





ARTICLE

Special Feature: Management of biological invasions in China

Restoration of native saltmarshes can reverse arthropod assemblages and trophic interactions changed by a plant invasion

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Abstract

Plant invasions profoundly impact both natural and managed ecosystems, and removal of the invasive plants addresses only part of the problem of restoring impacted areas. The rehabilitation of diverse communities and their ecosystem functions following removal of invasive plants is an important goal of ecological restoration. Arthropod assemblages and trophic interactions are important indicators of the success of restoration, but they have largely been overlooked in saltmarshes. We determined how arthropod assemblages and trophic interactions changed with the invasion of the exotic plant *Spartina alterniflora* and with the restoration of the native plant *Phragmites australis* following *Spartina* removal in a Chinese saltmarsh. We investigated multiple biotic and abiotic variables to gain insight into the factors underlying the changes in arthropod assemblages and trophic structure. We found that although *Spartina* invasion had changed arthropod diversity, community structure, feeding-guild composition, and the diets of arthropod natural enemies in the saltmarsh, these changes could be reversed by the restoration of native *Phragmites* vegetation following removal of the invader. The variation in arthropod assemblages and trophic structure were critically associated with four biotic and abiotic variables (aboveground biomass, plant density, leaf N, and soil salinity). Our findings demonstrate the positive effects of controlling invasive plants on biodiversity and nutrient cycling and provide a foundation for assessing the efficacy of ecological restoration projects in saltmarshes.

KEYWORDS

biological invasion, biotic interactions, consumer, ecological engineering, food web, producer, saltmarsh restoration

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INTRODUCTION

Biological invasions pose an increasing threat to both natural and managed ecosystems (Simberloff et al., 2013). In particular, invasive plants outcompete native plants and often form monocultures that profoundly affect native flora and fauna and ecosystem functioning (Carboni et al., 2021; Vilà et al., 2011). Saltmarshes are among the most important ecosystems along coastal zones and provide multiple ecological services (e.g., nutrient cycling, carbon sequestration, and biodiversity protection) (Adam, 2019). Perhaps in part due to their low plant diversity, however, saltmarshes are vulnerable to invasive plants: Plant invasion along with other human disturbances are the major causes of saltmarsh degradation worldwide (Gedan et al., 2009). Restoration of native saltmarshes damaged by invasive plants is becoming a key task for the management of natural resources in coastal areas (Adam, 2019).

Management that relies on ecological engineering principles relies on natural ecosystems to perform much of the design and construction in restoration (Mitsch, 1996). This approach has been effective for restoring native saltmarshes (Teal & Weishar, 2005). Following the removal of invasive plants, native vegetation can often recover naturally or via artificial transplanting (Andreu & Vilà, 2011). Given that natural animal assemblages and food webs are also changed by plant invasions, restoration projects typically expect that the return of native producers can facilitate the rehabilitation of native-associated fauna and trophic interactions (Benke, 2018; Ning et al., 2021). Because they affect the movement of energy and materials in ecosystems, trophic interactions associated with native producers can be used as indicators of ecosystem functioning recovery (Dibble & Meyerson, 2014; Montoya et al., 2015). To date, however, most restoration projects have monitored some target plant species or communities (e.g., Andreu & Vilà, 2011; Gaynor et al., 2019; Kerr et al., 2016) and have paid relatively little attention to the reestablishment of native faunal assemblages and food-web interactions (but see Feng et al., 2018; Ge et al., 2020; Gratton & Denno, 2005, 2006).

Faunal studies in saltmarshes have focused on groups of benthic animals, fish, and birds (e.g., Li et al., 2009; Nordström et al., 2014; Wang et al., 2014). Arthropod assemblages, in contrast, have received little attention, and few studies have assessed the effects of saltmarsh restoration on arthropod diversity and trophic interactions (but see Gratton & Denno, 2005, 2006). Arthropods are highly diverse and participate in many trophic interactions that

are responsible for multiple ecosystem processes (e.g., biomass removal, litter decomposition, and nutrient transfer) in saltmarshes (Bertness & Silliman, 2008). Moreover, arthropods are highly sensitive to environmental changes driven by human disturbance and, thus, can rapidly reflect the state of biodiversity and the processes influencing it (Bal et al., 2018). As a consequence, arthropods can serve as indicators of the effects of plant invasions on ecosystems and of the quality of restoration following the removal of invasive plants (Litt et al., 2014; Longcore, 2010).

In this study, we investigated how arthropod assemblages and their trophic interactions changed with the invasion by *Spartina alterniflora* (hereafter *Spartina*) and with the restoration of native *Phragmites australis* (hereafter *Phragmites*) following *Spartina* removal in the Yangtze estuary saltmarsh of China. *Spartina* is a perennial grass native to North America and was intentionally introduced into China for erosion control because of its well-developed root system, high tolerance to salinity, rapid growth, and high productivity (Li et al., 2009). However, these same traits have also contributed to *Spartina*'s becoming highly invasive. After its introduction into China in 1979, it has rapidly displaced native plants, making it a successful invader throughout the country's coastal areas (Meng et al., 2020). By the end of 2015, *Spartina* had occupied 545 km² in China, and the Yangtze estuary was among areas suffering the most serious invasion (Liu et al., 2018). *Spartina* invasion has resulted in multiple ecological consequences (e.g., rapid displacement of native plants, changes in benthos, fish, and birds, and alterations in carbon and nitrogen cycling). This invasion is considered the most serious ecological problem in the Yangtze estuary (Ju et al., 2017).

To control *Spartina* invasion in the Yangtze estuary, China's State Forestry Administration and the Shanghai government implemented an engineering project to restore native saltmarshes that had been invaded by *Spartina* in the Chongming Dongtan Nature Reserve from 2012 to 2017. The project removed *Spartina* in the reserve via mowing and waterlogging and transplanted *Phragmites* from nearby wetlands. These activities covered an area of 24.2 km² of *Spartina* saltmarsh and may be the largest restoration project for the control of invasive wetland plants worldwide (Ju et al., 2017; Tang, 2016). Previous research revealed that *Spartina* invasion changes arthropod diversity and interactions in the reserve (Wu et al., 2009). However, it was unknown whether those changes in arthropod characteristics had

been reversed following the return of native vegetation after *Spartina* removal. Moreover, it was also unclear whether those changes had been reversed over time as a consequence of continuous interactions between arthropods and *Spartina* in nonrestored areas (Ju et al., 2016, 2019; Sun et al., 2020).

Here we hypothesized that (1) *Spartina* invasion was associated with changes in the diversity of indigenous arthropods and their trophic interactions in the Yangtze estuary and (2) *Spartina*-induced arthropod changes would be reversed following the removal of *Spartina* and the restoration of native *Phragmites* vegetation. To test these hypotheses, we compared arthropod diversity, community structure, and trophic groups in five types of plant communities that represent different stages of *Spartina* invasion and removal in the estuary. We also determined the dietary characteristics of arthropod natural enemies among plant communities. We chose arthropod natural enemies as proxies for complex food webs because they occupy a high trophic level in food webs and can be useful for evaluating the flow of energy and the cycling of nutrients in ecosystems (Smith-Ramesh, 2017). Finally, we measured multiple biotic and abiotic environmental factors to identify potential causes of differences in arthropod assemblages and trophic structure among plant communities.

METHODS

Study site and plant communities

We conducted this study in Dongtan wetlands on Chongming Island (31°27'–31°51' N, 121°09'–121°54' E) in the Yangtze estuary. The wetlands contain approximately 120 saltmarsh plant species (Zuo et al., 2003), but the dominant species are native *Phragmites* and invasive *Spartina* (both plant species are detailed in Appendix S1: Section S1). We sampled replicate transects of five types of plant communities in the Dongtan wetlands: (1) the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), (2) the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (i.e., on the periphery of the plant community where *Spartina* was encroaching within a few meters) (TP), (3) the *Phragmites*–*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), (4) the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and (5) the restored *Phragmites* monoculture following *Spartina* removal (RP) (see Appendix S1: Section S2 for more details). To some degree, these communities represent a chronosequence, beginning with the noninvaded reference community (original *Phragmites* monoculture), followed by the invaded communities (at first with no *Spartina*, then with mixtures of the

two species, and then with *Spartina* monoculture), and then followed by the restored *Phragmites* community.

Arthropod sampling and the assignment of trophic groups

Adjacent types of plant communities were separated by ≥ 500 m. In each plant community type, we randomly designated 15 replicate transects (16 m \times 3–4 m per transect) along the main creek channel. All transects were located at the same elevation, and adjacent transects were separated by ≥ 50 m (Appendix S1: Figure S2g). We used vacuum suctioning (with a gasoline-powered arthropod sampler) to collect arthropods (approximately 3.2 m² of vegetation was sampled per transect; Appendix S1: Section S3) at three time points in 2018 (22–25 June, 24–27 July, and 23–26 August) (Ebeling et al., 2018; Gratton & Denno, 2005). We sampled from late June to late August because arthropods are most abundant during this period in the Dongtan wetlands (Wu et al., 2009). All arthropods were stored at -20°C and identified to the finest taxonomic category possible, usually at or below the family level or to the morphospecies level. We followed several references to identify the arthropod taxa (Xin et al., 1985; Zhang & Li, 2011; Zhang & Wang, 2017; Zheng & Gui, 1999; Zhong, 1990) (see Appendix S1: Section S3 for more details). The 349 morphospecies identified (Jiang et al., 2022a) were designated by three broad trophic groups (detritivores, herbivores, and carnivores, i.e., natural enemies) and then subdivided into eight feeding guilds: (1) scavengers/shredders/filter feeders (pooled as detritivores in the analysis), (2) leaf chewers, (3) leaf suckers, (4) stem borers, (5) nonspider predators, (6) parasitoids, (7) web-building spiders, and (8) hunting spiders. Samples that did not belong to these eight guilds were classified as (0) others or unknown (Gratton & Denno, 2005). Holometabolous arthropods have different feeding modes in different life stages. We used their larval stage to determine the feeding guilds. We counted the number of individuals of each morphospecies on each transect.

Arthropod natural enemy diets

We used stable isotopes to determine the diets of arthropod natural enemies collected from the five plant communities. Because of the large number of natural enemy species in our collection, we restricted our analysis to the three to six most abundant taxa for each of the four natural enemy guilds (i.e., nonspider predators, parasitoids, web-building spiders, and hunting spiders; see Appendix S1:

Table S1 for the selected samples). To determine the extent to which arthropod natural enemies depended on native or invasive plants for basal trophic resources, we used fresh leaves of *Phragmites* and/or *Spartina* to analyze plant stable isotope signatures in each plant community. We used five replicates of both arthropod and plant samples for each plant community. All samples were subjected to stable isotope analysis using an isotope ratio mass spectrometer. More details for this analysis are presented in Appendix S1: Section S4.

Biotic and abiotic variables

We measured multiple biotic and abiotic variables at the sampling sites. Because macro-environmental conditions (e.g., temperature, precipitation, and tide) were similar but soil characteristics would likely differ among plant communities (Peng et al., 2011), we selected six soil variables as proxies of the abiotic environment: soil water, soil salinity, soil pH, soil carbon (C), soil nitrogen (N), and soil phosphorus (P). These soil indicators have often been shown to be directly or indirectly related to arthropod diversity (e.g., Mitchell & Litt, 2016; Page et al., 2010) and trophic interactions (Lewis et al., 2014). For the biotic environment, we quantified five variables: plant (stem) density, aboveground biomass, leaf C, leaf N, and leaf P. These indicators are also known to be related to the diversity and feeding behavior of arthropods (Wimp et al., 2010; Wolkovich, 2010). The soil sampling was conducted concurrently with the last arthropod sampling (late August). The plant tissues were sampled at the end of the growing season (October), after plants had attained their peak biomass. Samples of *Phragmites* and *Spartina* in their mixtures were fully mixed, and the mixtures were used to measure the biotic variables. For each biotic or abiotic variable, each plant community was represented by 15 replicate transects. Appendix S1: Section S5 shows more details for the sampling and detection.

Data analysis

All statistical analyses were performed in R version 3.6.2 (R Core Team, 2019). To compare arthropod diversity among the five plant communities, we calculated species richness (i.e., the number of arthropod species per transect), individual density (i.e., the number of arthropod individuals per m²), and the Shannon–Wiener index of arthropods sampled on each transect (Wu et al., 2009). We used the Shapiro–Wilk test and Levene’s test in the car package to assess normality and heterogeneity assumptions. We used one-way analyses of variance

(ANOVAs) with least-significant difference (LSD) tests to compare differences in the richness and Shannon–Wiener index among plant communities (using the agricolae package) because the data were normally distributed with homogeneity of variances. We used a Kruskal–Wallis test with multiple comparisons to compare differences in species density among plant communities (using the agricolae package) because the data were not normally distributed. To examine the similarities of arthropod assemblages at the species level among plant communities, we conducted a nonmetric multidimensional scaling (NMDS) analysis based on Bray–Curtis dissimilarity measures, using the number of individuals of each arthropod species in the data sets of sampled arthropods; the significance of the results was tested with an analysis of similarities (ANOSIM). This analysis was performed with the vegan package.

To analyze the trophic structure of arthropods in response to *Spartina* invasion and its removal, we first conducted the NMDS and ANOSIM analyses to compare the similarity of arthropod assemblages at the feeding-guild level among plant communities, using the number of individuals of each feeding guild in the sample data sets. We also compared differences in the composition of feeding guilds (i.e., the individual density of each feeding guild) among plant communities. Because the density data were not normally distributed, we used the Kruskal–Wallis test with multiple comparisons for the analysis.

To evaluate differences in the diets of arthropod natural enemies among plant communities, we drew $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots of the natural enemies and plant samples to examine their stable isotope signatures. We evaluated the spread and extent of six metrics to suggest the trophic niche of arthropod natural enemies (Layman et al., 2007). These metrics were $\delta^{15}\text{N}$ range (NR), $\delta^{13}\text{C}$ range (CR), total convex hull area (TA), mean distance to centroid (CD), mean nearest neighbor distance (MNND), and standard deviation of the nearest neighbor distance (SDNND) (Appendix S1: Section S6 explains the significance of these metrics). These values were estimated with the SIBER package.

We conducted canonical correlation analyses (CCA) to determine relationships between biotic and abiotic variables (see Appendix S1: Section S7 for the selection of variables) and arthropod assemblages and between those variables and trophic structure (i.e., the composition of feeding guilds). The final results of both CCAs were visualized with biplots. To simplify the explanatory variables, we selected three biotic variables (i.e., aboveground biomass, plant density, and leaf N) and one abiotic variable (i.e., soil salinity) that contributed most in both CCAs (see Figure 5 in the results) to compare their differences among plant communities using the Kruskal–Wallis test

with multiple comparisons (the data were not normally distributed).

RESULTS

Arthropod assemblages and feeding guilds

We collected a total of 349 arthropod morphospecies from 15 orders and 103 families in the five plant communities (Jiang et al., 2022a). Among these plant communities, the numbers of both the families and species of arthropods were lowest in the *Spartina* monoculture (IS) and highest in the restored *Phragmites* monoculture (RP) (Table 1). The *Phragmites* monoculture being threatened by invasive *Spartina* (TP) had higher values of species richness and the Shannon–Wiener index than the original reference *Phragmites* monoculture (OP) (Figure 1). Species richness, individual density, and the Shannon–Wiener index were all higher in the *Phragmites*–*Spartina* mixture (PS) than in the original *Phragmites* monoculture (OP) or *Spartina* monoculture (IS) but did not differ between the latter two plant communities (i.e., OP and IS). Arthropod richness and density were higher in the restored *Phragmites* monoculture (RP) than in the original *Phragmites* monoculture (OP) or *Spartina* monoculture (IS).

Arthropod assemblages at the species level were clearly separated according to plant community in the ordination space of NMDS, but the assemblages in the three *Phragmites* monocultures (OP, TP, and RP) were closer to each other than to those in the *Spartina*

monoculture (IS) (Figure 2a). Arthropod assemblages were more similar among plant communities at the feeding-guild level than at the species level in the ordination space of NMDS (Figure 2b vs. a). The degree of similarity at the feeding-guild level was relatively high between the restored and the original *Phragmites* monocultures (RP and OP) but relatively low between the *Spartina* monoculture (IS) and any other plant community.

Differences in the trophic structure of arthropods among plant communities were also indicated by the changes in the abundances of each feeding guild. For example, compared to the original reference *Phragmites* community (OP), the *Spartina* monoculture (IS) supported an increased density of stem borers (Figure 3d), parasitoids (Figure 3f), and both spider guilds (Figure 3g,h) but a decreased density of detritivores (Figure 3a), leaf suckers (Figure 3c), and nonspider predators (Figure 3e). Following *Spartina* removal, the individual densities of all feeding guilds (Figure 3b–h) except detritivores (Figure 3a) in the restored *Phragmites* monoculture (RP) had returned to be similar (leaf chewers and stem borers) to or even higher (other feeding guilds) than those in the original *Phragmites* monoculture (OP).

Diets of arthropod natural enemies

The $\delta^{13}\text{C}$ signatures of arthropod natural enemies were indistinguishable from those of *Phragmites* in the original *Phragmites* monoculture (OP) (Figure 4a) or in the *Phragmites* monoculture being threatened by *Spartina* (TP) (Figure 4b). The $\delta^{13}\text{C}$ signatures of natural enemies in the *Phragmites*–*Spartina* mixture (PS) were intermediate with respect to the $\delta^{13}\text{C}$ signatures of *Phragmites* and *Spartina* (Figure 4c). In the *Spartina* monoculture (IS), the $\delta^{13}\text{C}$ signatures of some natural enemies were distinguishable from those of *Spartina*, but most species had $\delta^{13}\text{C}$ signatures that were close to those of *Spartina* (Figure 4d). The $\delta^{13}\text{C}$ signatures of natural enemies in the restored *Phragmites* monoculture (RP) were almost the same as those of *Phragmites* (Figure 4e). Although most natural enemies had higher $\delta^{15}\text{N}$ signatures than *Phragmites* or *Spartina* in the five plant communities, a few species had $\delta^{15}\text{N}$ signatures that were lower than that of *Phragmites* or *Spartina* in those plant communities (Figure 4b–e). Moreover, the analysis of Layman's metrics of arthropod natural enemies showed that, although CD, MNND, SDNND, and TA were similar among plant communities, the natural enemies collected from the *Spartina* monoculture (IS) had a much larger CR but a smaller NR than those from other plant communities (Figure 4f). CR was greater in the *Phragmites*–*Spartina*

TABLE 1 Arthropod composition at different taxon levels in the five plant communities.

Plant community	Orders	Families	Species
Original <i>Phragmites</i> monoculture (OP)	12	78	202
Threatened <i>Phragmites</i> monoculture (TP)	12	81	257
<i>Phragmites</i> – <i>Spartina</i> mixture (PS)	12	73	209
Invasive <i>Spartina</i> monoculture (IS)	13	67	153
Restored <i>Phragmites</i> monoculture (RP)	14	91	263

Note: Arthropods were sampled via vacuum suctioning methods. Plant communities included the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (TP), the *Phragmites*–*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and the restored *Phragmites* monoculture following *Spartina* removal (RP).

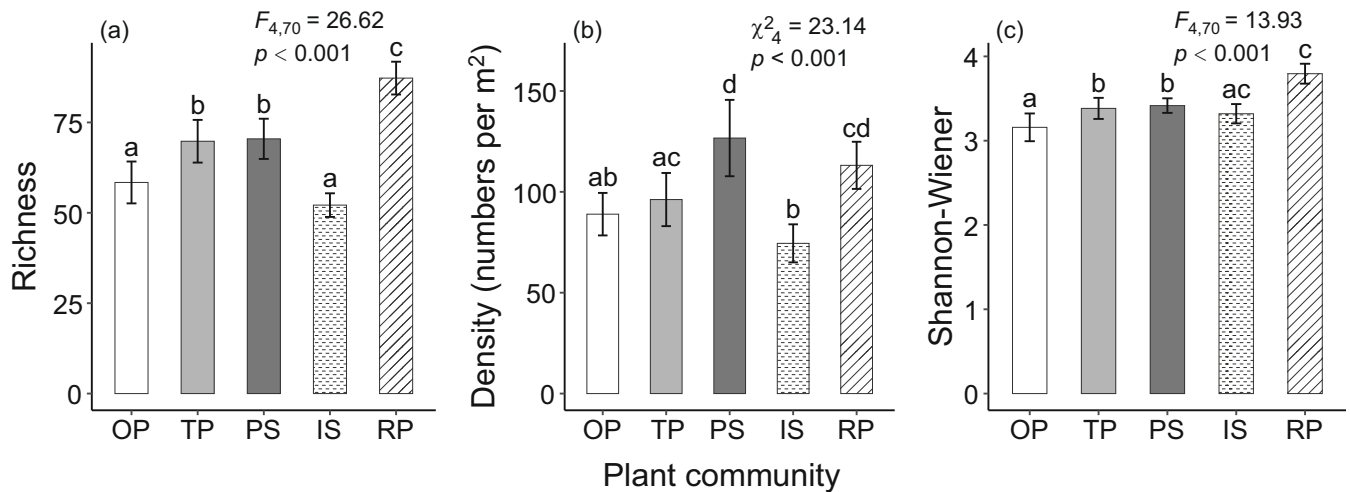


FIGURE 1 (a) Arthropod species richness, (b) individual density, and (c) the Shannon–Wiener index of arthropod assemblages in the five plant communities. Plant communities included the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (TP), the *Phragmites*–*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and the restored *Phragmites* monoculture following *Spartina* removal (RP). Values are means \pm 1.96 SE. Within each panel, $p < 0.05$ indicates a significant difference among plant communities, and means with the same letters did not differ at $\alpha = 0.05$ following a post hoc analysis.

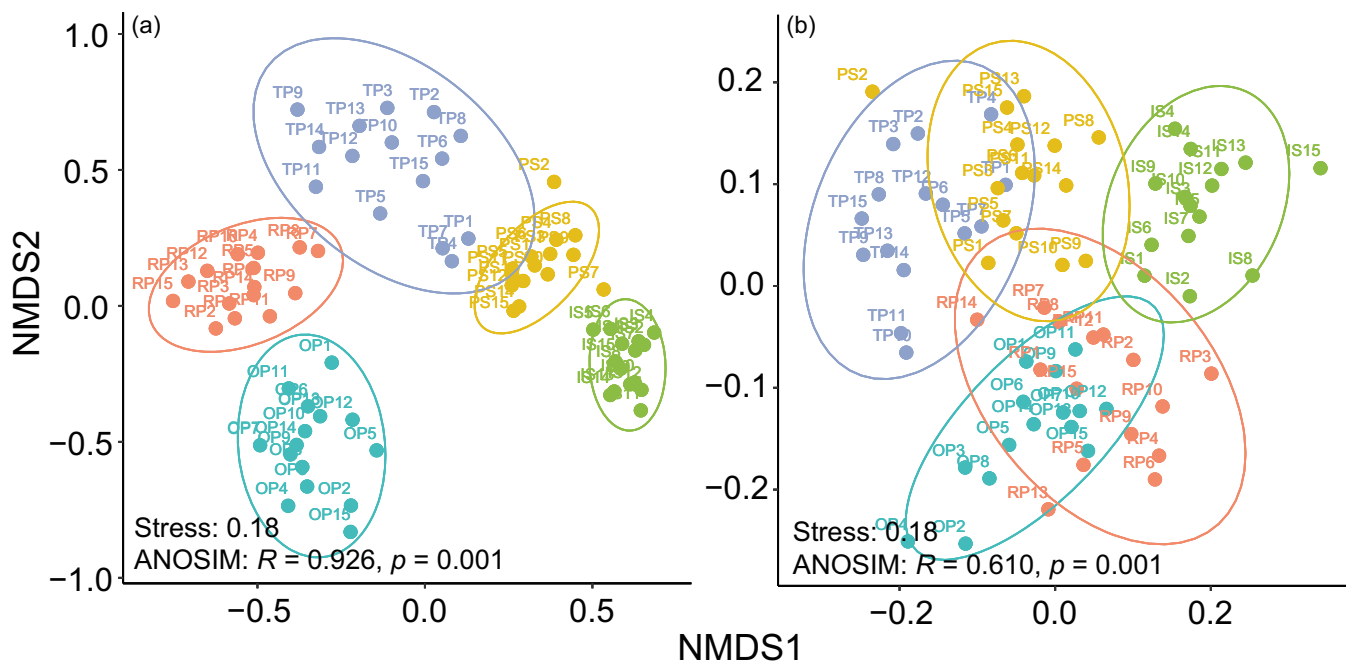


FIGURE 2 Nonmetric multidimensional scaling (NMDS) ordination plots explaining the differences in arthropod assemblages at the (a) species level and (b) feeding-guild level among the five plant communities. Different plant communities and sampling transects are indicated by different letters and numbers, respectively. Plant communities included the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (TP), the *Phragmites*–*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and the restored *Phragmites* monoculture following *Spartina* removal (RP). Ellipses indicate 95% confidence intervals for variables within each plant community. Results of the analysis of similarities (ANOSIM) showed that the dissimilarities of arthropod assemblages were greater among plant communities than within each plant community ($R > 0$, $p < 0.05$).

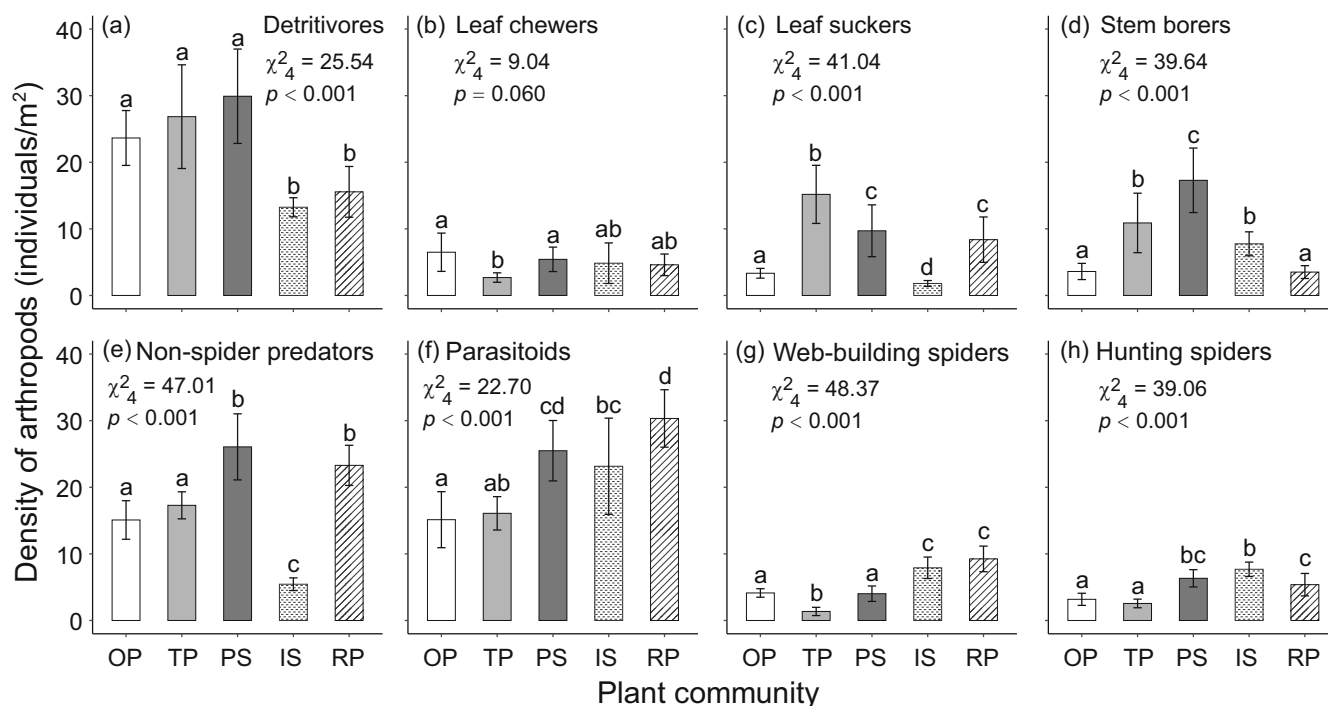


FIGURE 3 Density of arthropods from different feeding guilds affected by plant communities. Plant communities included the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (TP), the *Phragmites*–*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and the restored *Phragmites* monoculture following *Spartina* removal (RP). Each panel shows a feeding guild. Values are means ± 1.96 SE. Within each panel, $p < 0.05$ indicates a significant difference among plant communities, and means with the same letters did not differ at $\alpha = 0.05$ following a post hoc analysis.

mixture (PS) than in the original *Phragmites* monoculture (OP), but NR had the opposite pattern. In addition, neither CR nor NR differed significantly between the restored *Phragmites* monoculture (RP) and the original *Phragmites* monoculture (OP) (the boundary of 95% credibility intervals overlapped).

Effects of biotic and abiotic factors on arthropod assemblages and feeding guilds

CCA identified significant correlations between biotic and abiotic variables and arthropod assemblages or feeding guilds in the five plant communities (Appendix S1: Table S2). The first two axes of biotic and abiotic variables in the CCA biplots explained 68.5% and 76.9%, respectively, of the variation in arthropod assemblages (Figure 5a) and in the composition of feeding guilds (Figure 5b). In both CCA biplots, aboveground biomass, plant density, leaf N, and soil salinity are the main variables explaining the variation in arthropod assemblages and feeding guilds. Aboveground biomass (Figure 6a), plant density (Figure 6b), and soil salinity (Figure 6d) were significantly higher, but leaf N (Figure 6c) was significantly lower in the *Spartina*

monoculture (IS) than in the three *Phragmites* monocultures (OP, TP, and RP) (Figure 6c). Overall, differences in biotic and abiotic conditions were smaller among the three *Phragmites* monocultures (OP, TP, and RP) than between each *Phragmites* monoculture and the *Spartina* monoculture (IS).

DISCUSSION

Increasing evidence suggests that plant invasion can affect biodiversity and species interactions by changing the types of primary producers and habitat characteristics of native ecosystems (e.g., Gratton & Denno, 2005; Litt et al., 2014; Wu et al., 2009). However, few studies have simultaneously determined how arthropod assemblages and their trophic interactions are affected by plant invasions and the reintroduction of native plants following removal of the invasive plants (Gratton & Denno, 2005, 2006). Our study here considered the effects of both *Spartina* invasion and its subsequent removal on arthropod communities with an in-depth investigation of arthropod diversity, trophic groups, and interactions. We found that *Spartina* invasion had changed arthropod

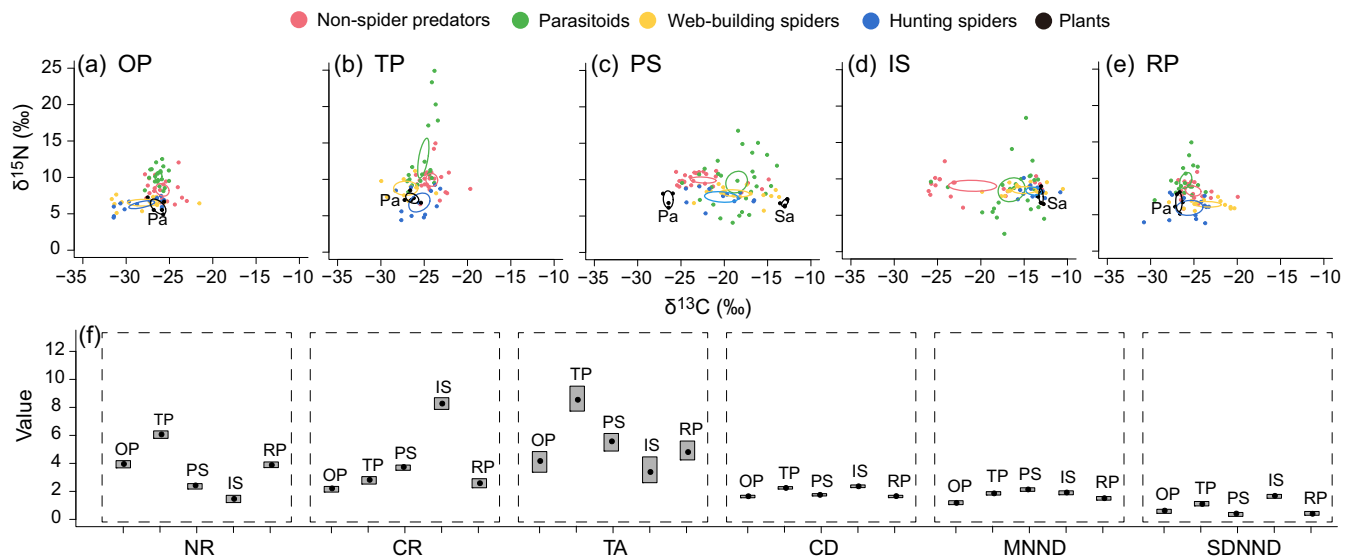


FIGURE 4 (a–e) Biplots of signatures of stable isotopes C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) and (f) probability values of six Layman's metrics for arthropod natural enemies or plants collected from different plant communities. Plant communities included the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (TP), the *Phragmites*–*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and the restored *Phragmites* monoculture following *Spartina* removal (RP). In the upper panels, different feeding guilds of natural enemies (species used are shown in Appendix S1: Table S1) are represented by different colored dots, and plants by black dots. Ellipses indicate 95% confidence intervals for the signatures of stable isotopes of each feeding guild and plant. In the bottom panels, six Layman's metrics show the range in $\delta^{15}\text{N}$ (NR), the range in $\delta^{13}\text{C}$ (CR), the total sample hull area (TA), the distance to the centroid (CD), the mean nearest neighbor distance (MNND), and the standard deviation of the mean nearest neighbor distance (SDNND) (Layman et al., 2007). The mode of each metric is represented by a black dot, and 95% credibility intervals are shown as boxes. Letters above the boxes indicate the plant communities. Boxes sharing an overlapped boundary of 95% credibility intervals indicate no obvious difference.

communities and their trophic interactions in marshes, and those changes could be reversed by the restoration of native vegetation following *Spartina* removal. The alterations in biotic and abiotic factors might have contributed to the changes in arthropod communities.

Arthropod diversity and community structure

In this study, most metrics of arthropod diversity were higher in the *Phragmites*–*Spartina* mixture than in the original reference *Phragmites* monoculture (Table 1, Figure 1), that is, the transitional plant community where *Spartina* was gradually displacing *Phragmites* supported higher arthropod diversity than the original *Phragmites* monoculture. This could have resulted from bottom-up effects: The increase in plant species richness provided diverse niches, allowing an increased number of consumer species to obtain habitat and food resources (Ebeling et al., 2018). This result is also consistent with the resource heterogeneity hypothesis, which states that increasing plant diversity should increase arthropod diversity because of increased niches and diet variety

(Borer et al., 2012). Compared to the original *Phragmites* monoculture, we found higher arthropod diversity even in the *Phragmites* monoculture that was being threatened by *Spartina* invasion (Table 1, Figure 1). We suggest that this could have been due to the migration of arthropods from the nearby mixed plant community (see also Wu et al., 2009). Although several indicators of arthropod richness did not differ between the original *Phragmites* monoculture and the *Spartina* monoculture, the total number of families and species of arthropods was much lower in the *Spartina* monoculture. Hence, arthropod diversity was lower in the *Spartina* monoculture than in the original *Phragmites* monoculture. The ordination space of NMDS also suggests that arthropod community structure was changed in the *Spartina* monoculture (Figure 2a). The complete displacement of native plants by invasive plants, therefore, appears to be detrimental to arthropod diversity in this system (Litt et al., 2014).

Given their short generation time and migration from nearby noninvaded habitats, arthropods can respond rapidly to the restoration of native vegetation following the removal of invasive plants (Dibble et al., 2013; Gratton & Denno, 2005). In this study, following *Spartina* removal, almost all metrics of arthropod diversity were

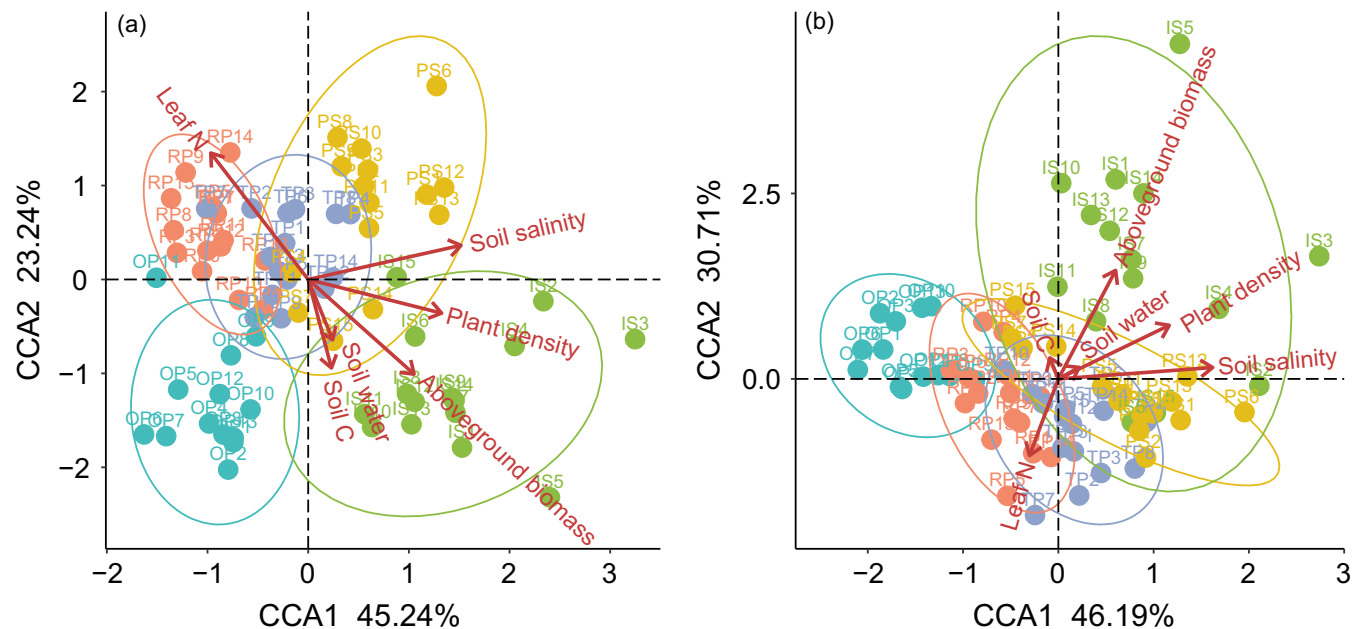


FIGURE 5 Canonical correspondence analysis biplots showing (a) correlations between environmental variables and arthropod assemblages or (b) the composition of feeding guilds in the five plant communities. In each panel, different plant communities and sampling transects are indicated by different letters and numbers, respectively. Plant communities included the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (TP), the *Phragmites*-*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and the restored *Phragmites* monoculture following *Spartina* removal (RP). Arrows indicate the relationships with environmental variables, and arrow lengths correspond to the variance in axis scores explained by each environmental variable. Ellipses indicate 95% confidence intervals for variables within each plant community.

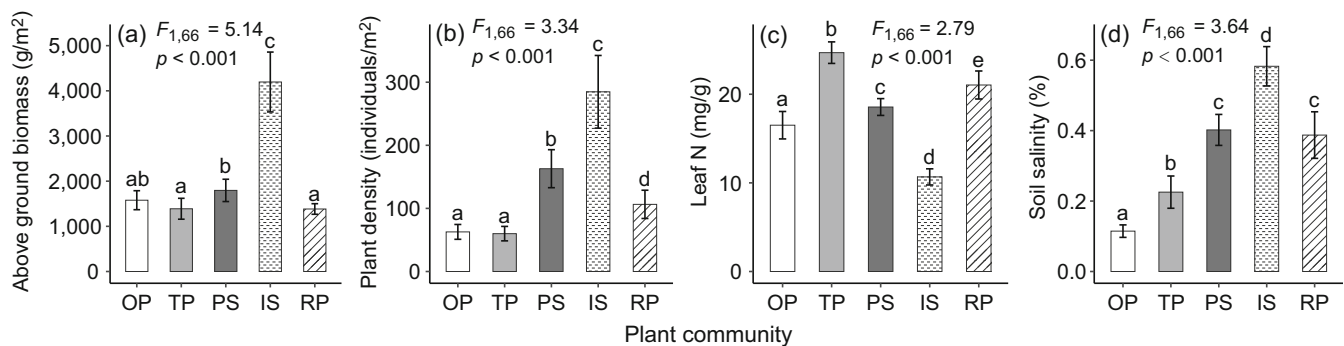


FIGURE 6 Results of multiple comparisons for the remaining four variables in the five plant communities after the permutation test for the constrained correspondence analysis. Plant communities included the original reference *Phragmites* monoculture that had never been affected by *Spartina* (OP), the *Phragmites* monoculture that had not yet been invaded but was being threatened by *Spartina* (TP), the *Phragmites*-*Spartina* mixture in which *Spartina* was gradually displacing *Phragmites* (PS), the invasive *Spartina* monoculture in which *Spartina* had completely displaced *Phragmites* (IS), and the restored *Phragmites* monoculture following *Spartina* removal (RP). Values are means \pm 1.96 SE. Within each panel, $p < 0.05$ indicates a significant difference among plant communities, and means with the same letters did not differ at $\alpha = 0.05$ following a post hoc analysis.

higher in the restored *Phragmites* monoculture than in the *Spartina* monoculture or the original reference *Phragmites* monoculture (Table 1, Figure 1). Moreover, arthropod assemblages at the species level showed a higher similarity between the restored and original

Phragmites monocultures than between either the *Phragmites* monoculture and the *Spartina* monoculture (Figure 2a). These results are consistent with the intermediate disturbance hypothesis (IDH), which contends that moderately disturbed plant communities will support

higher biodiversity than undisturbed or highly disturbed plant communities (Connell, 1978). In the Yangtze estuary, the removal of *Spartina* and the transplanting of *Phragmites* may have introduced an intermediate level of disturbance compared to established plant communities of the original reference area or the invaded area (Tang, 2016). The IDH, therefore, might help explain why arthropod diversity was greater in the restored *Phragmites* monoculture than in the *Spartina* monoculture and in the original *Phragmites* monoculture.

Our CCAs showed that four main variables (aboveground biomass, plant density, leaf N, and soil salinity) could jointly explain the variation in arthropod community structure among plant communities (Figure 5a, Appendix S1: Table S2). In addition, these four variables were more similar among the three *Phragmites* monocultures than between each *Phragmites* monoculture and the *Spartina* monoculture (Figure 6). These results suggest that changes in arthropod communities in response to *Spartina* invasion and its removal can be largely explained by differences in these biotic and abiotic variables among plant communities. According to previous studies, the changes in arthropod communities are not only driven by food resource availability (more-individuals hypothesis) (Kaspari et al., 2003; Storch et al., 2018) but also mediated by abiotic factors. This follows because abiotic conditions can affect arthropod survival and abundance (abiotic constraint hypothesis) (Chase, 1996). In this study, we speculate that plant-resource quality (e.g., leaf N) is the most critical factor, whereas the abiotic environment (e.g., soil salinity) and resource quantity (e.g., biomass and plant density) are concomitant factors that mediate arthropod communities among plant communities (see Appendix S1: Section S8 for more discussions).

Trophic structure of arthropods

In this study, the overall similarity of arthropod assemblages at the feeding-guild level in a NMDS ordination space was higher between the restored and the original *Phragmites* monocultures than between the *Spartina* monoculture and any other plant community (Figure 2b). Moreover, the abundance of feeding guilds changed with *Spartina* invasion and removal (Figure 3). In the *Spartina* monoculture, the density of almost every feeding guild differed significantly from that in the original *Phragmites* monoculture. Following *Spartina* removal, the individual densities of most feeding guilds in the restored *Phragmites* monoculture had returned to be similar or higher than that in the original *Phragmites* monoculture. However, the variation in feeding-guild composition among plant communities could also be explained by four biotic and abiotic

variables (aboveground biomass, plant density, leaf N, and soil salinity) (Figure 5b). These results indicate that complete takeover by *Spartina* invasion changed the trophic structure of arthropods, which can to some extent be reversed by the restoration of native biotic and abiotic conditions (Gratton & Denno, 2005; Litt et al., 2014; Ning et al., 2021). We provide a supplemental discussion regarding the changes in feeding guilds among plant communities in Appendix S1: Section S8.

Diets of arthropod natural enemies

Plant invasion can directly change the food resources of primary consumers or decomposers, which can then affect the dietary characteristics of consumers at higher trophic levels (Schirmel et al., 2011; Tang et al., 2012). In the current study, the $\delta^{13}\text{C}$ results (Figure 4a–c) indicate that natural enemies and their prey (i.e., consumers and decomposers with relatively low trophic positions) mainly relied on *Phragmites* in its monocultures but relied on both *Phragmites* and *Spartina* in their mixture to obtain basal trophic resources. Following the complete displacement of *Phragmites* by *Spartina*, most natural enemies in the *Spartina* monoculture had $\delta^{13}\text{C}$ signatures like those of *Spartina* (Figure 4d), indicating that these natural enemies and their prey relied on *Spartina* as their basal trophic resources in the invasive monoculture. However, a few natural enemies and their prey in the *Spartina* monoculture relied on *Phragmites* or other producers (e.g., aquatic origin plants or microorganisms) as basal trophic resources. Past studies indicated that if *Spartina* completely displaced *Phragmites*, the abundance of consumers eating *Phragmites* would decline, whereas the abundance of consumers eating *Spartina* would increase and become dominant in marshes (Ju et al., 2016; Wu et al., 2009). The effects of changes in consumers in relatively low trophic positions on natural enemy diets following *Spartina* invasion were not examined in the current study, but this issue warrants additional research.

Given the changes in basal trophic resources and species composition of arthropods, plant invasion may also affect the complexity of food webs of indigenous arthropods (Wu et al., 2009). In this study, although most arthropod natural enemies had higher $\delta^{15}\text{N}$ signatures than *Spartina* and/or *Phragmites* in the five plant communities, some natural enemies had $\delta^{15}\text{N}$ signatures that were lower than that of *Spartina* and/or *Phragmites* in those plant communities (Figure 4a–e). This result suggests that some natural enemies only feed on arthropods that consume food sources other than *Spartina* or *Phragmites* in the marshes. Nonetheless, the $\delta^{15}\text{N}$ range (NR) of arthropod natural enemies was lower in the

Spartina monoculture than in the original reference *Phragmites* monoculture (Figure 4f). A larger NR of natural enemies usually indicates a community with more trophic levels, and thus NR can indicate the complexity of food webs (Layman et al., 2007). The low NR of natural enemies in the *Spartina* monoculture suggests that invasion by *Spartina* that completely displaces *Phragmites* simplifies the structure of arthropod food webs in the marshes. A possible reason for this simplification is that arthropod natural enemies can feed on multiple levels of consumers in the reference *Phragmites* monoculture, that is, their prey in the reference plant community includes not only primary consumers or decomposers but also some secondary consumers whose trophic positions are relatively low (Gratton & Denno, 2006). This multiple-trophic-level feeding mode (i.e., omnivory), however, might have been weakened in the *Spartina* monoculture due to the changes in prey diversity and abundance (Jiang et al., 2022a, Figure 3). The dependence of natural enemies on multiple-trophic-level prey resources is a key feature linking material cycling and energy flow in ecosystems and is therefore important for maintaining ecosystem stability (Dibble & Meyerson, 2014; Perkins et al., 2018; Rooney et al., 2006). It follows that the simplification of the dietary structure of arthropod natural enemies caused by *Spartina* invasion that completely displaces *Phragmites* may affect the stability of saltmarsh ecosystems.

Following *Spartina* removal, the $\delta^{13}\text{C}$ signatures of arthropod natural enemies in the restored *Phragmites* monoculture were almost the same as those of the original *Phragmites* (Figure 4a,e), indicating that natural enemies and their prey in the restored *Phragmites* monoculture relied on *Phragmites* as their major basal trophic resources. In addition, the CR and NR of arthropod natural enemies (Figure 4f) indicate that the restoration of native vegetation following the invasive plant removal can not only restore the dependence of arthropod natural enemies and their prey on the native primary producer but also restore the complexity of the food-web structure of arthropods. In other words, once invaders are removed and native primary producers are restored, native-associated trophic interactions can return to their original state (Ning et al., 2021; Nordström et al., 2014, 2015). In this regard, our results suggest that the *Spartina* control project in Chongming Dongtan has promoted the restoration of native food-web interactions. Nevertheless, given the profound impacts of *Spartina* invasion on native biodiversity and ecosystem functioning, and the costs associated with restoration efforts, effective preinvasion prevention should be the primary goal of these ecosystems' conservation.

CONCLUSIONS

Consistent with our hypotheses, our results suggest that, following its 20-year invasion, *Spartina* has greatly changed arthropod diversity, community structure, and trophic interactions in the saltmarshes of the Yangtze estuary. These changes, however, can be reversed by an engineering project that involved the removal of *Spartina* and the restoration of native *Phragmites* following the principles of ecological engineering. The variation in arthropod assemblages and trophic interactions were mainly related to changes in four biotic and abiotic variables (aboveground biomass, plant density, leaf N, and soil salinity) among habitats. Because arthropod assemblages play an important role in the movement of energy and materials of saltmarshes, the restoration of their diversity and trophic interactions is of great significance to the rehabilitation of saltmarsh ecosystem functioning. In this sense, our results have implications for the management of invasive *Spartina*. To maintain biodiversity and trophic interactions in native saltmarshes, we propose that strict prevention measures be implemented in areas where *Spartina* is currently not introduced. This follows from evidence that prevention is more economical and effective than removal (Waage & Reaser, 2001). In addition, the examples from this ecological engineering project for *Spartina* removal and the restoration of native saltmarshes at Chongming Dongtan provide a good model for how to manage areas where *Spartina* has invaded aggressively. If additional engineering projects are carried out, we would expect these projects to contribute to reversing the negative effects of *Spartina* invasion on native biodiversity and ecosystem processes in China (Meng et al., 2020). Our results increase our understanding of the effects of invasive plants and their removal on the ecosystem structure and functions in saltmarshes and provide insight into the efficacy of the ecological restoration project in the Yangtze estuary.

AUTHOR CONTRIBUTIONS

Rui-Ting Ju, Jia-Jia Jiang, and Yu-Jie Zhao designed and performed the experiments. Jia-Jia Jiang and Rui-Ting Ju identified the morphospecies, designated trophic groups and feeding guilds, analyzed the data, and drew the figures. Lei Gao checked morphospecies, and Evan Siemann checked feeding guilds. All authors contributed to writing the paper.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Jiang et al., 2022a) are available from Dryad at <https://doi.org/10.5061/dryad.5x69p8d35> and novel code (Jiang et al., 2022b) is available from Zenodo at <https://doi.org/10.5281/zenodo.5721231>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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