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INVASIVE SPARTINA

The extended phenology of *Spartina* invasion alters a native herbivorous insect's abundance and diet in a Chinese salt marsh

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Abstract Plant invasions can alter the trophic interactions of invaded ecosystems because of phenological differences between native and invasive plants that may affect the population dynamics and diets of indigenous arthropod herbivores. This issue, however, has seldom been studied. We here report on how abundance and diet of a local tussock moth (*Laelia coenosa*) are affected by the invasive plant *Spartina alterniflora* in a Chinese salt marsh previously dominated by the moth's native host plant, *Phragmites australis*. We monitored the population dynamics of *L. coenosa* from four types of hosts: (1) *Phragmites* in its monoculture, (2) *Spartina* in its monoculture, and either (3) *Phragmites*, or (4) *Spartina* in *Phragmites*–*Spartina* mixtures. Additionally, we tested the diet of *L. coenosa* from the mixtures with isotope analysis. We found that the larval densities of *L. coenosa* were similar on *Spartina* and *Phragmites* in their respective monocultures and mixtures in summer but were greater on *Spartina* than on *Phragmites* in autumn. Stable isotope analysis showed that *Spartina* was a food resource for *L. coenosa*. The change in the insect's population dynamics associated with *Spartina* invasion might be caused by phenological differences between *Spartina* and *Phragmites* in that *Spartina* has a longer growing season than *Phragmites*. Our study indicates that the extended phenology of *Spartina* invasion has altered the abundance and diet of the indigenous herbivorous insect (*L. coenosa*) previously feeding on native *Phragmites*. We predict such alternation may increase the consuming pressure to native plants via apparent competition, and thereby may facilitate the further invasion of the exotic plants in the salt marsh.

Keywords Diet · Habitat · Invasion · Native insect · Salt marsh · Yangtze River estuary

Introduction

Invasion by exotic plants is a major threat to biodiversity and ecosystem integrity and function (Dukes and Mooney 2004; Gratton and Denno 2006). Arthropod biodiversity and abundance are often lower in invasive than in native plant communities (Wu et al.

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2009; also see the review by Bezemer et al. 2014). Some insect herbivores, however, can rapidly adapt or even evolve and thereby exploit exotic plants as new hosts because their native habitats are seriously disrupted (Agrawal and Kotanen 2003), which is often overlooked or ignored (Bezemer et al. 2014).

Previous studies have shown that differences in morphology, nutrition, and allelochemicals of exotic and native plants, as well in the predators and parasitoids that they support, may affect the preference of herbivorous insects for host plants in invaded areas (Bezemer et al. 2014). Although plant phenology is also known to greatly affect insect performance and population dynamics (Hunter 1992), there is little evidence concerning the effects of phenological differences between exotic and native plants on insect herbivores. The phenological effects of invasive plants, therefore, have been receiving increasing attention in food web ecology and invasion biology (Wolkovich and Cleland 2011).

We here report on how the abundance and diet of a tussock moth, *Laelia coenosa*, are affected by the invasive plant *Spartina alterniflora* (*Spartina* hereafter) in a salt marsh previously dominated by the moth's native host plant, *Phragmites australis* (*Phragmites* hereafter). The salt marsh is located in the Yangtze River estuary of China and has been heavily invaded by *Spartina*, leading to a replacement of native *Phragmites* and other natives. This invasion has caused multiple consequences to the native ecosystems (for a review, see Li et al. 2009), one of which is a shift in the habitat of certain native insect herbivores and/or their diet from *Phragmites* to *Spartina* in the salt marsh (Wu et al. 2009). The tussock moth *L. coenosa*, for example, has become increasingly prevalent in *Spartina* over the past 5 years (Fig. 1a, b), although *Phragmites* has historically been the main host for this moth in China (Zhao 2003).

Considering that *Spartina* and *Phragmites* differ in phenology (Liao et al. 2007), we hypothesized that this difference might have resulted in differences in *L. coenosa* performance between the exotic and native plants. To test this hypothesis, we studied the abundance and diet of *L. coenosa* larvae on *Phragmites* and *Spartina* from summer to autumn in the salt marsh. Our aims were to determine whether the longer growing season of *Spartina* versus *Phragmites* affects the native herbivore's abundance and diet in the invaded salt marsh and what are the possible consequences to the native ecosystems if any.

Methods

Study site

This study was conducted at the Chongming Dongtan National Nature Reserve in the Yangtze River estuary, Shanghai, China (31°25′–31°38′N, 121°50′–122°05′E). The whole wetland occupies an area of 32,600 ha and is dominated by native *Scirpus* spp. and *Phragmites* and by exotic *Spartina*. Over the study area, where there is no *Scirpus* spp., *Phragmites* and *Spartina* exist as either their respective monocultures or mixtures (Li et al. 2014).

Monitoring of population dynamics of *L. coenosa*

We monitored the population dynamics of *L. coenosa* at two wetland sites (A: 31°30.930′N, 121°57.411′E; B: 31°30.961′N, 121°57.438′E) 72 m apart. These two collecting sites were selected because numbers of *L. coenosa* were found to be much higher than in other regions in the last 5 years, and also because there were three habitat patterns in which four types of hosts could be investigated: (1) *Phragmites* in its monoculture (PMC); (2) *Spartina* in its monoculture (SMC); (3) *Phragmites* in a *Phragmites*–*Spartina* mixture (PMT); and (4) *Spartina* in a *Phragmites*–*Spartina* mixture (SMT). At each site, we investigated all of the four host types, i.e. PMC, SMC, PMT and SMT. The mixed habitat (PMT, SMT) was transitional in that *Phragmites* was being gradually replaced by the invasive *Spartina*. Five replicate plots (1 × 1 m per plot) were evaluated for each host type. In each replicate, we randomly selected 20 individual shoots of *Spartina* or *Phragmites* in their respective monocultures, 20 *Phragmites* individuals in the PMT, and 20 *Spartina* individuals in the SMT. The number of *L. coenosa* larvae on these plants were counted. In 2011, we surveyed all plots three times (23 June, 26 July, and 20 September) based on the moth's generation numbers in the year and the greatest abundance for each generation's larva. Both *Phragmites* and *Spartina* were growing healthily and had green leaves in June and July. From late September, however, *Phragmites* started to lose its leaves but *Spartina* still had more healthy green leaves. The first and second generations

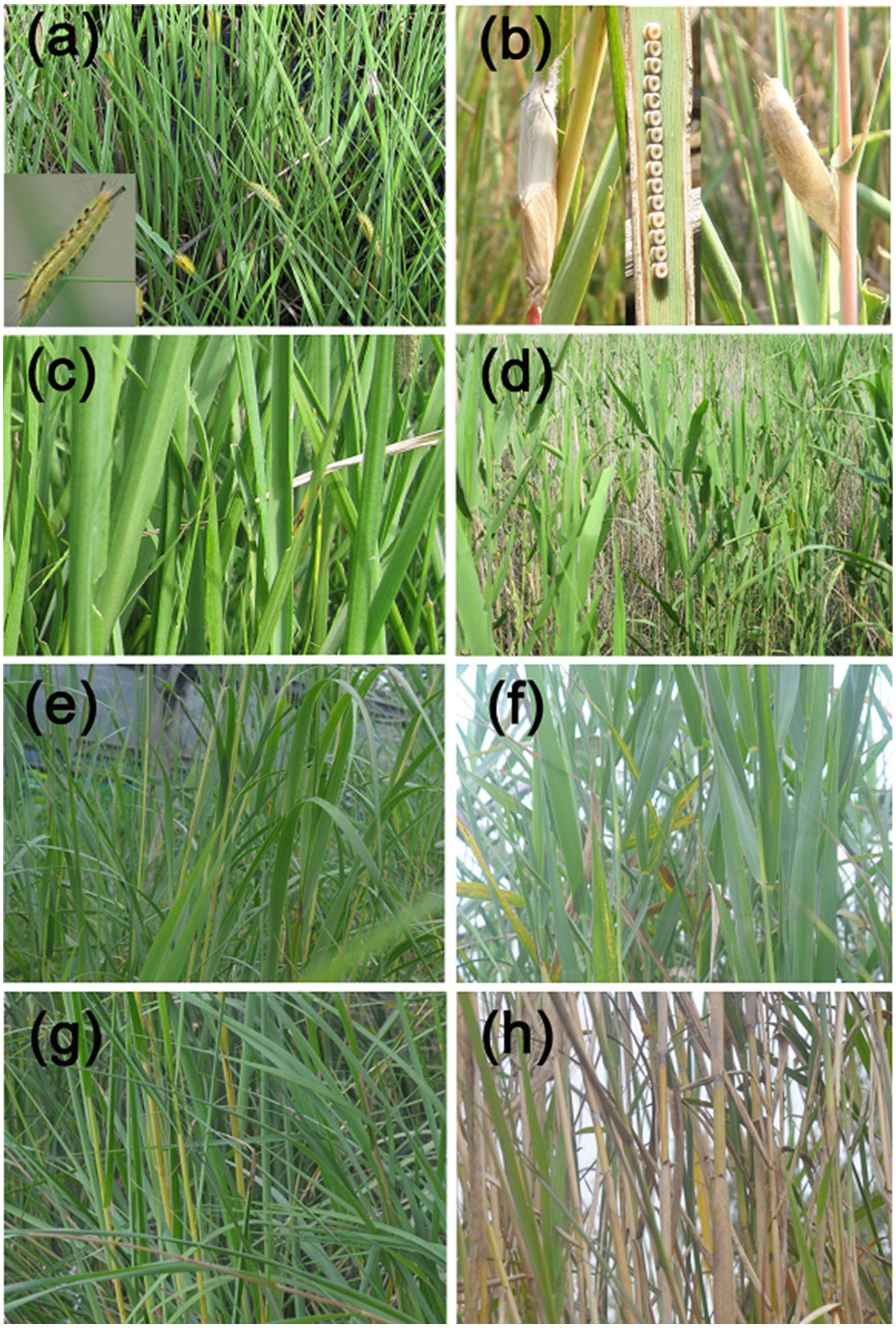


Fig. 1 *Laelia coenosa* and seasonal development of *Spartina* and *Phragmites* at the Chongming Dongtan National Nature Reserve, China. **a** Larva of *L. coenosa* on *Spartina*; **b** egg, adult, and cocoon with pupa of *L. coenosa* on *Spartina*; **c**, **e**, **g** *Spartina* in late June, late July, and late September, respectively; **d**, **f**, **h** *Phragmites* in late June, late July, and late September, respectively

of *L. coenosa* appeared in June and July, respectively, while the third generation appeared and began to prepare for overwintering from late September till late October.

Isotope analysis of the diet of *L. coenosa*

To determine the diet of *L. coenosa*, we randomly collected five larvae from each mixed habitat at site A and B on 23 June 2011. The specimens were divided into two groups: one group collected from *Phragmites*, and the other from *Spartina*. The samples were dried at 75 °C for 72 h and then ground into a fine powder with a mortar and pestle; the powder was passed through a 0.15-mm screen. The powders (0.5–1.0 mg dry mass per sample) were subjected to a stable isotope analysis (Wu et al. 2009) with an isotope ratio mass spectrometer (DELTA plus Advantage, Thermo Scientific, USA) at Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Jiangsu Province. Stable isotope patterns for *Phragmites* and *Spartina* plants were analyzed by the same method. Leaf tissues of *Phragmites* or *Spartina* for isotope analysis were collected from 10 randomly selected plants from each of sampled plot, immersed and rinsed with deionized water before use (Wu et al. 2009). Each treatment was replicated four times.

Data analysis

All data for different habitat treatments at the same collecting time and site and for isotope analysis were subjected to one-way ANOVAs. Before analyses, all data were checked for normality and equal variance. The results are represented as means and SE, and means were compared with Tukey's test. The analyses were performed with the statistical package SPSS NLN, 15.0 (SPSS Inc., Chicago, USA). All data of isotope analysis were multiplied by 10 and then log-transformed before the statistical analysis.

The stable isotope ratios were calculated by the following equation:

$$\delta(X) = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right) - 1\right] \times 1000 \qquad (1)$$

where X is ^{13}C, R is the ratio of ^{13}C/^{12}C, and δ is a notation for the ratios and expressed as ‰. The analytical precision of the measurement is 0.2 ‰ for δ^{13}C.

Results

At each site, the larval density of each plant type decreased with plant growing season prolonging, but the decrease was greater on *Phragmites* than on *Spartina* (Fig. 2). In summer (June–July), *L. coenosa* larval densities were similar on *Spartina* and *Phragmites* in their either monocultures or mixtures, although monocultures support higher densities than mixtures (Fig. 2a–d). In autumn (late September), however, the densities were much higher on *Spartina* than on *Phragmites* both in monocultures and mixtures (Fig. 2e, f).

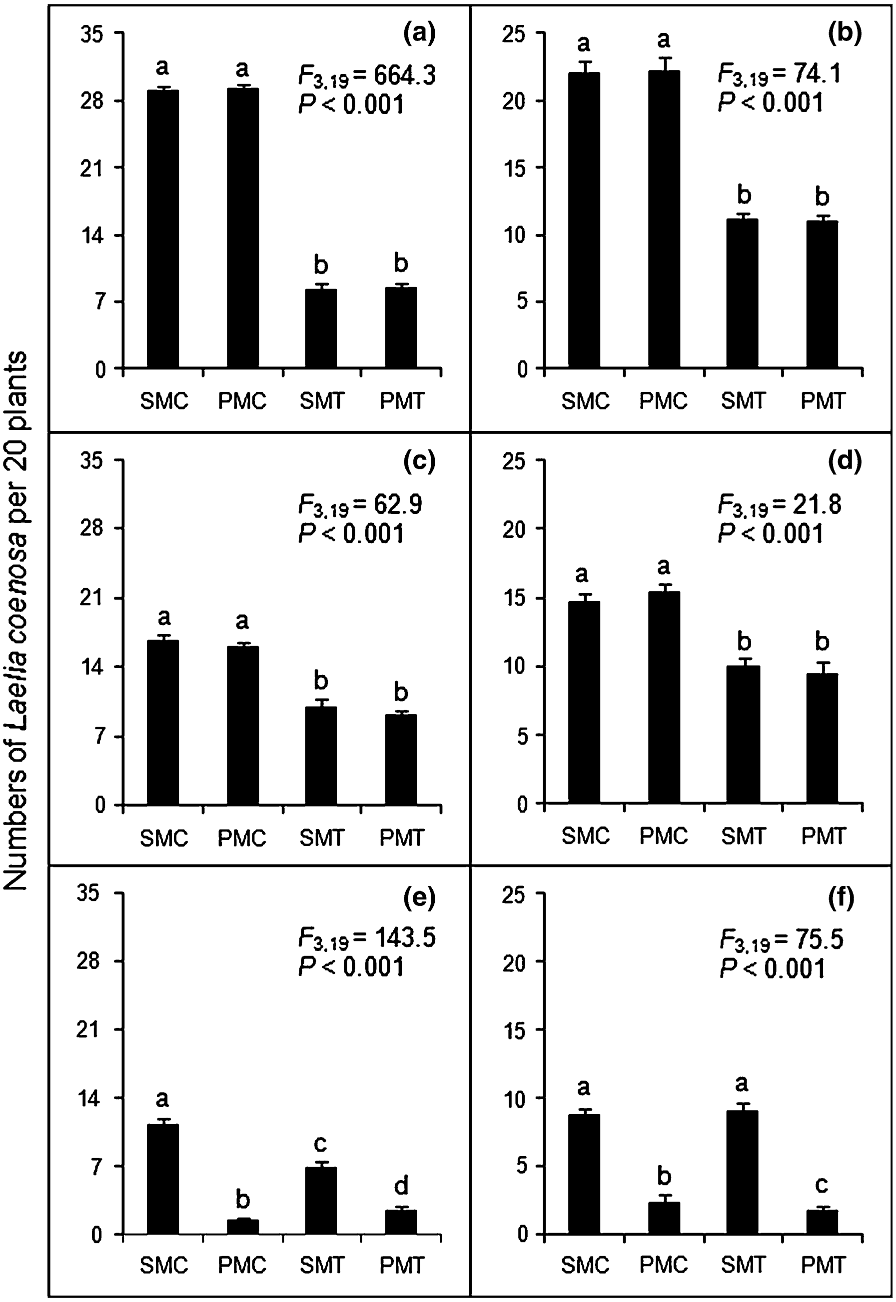
Stable isotope patterns of *Phragmites*, *Spartina*, and *L. coenosa* collected from *Phragmites* and *Spartina* were significantly different ($F_{3,\ 15} = 82.3$, $P < 0.001$) (Fig. 3). The δ^{13}C value of *L. coenosa* collected from *Phragmites* plants was almost the same as that of *Phragmites*, while that of *L. coenosa* collected from *Spartina* plants was intermediate with respect to the values of *Phragmites* and *Spartina* (Fig. 3), indicating that in the mixed habitat, *L. coenosa* collected from *Phragmites* still had selected *Phragmites* as their basal dietary resource, but those collected from *Spartina* had fed not only on *Spartina* but also on *Phragmites*.

Discussion

Invasive plants disrupt many trophic interactions in native communities (van Hengstum et al. 2014). Although effects of exotic plants on native arthropods have been frequently reported (e.g., Wolkovich 2010; Tang et al. 2012), the impact of invasive plants on the population dynamics and diets of native insects has rarely been examined (Bezemer et al. 2014). In the present study, we monitored the population dynamics of native *L. coenosa* on the native *Phragmites* and the invasive *Spartina* and examined its use of the native and the invasive plants as food sources. We found that although some *L. coenosa* still depended on *Phragmites*, many *L. coenosa* larvae lived in the exotic plants in both *Spartina* monocultures and mixed habitats of *Spartina* and *Phragmites*. Isotope analysis indicated that the larvae consumed *Spartina* tissue. These results suggest that *Spartina* may have been a new host species for *L. coenosa*.

Temporal variation in the quantity of the plant resources may support different population sizes of herbivores (Hunter and Price 1992). As such, difference in food supply between *Spartina* and *Phragmites* may be an important factor determining which plant species *L. coenosa* lives on and consumes, although both plants can be hosts for the insect. In eastern China, *Spartina* leaves usually start to develop in early

Fig. 2 Larval densities of *L. coenosa* on *Spartina* and *Phragmites* as affected by host type, collecting time, and site. Values are means + SE. Within each panel, means with the same letters are not significantly different (Tukey's test: $P < 0.05$). The host types SMC, PMC, SMT, and PMT represent, respectively, *Spartina* in its monoculture, *Phragmites* in its monoculture, *Spartina* in a mixed habitat of *Spartina* and *Phragmites*, and *Phragmites* in a mixed habitat of *Spartina* and *Phragmites*. (**a**, **b**), (**c**, **d**), and (**e**, **f**) indicate densities on 23 June, 26 July, and 20 September, respectively. (**a**, **c**, **e**) and (**b**, **d**, **f**) indicate densities at site A and site B, respectively



March and senesce in late November, while *Phragmites* leaves emerge in late March and wither in early October. Because the length of the growing season is 270 days for *Spartina* but only 220 days for *Phragmites* in the Yangtze River estuary (Liao et al. 2007), the temporal differences in the population densities of *L. coenosa* in the monocultures and mixtures may have been caused by phenological differences between the two plant species. In the summer growing season (June and July), both *Spartina* and *Phragmites* produce abundant green, soft leaves (Fig. 1c–f) that supply adequate nutrients to insect herbivores and thus, generate the same higher abundance of *L. coenosa* on the exotic and native plants. In autumn (late September), however, *Spartina* still provides sufficient green leaves for *L. coenosa* but *Phragmites* does

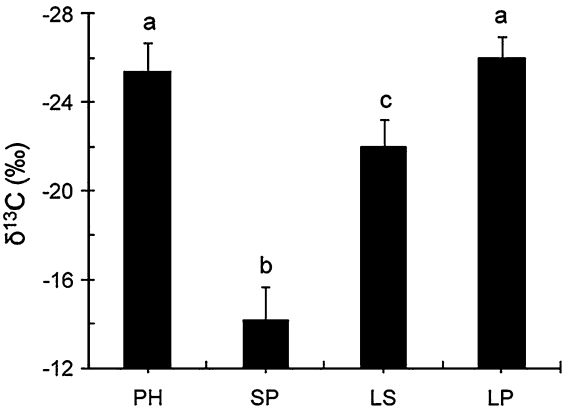


Fig. 3 Distribution of δ^{13}C isotope in *Phragmites* plants (PH), *Spartina* plants (SP), *L. coenosa* larvae that were collected from either *Spartina* (LS) or *Phragmites* (LP) in the mixtures of PH and SP. Values are means + SE. Means with the same letters are not significantly different (Tukey's test: $P < 0.05$)

not because the latter senesces (Fig. 1g, h), and therefore, *Spartina* can support more larvae than *Phragmites*, as temperature is still suitable for the larval development (Zhao 2003).

On the other hand, as suggested by previous researchers (e.g., Feeny 1970; Coley 1980), phenological changes in plant foliar quality, such as seasonal increases in leaf toughness and concentrations of secondary chemicals, may also play an important role in explaining variations in insect abundance among different plants or seasons. In this study, larval density of *L. coenosa* decreased with sampling date, but the decrease was greater on *Phragmites* than on *Spartina*. Other than effects of temperature, seasonal changes in *L. coenosa* abundance between *Spartina* and *Phragmites* may be further explained by effects of different physical and chemical characteristics between the two plant species in different seasons. In addition, larval densities of *L. coenosa* in summer were much higher in monocultures than in mixtures, which may be caused by differences in disturbances (e.g., allelochemicals, predators and parasitoids) between the two community patterns (Bezemer et al. 2014).

Stable isotope analysis provides a relatively quick and logical result for exploring what resources are being used by consumers (Hobson 1999). The stable isotopes of ^{13}C and ^{12}C (expressed as δ^{13}C) are relatively conservative as 'carbon' is transferred from plants to herbivores via a food web (Gratton and Denno 2006) and thus, the C isotope signatures can be used to determine the food sources for herbivores (Vander Zanden et al. 1999). In our study, *Phragmites* (C_3 plant) and *Spartina* (C_4 plant) have distinguishing δ^{13}C isotope signatures (Gratton and Denno 2006) that allow us to identify the food sources of *L. coenosa* through comparing their δ^{13}C signatures among different treatments (Wu et al. 2009). Our results indicate that the insects collected from *Phragmites* still use *Phragmites* as their food resource, but those living in *Spartina* community have fed on both *Spartina* and *Phragmites*, suggesting that *L. coenosa* collected from *Spartina* in the mixture may have come from those feeding on *Phragmites*. Although we did not test δ^{13}C signatures in the monocultures, we predict that the insect may feed on both *Spartina* and *Phragmites* in their respective monocultures. Consistent with our findings, previous studies have shown that a native butterfly, *Euphydryas editha*, can shift its diet from its native host plant (*Collinasia parviflora*) to an exotic plant (*Plantago lanceolata*); *E. editha* evolved such that the proportion that preferred the exotic host to the native host rapidly increased due to ten-year feeding on *P. lanceolata* (Thomas et al. 1987; Singer et al. 1993). Our earlier study (Wu et al. 2009) also predicted that if native *Phragmites* was widely replaced by exotic *Spartina* in China, the native insects that feed on *Phragmites* might expand their diets to include *Spartina* and might even also evolve to prefer *Spartina*.

In the current situation, two issues need to be considered. First, as the phenology of *Spartina* extends, the overwintering of *L. coenosa* may be delayed and its generation number may increase due to the extended period of food resources the insect can use (referred to as "resource effect" of *Spartina*). Second, *Spartina* has standing litter throughout the year while *Phragmites* is often harvested for industrial use. The latter leaves only the litter of culm in winter even if it is not harvested. Therefore, *L. coenosa* can be sheltered effectively by *Spartina* in the overwintering period when the tide comes (referred to as "pool effect" of *Spartina*). If the "resource" and "pool" effects are additive, we can predict that *L. coenosa* abundance may increase considerably, which will ultimately alter interactions between native consumers and native plants.

Nonetheless, the efficiency of the insect's control over *Spartina* may be devalued because the third generation of *L. coenosa* occurs in the late growing season of *Spartina* (i.e. at the mature stage of its seeds), which leads to little regulating influence on *Spartina* at population level. Till now, the ability of *L. coenosa* feeding on *Phragmites* is still stronger than on *Spartina* in the salt marsh (personal observation by the authors), indicating that although the exotic plant supports its higher abundance, the insect cannot effectively control *Spartina* at population level. However, because *Phragmites* is the traditional natural host for the insect (Zhao 2003), the plant has been found to be seriously damaged by *L. coenosa* in eastern China including Chongming Dongtan. The differences in damaging ability between the invasive and native plants by the moths may lead to "apparent competition" (Holt and Kotler 1987; Noonburg and Byers 2005) that will further facilitate *Spartina* to displace *Phragmites* via increasing the pressure of local consumers to native plants (i.e. indirect invasion of *Spartina*). Effect by apparent competition may create an advancing invasion front unlikely to retreat, and could interact with other mechanisms of biological invasion (Orrock et al. 2008), hindering the conservation and restoration of the invaded ecosystem.

In conclusion, our results suggest that *Spartina* invasion has altered the population abundance and has extended the diet of the indigenous herbivorous insect, *L. coenosa* that previously feeds on native *Phragmites*, which may be caused by phenological differences between the invasive and native plants. Such differences can be predicted to change the trophic interactions of the invaded ecosystem and may facilitate further invasion of exotic *Spartina* curtailing the reestablishment of native *Phragmites*.

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