT	100 (C)	0	100 (C)	0	100 (C)	0		
Delphacidae	HV	100 (C)	0	100 (C)	0	96 (S)	4 (S)		
Dermaptera									
Labiduridae	MF			96 (S)	4 (S)	85 (C)	15 (C)		
Diptera									
Coenomyiidae	SP					93 (S)	7 (S)		
Lauxaniidae	PT					51 (S)	49 (S)		
Pallopteridae	PT			59 (C)	41 (C)	43 (S)	57 (S)	18 (S)	82 (S)
Phoridae	PT			85 (S)	15 (S)	69 (S)	31 (S)	37 (S)	63 (S)
Sarcophagidae	SP			51 (S)	49 (S)				
Simuliidae	PT	100 (S)	0						
Tachinidae	PT					56 (S)	44 (S)	11 (S)	89 (S)
Ephemeroptera									
Leptophlebiidae	MF	100 (S)	0						
Hemiptera									
Lygaeidae	HV			94 (C)	6 (C)	91 (C)	9 (C)		
Hymenoptera									
Formicidae	MF					94 (C)	6 (C)		
Ichneumonidae	PT			90 (C)	10 (C)	77 (C)	23 (C)		
Neuroptera									
Chrysopidae	CV	91 (S)	9 (S)	79 (S)	21 (S)	50 (C)	50 (C)		
Odonata									
Caeneagriidae	CV	100 (S)	0	100 (S)	0	100 (S)	0		
Orthoptera									
Gryllidae	MF					65 (S)	35 (S)	0	100 (S)
Tettigonidae	MF	48 (S)	52 (S)			76 (S)	24 (S)	1 (S)	99 S
Spiders	CV			86 (S)	14 (S)	68 (S)	32 (S)	49 (S)	51 (S)

Codes in parentheses indicate sampling methods by which arthropods were caught: S: net sweeping method, and C: both net sweeping and plant harvesting methods. The codes for feeding habits are defined as: CV: carnivorous; HV: herbivorous; SP: saprophagous; PT: parasitoid; and MF: mixed feeding (strategies)

density of insects in *Spartina* monoculture obtained through plant harvesting method. It is also suggested that fewer insects relied on *Spartina* as food and/or the habitats that *Spartina* created. Some insects we found through net sweeping might be opportunitists that might have randomly appeared in *Spartina* monoculture, which can be viewed as one of the limitations of net sweeping. For this reason, some of insect diversity indices obtained through net sweeping were not significantly different. In this sense, plant harvesting is better than net sweeping for estimating insect diversity indices, especially for determining the effects of plant invasions.

Our results support the view that most of native insects preferred native plants to exotic ones. It is suggested that *Spartina* would be little affected, at least less affected by native insects than *Phragmites*. It is highly possible that *Spartina* might have experienced, to a certain degree, natural enemy release in its non-native range, which has been confirmed in 'young' introduced *Spartina alterniflora* population from San Francisco, California (Daehler and Strong 1997). It might be also the enemy release that has facilitated rapid growth and spread of *Spartina* in the Yangtze River estuary. Although this enemy release hypothesis (ERH) has been tested for many species (see review by Keane and Crawley 2002), further studies are still needed to test for ERH in relation to fitness differences in *Spartina*

At Chongming Dongtan, *Spartina* and *Phragmites* form either their respective monocultures or mixtures in which *Phragmites* is generally taller than *Spartina*, which produces a mosaic of three types of plant communities in the saltmarshes. The greatest species number, diversity and density of native insects observed in *Phragmtes–Spartina* mixture suggest that plant communities with more species provided more heterogeneous habitats that can accommodate a greater array of insects (Denno et al. 2004; Langellotto and Denno 2004). However, another possibility might also exist that the exotic plant accumulates native insect pests that harm native plants. Although such effects have not yet been tested in relation to insects, a recent study has shown that exotic invasive plant can accumulate native soil pathogens which inhibit native plants, which facilitates the invasion of *Chromolaena odorata* in India (Mangla et al. 2008).

Diet choice of native arthropods in response to *Spartina* invasion

In the present study, the ^{13}C and δ^{15}N patterns suggest that arthropod food webs have shifted after *Spartina* invaded the saltmarshes in the Yangtze River estuary. Other studies have also reported similar results that invasive species alter food web structure (Spencer et al. 1999; Vander Zanden et al. 1999; Gratton and Denno 2005, 2006; Levin et al. 2006). Our dietary analysis revealed that some native insects such as generalist grasshoppers changed their diet when they inhabited *Spartina* monoculture. Furthermore, our study shows that the insects like Coccinellidae still fed only on native plant *Phragmites*, even in *Spartina* monoculture. Therefore, those feeding only on *Phragmites* may be threatened after *Spartina* further invades the Dongtan wetland on Chongming Island. The δ^{13}C values of some insects stayed between C_3 (*Phragmites*) and C_4 plants (*Spartina*), which reflected the fact that these insects moved between these two plants, and fed on both of them. However, most insects in *Spartina* monoculture still used *Phragmites* as their basal food resource. Therefore, if exotic *Spartina* replaced the native plants, and occupied the whole area, the abundances of the insects relying mainly on *Phragmites* would be reduced, and those of the insect feeding mainly on *Spartina* would become the dominant species in arthropod community.

The δ^{15}N values for some insects like flies (Phoridae) and grasshoppers in *Spartina* monoculture were lower than those in *Phragmites* monoculture and *Phragmites–Spartina* mixture, indicating that the position of these insects in food web was lower in *Spartina* monoculture than that in other plant communities. The δ^{13}C values of spiders were close to those of *Spartina*, and their δ^{15}N values were lower in *Spartina* monoculture than in other communities. It implies that spiders as a top predator in the arthropod food-web were also altered after *Spartina* invasion, and that *Spartina* invasion might have simplified the arthropod food web. In addition, the δ^{13}C values of some insect taxa (e.g., Pedilidae, Caenagriidae, Leptophlebiidae, Simuliidae) in the reference *Phragmites* monoculture were lower than those of *Phragmites*, reflecting that these taxa might have fed on other food sources with lower δ^{13}C values. Detritus or algae can also be the main food source for some insects in saltmarshes (Gratton and Denno 2006). Stable isotope analysis of soil samples is an indirect method to determine whether detritus or algae are the food source of insects. Our results show that the δ^{13}C value of soil was much higher than that of *Phragmites* and *Spartina*. The δ^{13}C values of all arthropods were much lower than that of soil, being between those of *Phragmites* and *Spartina*. The possibility might be low that detritus or algae were the basal food sources of arthropods.

Exotic *Spartina* locally replaced native *Phragmites* in the Yangtze River estuary, which is a threat to the native insects feeding on native *Phragmites*. Most of those insects would decrease in abundance due to the lack of food sources and habitats, whereas other insects that feed mainly on exotic *Spartina* would expand rapidly due to the release of opportunity niches. There might be a possibility that just a few dominate the arthropod communities in the saltmarshes in the Yangtze River estuary with further expansion of *Spartina*. Therefore, it is necessary to mange *Spartina* invasions appropriately so as to maintain the native biodiversity and the integrity of the saltmarshes in the Yangtze River estuary.

In this study, arthropod communities were investigated only in a growing season (June and August), albeit in a season when arthropod diversity may be the highest. We made the assumptions: I) that the arthropod diversity observed in growing season can basically reflect that for the whole year, II) that the isotopic values of the taxa sampled reflect the resources they have been consuming over the growing season (Gratton and Denno 2006). However, it is well known that species richness and abundance are seasonally and inter-annually variable, which may make assumption I invalid. For this reason, it is likely to miss certain species that may be actually abundant in our study area. A single-season dataset obviously prevents us from obtaining a general picture of the effects of *Spartina* invasions on arthropod communities although it is probably valid only for the comparative purpose. For assumption II, it can be valid for long-lived arthropods like spiders and for host-specific herbivores that do not change their plants hosts (Gratton and Denno 2006), but what remains unknown is whether assumption II holds valid for other organisms in our study. Furthermore, it is also uncertain whether the differences in arthropod communities between plant communities and the patterns of C and N isotopes would hold true at other times of the year or in different years. It is not possible for us to exclude the possibility that *Spartina* supports other arthropod species at other times of the year or in different years.

In conclusion, like the replacement of *Spartina* by *Phragmites* in the saltmarshes in the USA (Gratton and Denno 2005, 2006), *Spartina* invasion into *Phragmites* communities in the Yangtze River estuary altered the arthropod assemblages, especially led to reduced abundance of concealed feeding insects. A stable isotope analysis of the arthropod assemblages showed that although most of native arthropods of the saltmarshes in the Yangtze River estuary did prefer *Phragmites* to *Spartina* even in *Spartina* monoculture, some of native arthropods (perhaps generalists) shifted their diets to *Spartina*. With further invasions in the Yangtze River estuary, these arthropods with dietary shift will become more abundant, which will eventually alter arthropod food web, and affect integrity and functioning of native ecosystems. Considering that *Spartina* invasions affect other aspects of biodiversity and ecosystem processes in the estuarine wetlands (Li et al. 2008), and that Chongming Dongtan has been set aside for conserving the native biodiversity and maintaining the ecosystem integrity, *Spartina* invasions in the Yangtze River estuary need to be managed appropriately.

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Appendix I

Relative abundance of arthropod taxa in three plant communities in Dongtan saltmarsh of the Yangtze River estuary, expressed as %

Order/Family	Relative abundance (%)		
	Phragmites monoculture	*Phragmites*–*Spartina* mixture	*Spartina* monoculture
Coleoptera			
Aglycyderidae	0	0	<1 (S)
Bostrychidae	0	0	<1(S)
Carabidae	0	<1 (C)	0
Chrysomelidae	0	0	<1 (H)
Coccinellidae	15 (C)	10 (C)	5 (S)
Dermestidae	<1 (S)	1 (C)	<1 (S)
Elateridae	<1 (S)	0	0
Lyctidae	<1 (H)	<1 C	0
Nitidulidae	<1 (S)	<1 (H)	0
Oedemeridae	<1 (H)	0	0

Appendix I continued

Order/Family	Relative abundance (%)		
	Phragmites monoculture	*Phragmites–Spartina* mixture	*Spartina* monoculture
Pedilidae	<1 (C)	<1 (S)	0
Sarothriidae	0	<1 (C)	0
Scaphidiidae	1 (C)	1 (C)	<1 (S)
Staphylinidae	<1 (H)	<1 (S)	0
Tenebrionidae	1 (S)	1 (C)	<1 (S)
Xylophilidae	<1 (S)	0	0
Dermaptera			
Labiduridae	<1 (S)	<1 (C)	0
Diptera			
Anthomyiidae	<1 (S)	0	0
Bibionidae	<1 (S)	<1 (C)	<1 (S)
Calliphoridae	<1 (S)	0	0
Canaceidae	0	<1 (S)	<1 (S)
Cecidomyiidae	<1 (C)	1 (C)	1 (C)
Chironomidae	<1 (S)	<1 (S)	5 (S)
Chloropidae	0	0	1 (S)
Clusiidae	0	<1 (S)	0
Coelopidae	0	0 C	<1 (C)
Coenomyiidae	<1 (S)	1 (S)	0
Cordyluridae	0	0	<1 (S)
Culicidae	0	<1 (S)	<1 (S)
Dixidae	0	0	<1 (S)
Dolichopodidae	<1 (S)	0	0
Empididae	<1 (S)	<1 (S)	<1 (C)
Gastrophilidae	1 (S)	<1 (S)	<1 (S)
Hypodermatidae	<1 (S)	<1 (S)	0
Lauxaniidae	<1 (S)	2 (S)	1 (C)
Lonchaeidae	<1 (S)	0	<1 (S)
Muscidae	0	<1 (S)	0
Mycetophilidae	<1 (S)	0	<1 (S)
Ochthiphilidae	<1 (S)	<1 (C)	<1 (S)
Oestridae	0	<1 (S)	0
Otitidae	1 (C)	<1 (S)	<1 (S)
Pallopteridae	5 (C)	17 (S)	21 (S)
Platypezidae	0	<1 (S)	0
Rhinophoridae	0	0	<1 (S)
Ropalomeridae	<1 (S)	0	<1 (S)
Sarcophagidae	0	<1 (S)	0
Scastopsidae	<1 (S)	<1 (S)	0
Scatopsidae	0	<1 (S)	1 (S)
Sciomyzidae	<1 (S)	0	0
Simuliidae	<1 (S)	<1 (C)	<1 (S)

Appendix I continued

Order/Family	Relative abundance (%)		
	Phragmites monoculture	*Phragmites–Spartina* mixture	*Spartina* monoculture
Stratiomyiidae	<1 (S)	<1 (S)	0
Synneuridae	<1 (S)	0	0
Syrphidae	2 (S)	<1 (C)	<1 (S)
Thaumaleidae	0	<1 (C)	0
Therevidae	<1 (S)	<1 (S)	0
Tipulidae	<1 (S)	<1 (S)	2 (S)
Trichoceridae	0	<1 (S)	<1 (S)
Trypetidae	0	<1 (S)	<1 (S)
Hemiptera			
Corixidae	<1 (S)	0	0
Isometopidae	<1 (C)	<1 (S)	<1 (S)
Lygaeidae	3 (C)	15 (C)	<1 (S)
Miridae	0	<1 (S)	<1 (S)
Nabidae	0	0	<1 (S)
Urostylidae	<1 (S)	0	0
Homoptera			
Achilidae	<1 (S)	<1 (S)	<1 (S)
Aphididae	<1 (S)	<1 (S)	<1 (S)
Coccidae	41 (C)	12 (C)	0
Delphacidae	11 (C)	5 (C)	2 (S)
Fulgoridae	0	<1 (C)	0
Gyponidae	0	<1 (S)	0
Phylloxeridae	<1 (S)	0	0
Hymenoptera			
Aphelinidae	<1 (C)	<1 (C)	0
Braconidae	<1 (S)	0	0
Chalcidae	<1 (S)	<1 (H)	0
Cleonymidae	<1 (S)	<1 (S)	<1 (S)
Cynipidae	0	<1 (S)	0
Dryinidae	<1 (C)	0	0
Elasmidae	<1 (S)	<1 C	0
Encyrtidae	<1 (S)	0	0
Eucharitidae	<1 (S)	0	0
Eucoilidae	<1 (S)	<1 (S)	0
Eulophidae	<1 (C)	1 (C)	<1 (S)
Eupelmidae	0	<1 (H)	0
Figitidae	<1 (C)	<1 (S)	<1 (S)
Formicidae	<1 (S)	5 (C)	<1 (S)
Ibaliidae	<1 (S)	0	0
Ichneumonidae	3 (C)	3 (C)	<1 (C)
Mymaridae	0	<1 (S)	<1 (S)
Perilampidae	<1 (S)	<1 (S)	0

Appendix I continued

Order/Family	Relative abundance (%)		
	Phragmites monoculture	*Phragmites*–*Spartina* mixture	*Spartina* monoculture
Platygasteridae	<1 (S)	<1 (H)	0
Pteromalidae	<1 (S)	<1 (S)	<1 (S)
Scelionidae	0	<1 (S)	0
Tetracampidae	<1 (S)	<1 (S)	<1 (S)
Thysanidae	0	<1 (S)	0
Trigonalidae	0	<1 (S)	0
Lepidoptera			
Geometridae	<1 (S)	0	<1(S)
Gracilariidae	0	0	<1 (H)
Tineidae	0	<1 (S)	0
Neuroptera			
Chrysopidae	<1 (S)	<1 (C)	<1 (S)
Hemerobiidae	0	<1 (S)	0
Sisyridae	<1 (S)	0	0
Odonata			
Caenagriidae	<1 (S)	<1 (S)	<1 (S)
Orthoptera			
Acridiidae	0	0	<1 (S)
Gryllidae	0	<1 (S)	1 (S)
Tettigoniidae	0	<1 (S)	<1 (S)
Psocptera			
Psyllipsocidae	<1 (C)	<1 (S)	3 (C)
Thysanoptera			
Phloeotripidae	<1 (C)	1 (C)	9 (S)
Spider	<1 (S)	<1 (S)	<1 (S)

Codes in parentheses indicate sampling methods by which arthropods were sampled: S: Net sweeping method, H: Plant harvesting method; and C: Both net sweeping and plant harvesting methods

References

Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. Ecol Lett 6:712–715

An SQ, Gu BH, Zhou CF et al (2007) *Spartina* invasion in China: implications for invasive species management and future research. Weed Res 47:183–191

Benoit LK, Askins RA (1999) Impact of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. Wetlands 19:194–208

Bernay EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Chapman and Hall, New York

Carroll SP, Dingle H, Klassen SP (1997) Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. Evolution 51:1182–1188

Chambers RM, Meyerson LA, Saltonstall K (1999) Expansion of *Phragmites australis* into tidal wetlands of North America. Aquat Bot 64:261–273

Chen ZY, Li B, Chen JK (2004) Ecological consequences and management of *Spartina* spp. invasions in coastal ecosystems. Biodivers Sci 12:280–289 (in Chinese with English abstract)

Chen ZY, Fu CZ, Wang HY et al (2005) Effects of *Spartina alterniflora* invasive on the benthic macro-onvertebrates community at Dongtan of Chongming salt marsh, the Yangtze river estuary. Wetland Sci 1:1–7 (in Chinese with English abstract)

Chen HL, Li B, Fang CM et al (2007) Exotic plant influences soil nematode communities through litter input. Soil Biol Biochem Soil 39:1782–1793

Chung CH (1989) Ecological engineering of coastline with salt marsh plantations. In: Mitsch WJ, Jorgensen SA (eds) Ecological engineering: an introduction to eco-technology. Wiley, New York, pp 255–289

Chung CH (2006) Forty years of ecological engineering with *Spartina* plantations in China. Ecol Eng 27:49–57

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth, Plymouth

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Daehler CC, Strong DR (1997) Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. Oecologia 110:99–108

Davis LV, Gray IE (1966) Zonal and seasonal distribution of insects in North Carolina salt marshes. Ecol Monogr 36:275–295

Denno RF, Mitter MS, Langellotto GA et al (2004) Interactions between a hunting spider and a web-builder: consequences of intraguild predation and cannibalism for prey suppression. Ecol Entomol 29:566–577

Dukes JS, Mooney HA (2004) Disruption of ecosystem processes in western North America by invasive species. Rev Chil Hist Nat 77:411–437

Frenzel M, Brandl R (2003) Diversity and abundance patterns of phytophagous insect communities on alien and native host plants in the Brassicaceae. Ecography 26:723–730

Gao H, Peng XW, Li B et al (2006) Effects of the invasive plant *Spartina alterniflora* on insect diversity in Jiuduansha wetlands in the Yangtze River Estuary. Biodiversity Science 14:400–409 (in Chinese with English abstract)

Gratton C, Denno RF (2005) Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. Restor Ecol 13:358–372

Gratton C, Denno RF (2006) Arthropod food web restoration following removal of an invasive wetland plant. Ecol Appl 16:622–631

Herrera AM, Dudley TL (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. Biol Invasions 5:167–177

Hinkle RL, Mitsch WJ (2005) Salt marsh vegetation recovery at salt hay farm wetland restoration sites on Delaware Bay. Ecol Eng 25:240–251

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139:1–10

Levine JM (2008) Biological invasions. Curr Biol 18:R57–R60

Levine JM, Vila M, D'Antonio CM et al (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc Lond B 270:775–781

Levin LA, Neira C, Grosholz ED (2006) Invasive cordgrass modifies wetland trophic function. Ecology 87:419–432

Li B, Liao CZ, Zhang XD et al (2008) *Spartina alterniflora* invasions in the Yangtze River estuary, China: an overview of current status and ecosystem effects. Ecol Eng (in press)

Liao CZ, Luo YQ, Jiang LF et al (2007) Invasion of Spartina alterniflora enhanced ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China. Ecosystems 10:1351–1361

Liao CZ, Luo YQ, Fang CM et al (2008) Litter pool sizes, decomposition, and nitrogen dynamics in Spartina alterniflora-invaded and native coastal marshlands of the Yangtze Estuary. Oecologia 156:589–600

Lindsay EA, French K (2006) The impact of the weed *Chrysanthemoides monilifera* ssp. rotundata on coastal leaf litter invertebrates. Biol Invasions 8:177–192

Lodge DM, Williams S, MacIsaac HJ et al (2006) Biological invasions: recommendations for US policy and management. Ecol Appl 16:2035–2054

Mangla S, Inderjit, Callaway RM (2008) Exotic invasive plant accumulates native soil pathogens which inhibit native plants. J Ecol 96:58–67

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Olckers T, Hulley PE (1991) Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop relative to indigenous *Solanum* species in Natal Kwazulu and the Transkei. J Entomol Soc South Afr 54:39–50

Quan WM, Fu CZ, Jin BS et al (2007) Tidal marshes as energy sources for commercially important nektonic organisms: stable isotope analysis. Mar Ecol Prog Ser 352:89–99

Schowalter TD (2000) Insect ecology, an ecosystem approach. Academic Press, San Diego

Spencer CN, Potter DS, Bukantis RT et al (1999) Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. J Plankton Res 21:51–64

Speight MR, Hunter MD, Watt AD (1999) Ecology of insects: concepts and applications. Blackwell Science, Oxford

Sutherland WJ (2003) Ecological census techniques: a handbook. Cambridge University Press, Cambridge

Tallamy DW (2004) Do alien plants reduce insect biomass? Conserv Biol 18:1689–1692

Vander Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464–467

Vince SW, Valiea I, Teal JM (1981) An experimental study of the structure of herbivorous insect communities in a salt marsh. Ecology 62:1662–1678

Vitousek PM, Mooney HA, Lubchenco J et al (1997) Human domination of earth's ecosystems. Science 277:494–499

Wang Q (2007) The dynamics of plant community distribution of the salt marshes in the Yangtze River estuary as influenced by *Spartina alterniflora* invasions. Dissertation. Fudan University, Shanghai (in Chinese with English abstract)

Wang Q, An SQ, Ma ZJ et al (2006a) Invasive *Spartina alterniflora*-biology, ecology and management. Acta Phytotaxon Sin 44:559–588 (in Chinese with English abstract)

Wang Q, Wang CH, Zhao B et al (2006b) Effects of growing conditions on the growth of and interactions between salt marsh plants: implications for invasibility of habitats. Biol Invasions 8:1547–1560

Wang M, Chen JK, Li B (2007) Characterization of bacterial community structure and diversity in rhizosphere soils of three plants in rapidly changing salt marshes using 16S rDNA. Pedosphere 17:545–556

Xin JL, Yang QS, Hu CY (1985) Insect morphology taxonomy. Fudan University Press, Shanghai (in Chinese)

Zheng LY, Gui H (1999) Insect taxonomy. Nanjing Normal University Press, Nanjing (in Chinese)

Zhong JM (1990) Taxonomy of insect larva. Agriculture Press, Beijing (in Chinese)