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Coastal exotic plant serves as a habitat for a notorious wetland pest in unfavorable seasons: A case study of exotic *Spartina alterniflora* in China

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Coastal biological invasions pose a wide-reaching threat to various ecosystems, affecting both vegetation and herbivores in native communities. Although herbivores often exert strong top-down control on vegetation, the impact of invasive species on consumers that strongly regulate native species in invaded ecosystems remains unclear. Therefore, through field surveys and feeding preference experiments, this study examined the effects of the invasive *Spartina alterniflora* Loisel. (hereafter, *Spartina*) on the native moth *Laelia coenosa* Hübner (hereafter, *Laelia*), a notorious pest that has been documented to cause significant damage to native *Phragmites australis* (Cav.) Trin. ex Steud. (hereafter, *Phragmites*) marshes in coastal wetlands of China. Field surveys showed that *Laelia* larvae were more abundant and had higher grazing rates in *Phragmites* than in *Spartina* marshes in summer, but these patterns reversed in autumn. Feeding experiments consistently showed that the dietary preference of *Laelia* larvae switched from *Phragmites* in summer to *Spartina* in autumn, likely because *Spartina* has a longer growing season and relatively higher nutritional quality than *Phragmites* in autumn. Thus, by providing shelters (i.e., dietary sources and habitats) during unfavorable seasons, *Spartina* invasions may facilitate this insect pest *Laelia* and potentially amplify its damage to native wetland vegetation. Our work reveals a novel, indirect mechanism of coastal invasion impacts and highlights the importance of incorporating seasonal variation in plant-herbivore interactions.

KEYWORDS

salt marshes, Coastal invasions, insect, plant-herbivore interactions, *Phragmites australis*, *Spartina alterniflora*

1 Introduction

Coastal biological invasions pose a significant threat to biodiversity and ecosystem function (Vila et al., 2011; Tekiel and Barney, 2015), as well as the economy and human health (Mack et al., 2000; Liao et al., 2008; Pejchar and Mooney, 2009; Ehrenfeld, 2010; Pysek et al., 2012). Recently, a growing body of literature has demonstrated that consumers may drive the success of invading species in colonizing new areas (Agrawal and Kotanen, 2003; Strauss et al., 2012; Li et al., 2014; Zhai et al., 2024). Invasive plants may facilitate changes in consumer pressure by offering new food sources or protective cover as refuges for native consumers (Dutra et al., 2011; Stewart et al., 2021; Peller and Altermatt, 2024). One of the predominant, and most extensively tested hypotheses linking herbivores and invasion processes is the Enemy Release Hypothesis (ERH). This hypothesis indicates that invasive species release from natural enemies (i.e. herbivores, pathogens) and gain a competitive advantage in their introduced ranges compared to their co-occurring native counterparts (Keane and Crawley, 2002). While a rapidly increasing number of studies have been conducted to test this hypothesis, the conclusions drawn from different studies appear to be mixed. Several empirical studies support this hypothesis (Keane and Crawley, 2002; Agrawal et al., 2005; Parker and Gilbert, 2007), however, numerous exceptions exist (Agrawal and Kotanen, 2003; Colautti et al., 2004; Parker and Hay, 2005; Chun et al., 2010). There is still no general pattern for explaining the interactions between invasive species and native herbivores and the ERH is a context-dependent hypothesis.

Therefore, understanding the impact of invasive plants on native consumers is important, as the indirect effects mediated by consumers can alter the dynamics of coexistence within native communities. Whether the invasive species are released from herbivores may depend on an array of physical and biological factors: environmental conditions (e.g. light, latitudinal gradients, the presence and absence of neighboring plants, etc.) (Bezemer et al., 2014; Biswas et al., 2015), plant conditions (e.g. the degree of invasiveness, residence time, range sizes spread, the density of the host plant, plant diversity, etc.) (Cappuccino and Carpenter, 2005; Pearse and Hipp, 2014; Biswas et al., 2015; Schultheis et al., 2015), herbivores characteristics (specialists and generalists' native herbivores) (Harvey et al., 2010a; Fortuna et al., 2012), and herbivores' natural enemies such as parasitoids and predators (Ode, 2006; Harvey et al., 2010b). However, comparisons of herbivores on invasive vegetation and natives overlooks the growing season variability of invasive plants and natives, especially in autumn. Autumn is a hugely important season in plant leaf senescence, insect migration and diapause in temperate and arctic ecosystems (Fridley, 2012; Gallinat et al., 2015). For instance, many invasive plants extend their growing season in comparison with natives in autumn; insects can add generations, delayed migration and diapause in warmer autumn (Bale et al., 2002; Fridley, 2012; Gallinat et al., 2015). In addition, some studies also suggested vegetation quality and dietary selection of insects have seasonal changes (Awmack and Leather, 2002; Bale et al., 2002). However, season variability has received less attention in invasion ecology.

Spartina alterniflora, one of the most aggressive invasive species in coastal wetlands around the world, has been well-studied for its impact on native ecosystems and the mechanisms behind these effects (Zhao et al., 2015; Ma et al., 2019; Sun et al., 2020). *Spartina* species not only occupies a space where the native salt marshes vegetation is absent, representing an "empty niche", but also competes with native species (e.g. *Phragmites australis*, *Suaeda salsa* (L.) Pall. and *Scirpus mariqueter* Tang & F. T. Wang) for space in coastal wetlands (Tang et al., 2016; Ma et al., 2020; Zheng et al., 2022). Therefore, *Spartina* invasions significantly affect the physical structures of the native ecosystems and biotic communities. The invasion of *Spartina* in coastal marshes has been reported to cause distribution and dietary changes of herbivores, however, the results from past studies are mixed. Some studies suggested that herbivores prefer native vegetation to invasive *Spartina* in coastal wetlands: insect community (e.g. *Calliptamus barbarus* Costa, *Protohermes costalis* Walker and *Rhopalosiphum rufiabdominalis* S.) (Gao et al., 2006; Peng et al., 2006; Wu et al., 2009), crabs species (e.g. *Helicana wuana* Rathbun) (Zhang et al., 2023); but others advocated that herbivores prefer invasive *Spartina* to native species: crabs species (e.g. *Sesarma dehaani* H.Milne Edwards, *Helice tientsinensis* Rathbun) (Wang et al., 2008; Qin et al., 2010), nekton species (e.g. *Chelon haematocheilus* Temminck & Schlegel, *Synechogobius ommaturus* Richardson) (Quan et al., 2007); and some studies found that it is not distinctly different: snail species (e.g. *Assiminea latericea* H. Adams & A. Adams and *Cerithidea largillierti* R. A. Philippi) (Wang et al., 2014). Therefore, there is an ongoing debate as to the relative importance of invasive *Spartina* and native species to herbivores in coastal wetlands.

Here, we examined how the abundance and diet of the native insect *Laelia coenosa* are affected by the invasive *Spartina* from summer to autumn in coastal marshes through laboratory and field experiments. The salt marsh is located in the Yancheng National Nature Reserve of China and has been heavily invaded by *Spartina*. First, we monitored the density of *Laelia coenosa* larvae on *Phragmites* and *Spartina* from summer to autumn in high, middle and low marshes. Next, we compared the degree of leaf damaged by *Laelia coenosa* larvae for *Phragmites* and *Spartina* to examine whether the native insect *Laelia coenosa* prefers native *Phragmites* to invasive *Spartina* to support the Enemy Release Hypothesis. Finally, we explored whether the Enemy Release Hypothesis is constant in summer and autumn. Specifically, we assessed the larval feeding preference of *Laelia coenosa* on *Spartina* and native *Phragmites* in the laboratory in the different growing seasons.

2 Materials and methods

2.1 Study sites

The study was conducted at the Yancheng National Nature Reserve in Yancheng city of Jiangsu Province of China (32°20'–34° 37'N, 119°29'–121°16'E) (Figure 1A), which has experienced the widest and most extensive areal coverage of *Spartina* in China (Zuo

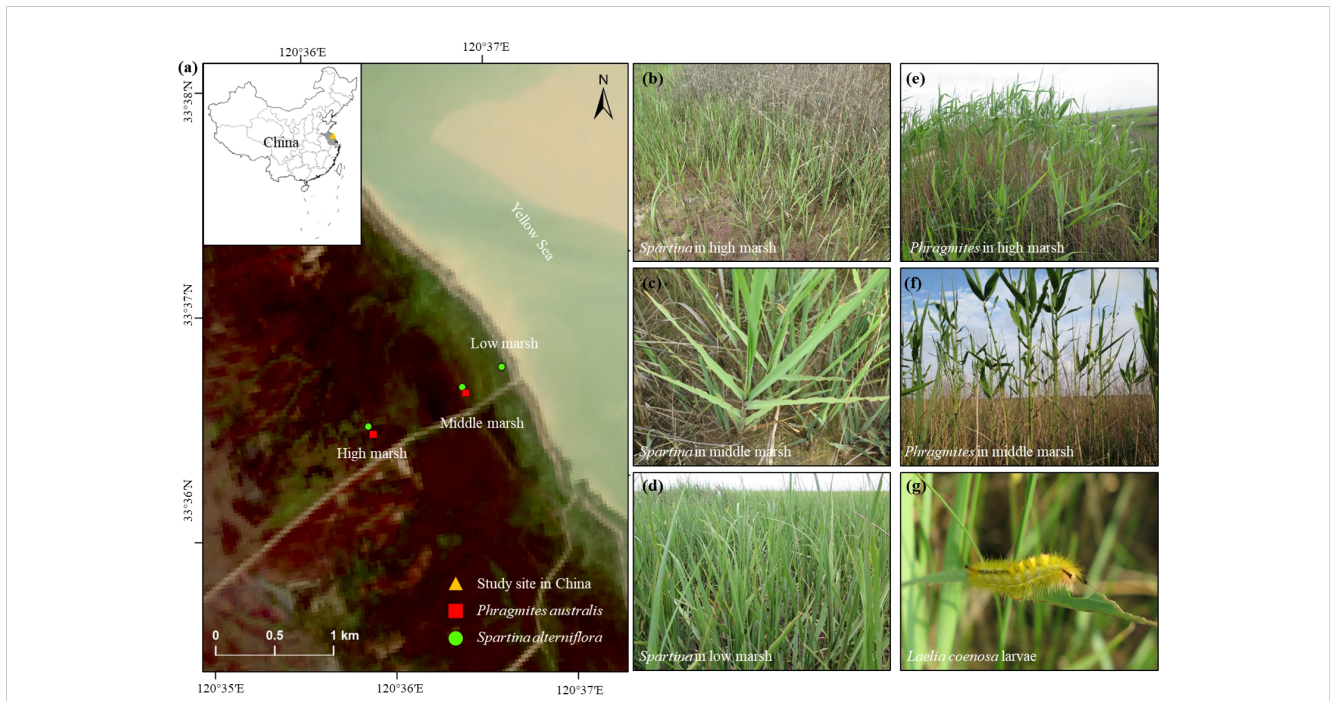


FIGURE 1

Location of the Yancheng National Nature Reserve in Jiangsu Province of China and sampling sites in the Yancheng National Nature Reserve with a true color remote sensing image on August 28, 2016 (A). Photographs of sample sites in summer: (B) the high marsh dominated by *Spartina* monoculture; (C) the middle marsh dominated by *Spartina* monoculture; (D) the low marsh dominated by *Spartina* monoculture; (E) the high marsh dominated by *Phragmites* monoculture and (F) the middle marsh dominated by *Phragmites* monoculture. Photograph of *Laelia coenosa* larvae in summer (G). Photographs were taken by Zezheng Liu.

et al., 2012). The Yancheng National Nature Reserve lies in the transition belt between subtropical and warm-temperate zones with distinctive seasons and a rainy summer. The average annual temperature and precipitation are 11.4–13.8°C and 1000–1080 mm, with 54% of precipitation occurring in summer (June–August) (Liu et al., 2007; Zhou et al., 2009). The average seasonal precipitation of Yancheng city amounts to 545.56 mm in summer (June–August) and 203.03 mm in autumn (September–November) from 1960 to 2020, respectively (Qi et al., 2023). The average seasonal temperature of Yancheng city amounts to 25.8°C in summer (June–August) and 16.70°C in autumn (September–November) from 1981 to 2018, respectively (Sheng, 2019). The salt marsh is dominated by native *Phragmites australis*, *Suaeda salsa* and by exotic *Spartina alterniflora*. The distribution of vegetation succession from land to seaward is *Phragmites australis*, *Suaeda salsa*, *Spartina alterniflora*, and tidal flat (Zhang et al., 2013). The three species have some overlap in their distribution zones.

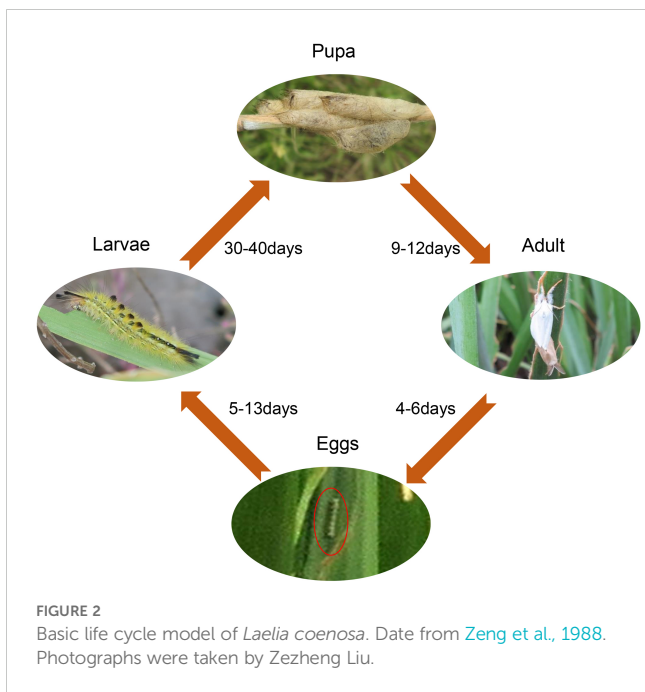
2.2 Study species

Laelia coenosa, a generalist herbivorous insect, is a moth of the *Lepidoptera* order, *Lymantriidae* family found in North Africa, southern and central Europe, through Russia and eastern Asia up to Japan (Zeng et al., 1988). It is common and widespread in China, and widely distributed in inland (e.g. Hunan, Hubei, Anhui, and Jiangxi Province) and coastal (e.g. Hebei, Shandong, Jiangsu, and

Shanghai Province) zones (Zeng et al., 1988; Xia et al., 1993; Ma et al., 2015). It generally produces two or three generations per year (Supplementary Table S1) and each generation has a four-stage life cycle: egg, larva, pupa and adult (Figure 2). In our study sites, the larvae of *Laelia coenosa* occurred during two periods: from mid-April to mid-June for the first generation, and from mid-June to late September for the second generation (Supplementary Table S1) (Xia et al., 1993). Hibernation takes place as an egg or larvae between the middle of October and early March of next year (Zeng et al., 1988). *Laelia coenosa* has long larvae life stages (Figure 1G), which primarily feed on a wide range of host plants including *Poaceae* and some *Cyperaceae*, especially *Phragmites* and *Miscanthus*, and 30%~40% production of reeds lost mainly by late-instar larvae (Zeng et al., 1988).

2.3 Sampling and analysis

To examine the spatial-temporal distribution of native insect *Laelia coenosa*, five distinct zones (habitats) were delimited based on elevation and vegetation type in June (summer) and September (autumn): (1) the high marsh dominated by *Phragmites* monoculture; (2) the high marsh dominated by *Spartina* monoculture; (3) the middle marsh dominated by *Phragmites* monoculture; (4) the middle marsh dominated by *Spartina* monoculture; (5) the low marsh dominated by *Spartina* monoculture (Figures 1B–F). In each sampling habitat at each



sampling season, 0.5×0.5 m quadrat was randomly placed for sampling. The sample sizes are 16 except those in *Phragmites* marsh whose sample sizes are 8. From the quadrat, numbers of native insect *Laelia coenosa* were counted, and leaves of five plants randomly selected were collected. In summer, all leaves of selected plants were collected, whereas only the up leaves were collected in autumn because the other leaves obviously were not consumed by

the second-generation larvae in autumn, but consumed by the first generation in summer. Samples were stored on ice during transportation to the laboratory.

To assess the degree of leaf damage, the area of leaf damaged and percentage of leaf area damaged were calculated. The area of leaf damaged was calculated for each leaf as “complete area of damaged leaves” minus “remaining leaf area”. The complete area of damaged leaves was estimated separately for *Phragmites* and *Spartina* by using regression equations between leaf area and length × width from 115 and 59 undamaged leaves of *Phragmites* and *Spartina* from the Yancheng National Nature Reserve salt marshes (Figure 3). When leaves width and length are not available because leaves are severely damaged, we used “average complete area of damaged leaves” minus “remaining leaf area” as the area of leaf damaged. The average complete area of damaged leaves is the mean value of undamaged leaf area in the same habitat as damaged area calculated. The percentage of leaf area damaged was calculated as “area of leaf damaged” divided by “complete area of damaged leaves” or “average complete area of damaged leaves”. The length, width, and area of leaves were measured with a Yaxin-1241 leaf area meter. In autumn, we also calculated the percentage of leaf number damaged between *Spartina*-invaded and non-invaded *Phragmites* habitats by dividing the number of damaged leaves by the total number of leaves.

2.4 Dietary preferences experiment

The two-choice experiment was designed to investigate the feeding preference of *Laelia coenosa* between native *Phragmites*

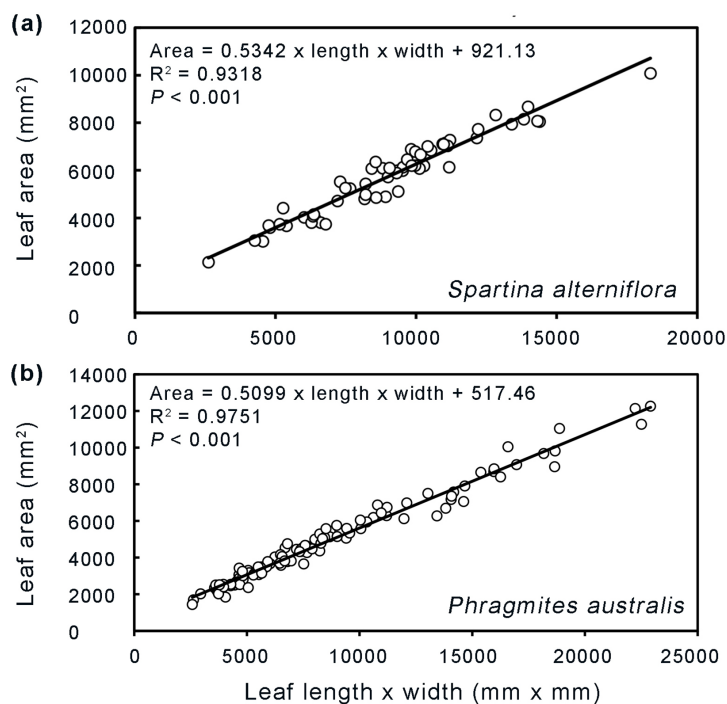


FIGURE 3
Relationship between leaf area and length×width for *Spartina alterniflora* (A) and *Phragmites australis* (B).

and exotic *Spartina*. One larva of *Laelia coenosa* and two leaves of each plant species were placed in a loosely capped 1500 mL wide-mouthed plastic bottle, covering the top with a gauze net in case larvae escaped. To keep the experiment systems moist, pure water (10–20 mL) was added to the jar at a depth of approximately 0.5 cm. All the plastic jars were subjected to 24 hours' nature photoperiod in June and September at field temperature. All larvae of *Laelia coenosa* were collected from the same area of the middle marsh zone, and the length and color were approximately consistent. The mean length of *Laelia coenosa* was 37.18 ± 4.96 mm and 30.1 ± 5.86 mm in June and September respectively (Supplementary Figure S1). While collecting the larvae in June and September, we also collected the top leaves of *Spartina alterniflora* and *Phragmites australis* and trimmed them to a length of 20 cm. The feeding experiment was used with twelve replicates, however, only eight replicates data are available, due to the death of *Laelia coenosa*. The leaf area of damaged was calculated as the leaf area before the experiment minus the remaining leaf area after experiment. The percentage of damaged was calculated as the leaf area of damaged divided by leaf area before the experiment. The leaf area was measured before and after feeding trials with a Yaxin-1241 leaf area meter.

2.5 Statistical analysis

The density of *Laelia coenosa* larvae and degree of leaf area damaged for different habitat treatments at the same season were subjected to one-way ANOVAs. *Laelia coenosa* feeding preferences were examined using paired t-tests (two-sided). Before statistical analyses, all data were checked for normality and were log-transformed to improve the normality distribution. The results are represented as means and SE, and the level of statistical significance was set at $P < 0.05$. All statistical analyses were performed with the statistical package SPSS NLN, 15.0 (SPSS Inc., Chicago, USA).

3 Results

3.1 Spatial-temporal distribution pattern of *Laelia* larvae

In total, 582 larvae of *Laelia coenosa* were surveyed in sampling sites in this study. Distribution pattern of larvae at all five sampling plots in two sampling seasons is shown in Figure 4. *Laelia coenosa* showed significantly different along the sampling plots among the two growing seasons. Generally, the density of larvae in summer was higher than in autumn in five sampling sites ($P < 0.01$). We surveyed 523 larvae of *Laelia coenosa* in summer, while the number of larvae in autumn was 59 in all sampling sites. In summer (the first generation of *Laelia coenosa*), *Laelia coenosa* exhibited the highest level in *Phragmites* middle marsh, reaching a density of 23.38 ± 6.22 ind./0.25 m². The lowest density also appeared in the middle marsh, however, in *Spartina* habitat with a density of 3.31 ± 0.45 ind./0.25 m². Compared to the middle marsh, the density of the native insect *Laelia coenosa* did not significantly differ among the two habitats in the high marsh, with the density of 6.00 ± 0.65 and 6.25 ± 0.87 ind./

0.25 m² in *Phragmites* and *Spartina* habitats, respectively (Figure 4). The density of larvae in *Spartina* low marsh is second to that in *Phragmites* middle marsh, with a density of 8.44 ± 1.34 ind./0.25 m² (Figure 4). However, *Laelia coenosa* preferred *Spartina* marsh, and was absent from *Phragmites* habitat in autumn (the second generation of *Laelia coenosa*) (Figure 4). *Laelia coenosa* exhibited the highest level in *Spartina* low marsh, reaching a density of 2.50 ± 0.30 ind./0.25 m². Therefore, season and vegetation species significantly affected the abundance of the native insect *Laelia coenosa*.

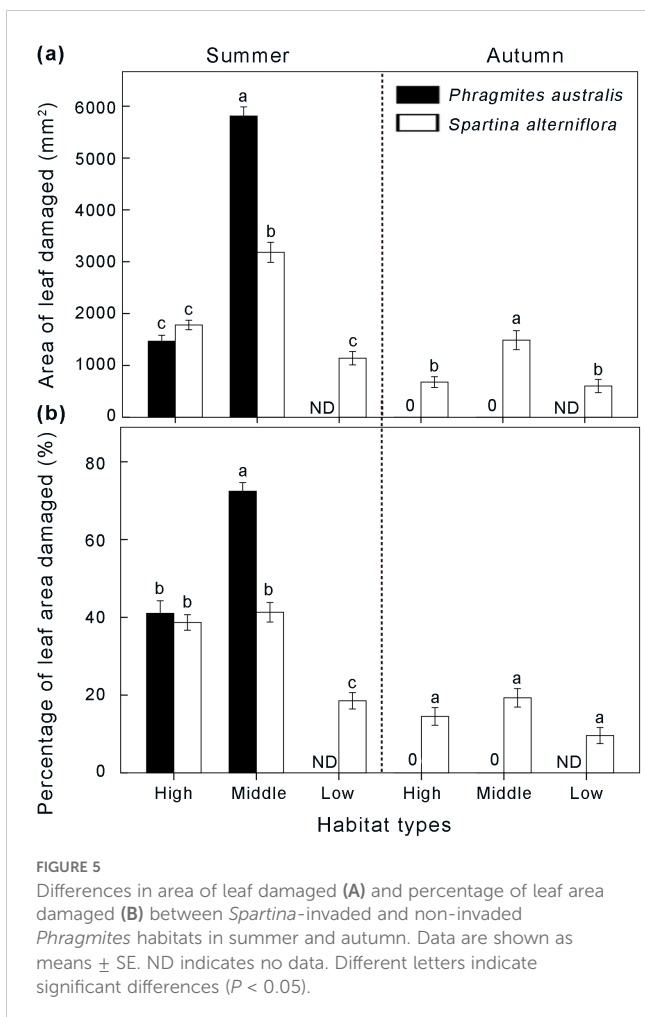
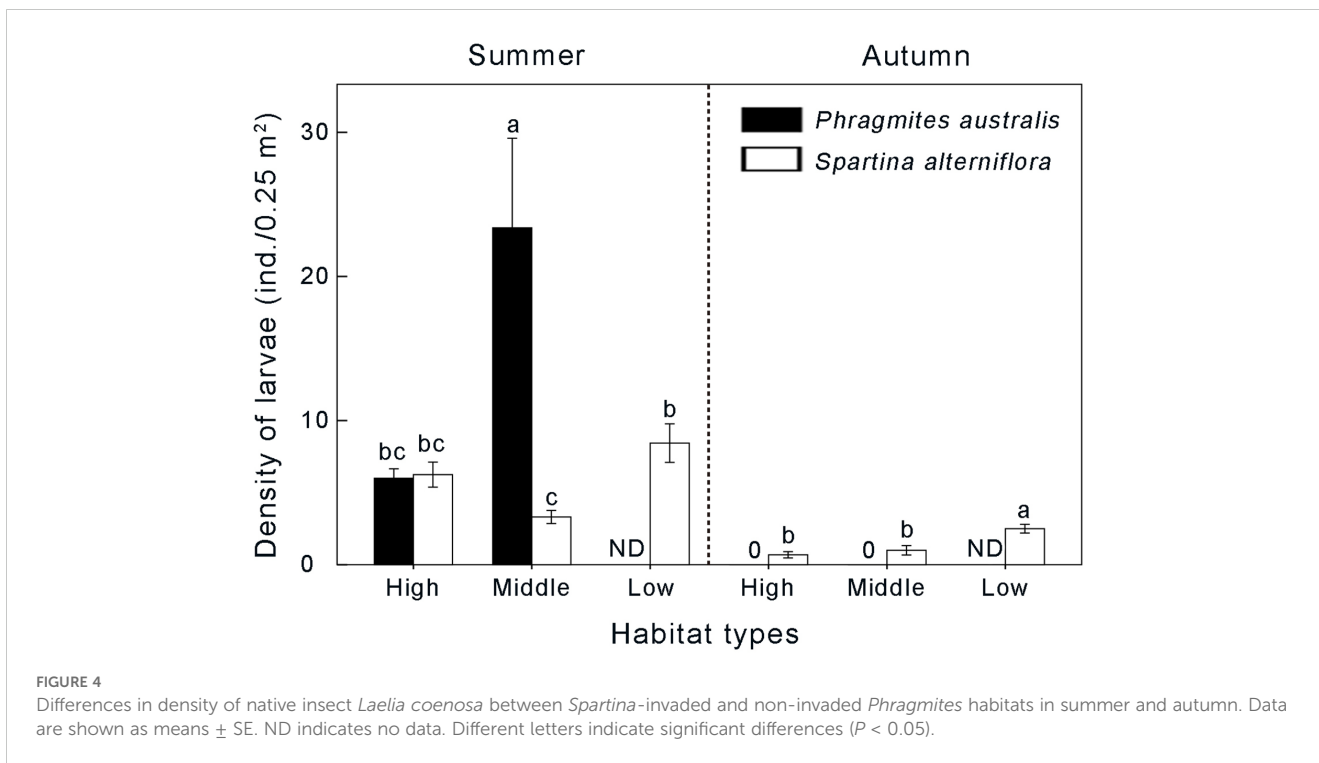
3.2 Degree of leaf damage for *Phragmites* and *Spartina*

Similar to the spatial-temporal distribution pattern of larvae, the degree of leaf damage also exhibited significant differences along the sampling habitats between the two growing seasons (Figure 5). In summer, leaves damaged by the first generation of *Laelia coenosa* showed the highest average extent of damage in the middle marsh area of the *Phragmites* community ($72.41 \pm 2.11\%$) (Figure 5B), with a damaged area of 5810.28 ± 173.91 mm² for each leaf (Figure 5A). In the middle marsh, the area of leaf damaged and percentage of leaf area damaged in *Phragmites* community were significantly higher than in *Spartina* community ($P < 0.05$) (Figure 5). In the high marsh, however, there was no significant difference in the area of leaf damaged and percentage of leaf area damaged between *Phragmites* community and *Spartina* community ($P > 0.05$) (Figure 5). The area of leaf damaged in *Spartina* community did not significantly differ in the high and low marshes, with 1778.66 ± 86.96 mm² and 1138.34 ± 134.39 mm² for each leaf, respectively ($P > 0.05$) (Figure 5). In autumn, the degree of leaf damage by the second generation of *Laelia coenosa* in the middle marsh area of the *Spartina* community reached the highest level (1478.26 ± 189.72 mm²), which was significantly higher in the high and low marshes ($P < 0.05$) (Figure 5). However, native *Phragmites* didn't provide food for the native insect *Laelia coenosa* in autumn.

In autumn, more than 60% of the leaves were affected by leaves of *Laelia coenosa* (Figure 6). In general, the proportion of damaged *Spartina* leaves was significantly higher than that of the *Phragmites* community ($P < 0.001$). The proportions of damaged *Spartina* leaves were more than 90% at different elevation levels, with $90.63 \pm 1.90\%$, $97.98 \pm 0.95\%$ and $92.16 \pm 1.89\%$ in high, middle and low marshes, respectively. The proportions of damaged *Phragmites* leaves were significantly higher in the middle elevation marsh ($86.58 \pm 2.28\%$) than in the high elevation marsh ($65.97 \pm 2.39\%$) ($P < 0.001$) (Figure 6).

3.3 Feeding preference for *Phragmites* and *Spartina*

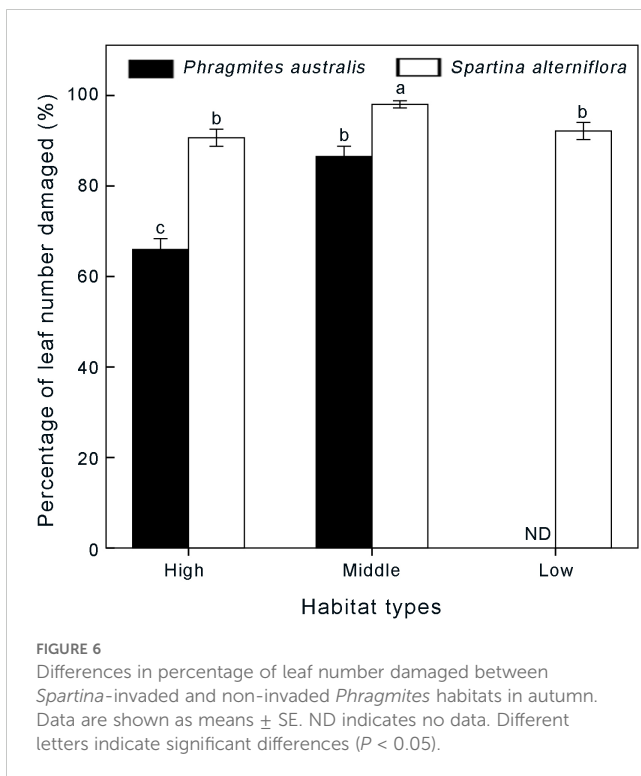
In the lab feeding trial, the amount of *Phragmites* consumed by *Laelia coenosa* was significantly higher than *Spartina* in summer, whereas *Laelia coenosa* preferred *Spartina* in autumn (Figure 7). In



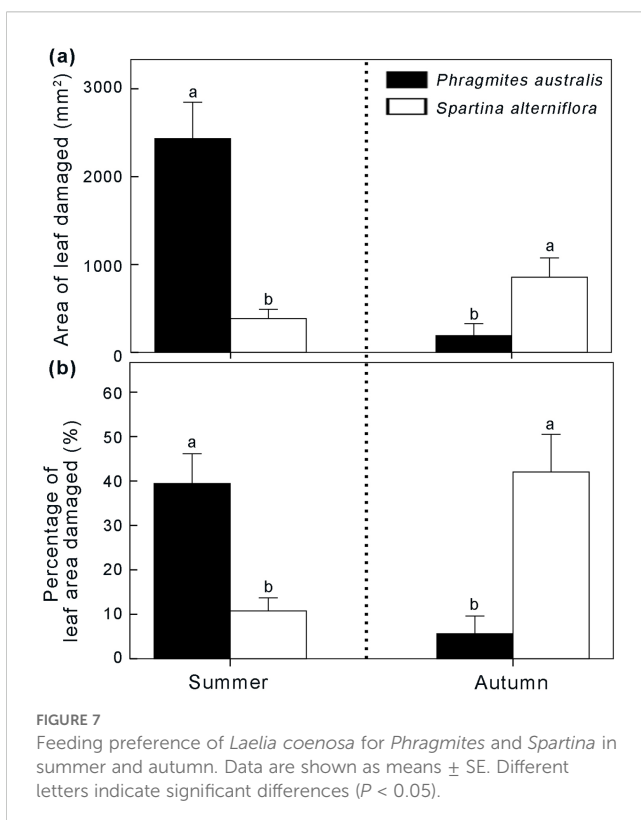
summer, the leaf area of *Phragmites* consumed by larvae was $2433.88 \pm 410.10 \text{ mm}^2$, more than six times higher than that of *Spartina* ($378.9 \pm 106.98 \text{ mm}^2$, $P < 0.001$) (Figure 7A). The percentage of *Phragmites* consumed by *Laelia coenosa* was also higher than that of *Spartina* ($39.48 \pm 6.72\%$ vs. $10.57 \pm 3.01\%$, $P < 0.001$) (Figure 7B). In autumn, however, the leaf area of *Phragmites* consumed by larvae was only a quarter as high as that of *Spartina* ($187.22 \pm 133.73 \text{ mm}^2$ vs. $851.41 \pm 218.43 \text{ mm}^2$, $P < 0.001$) (Figure 7A). Therefore, we could predict a shift in feeding preference by *Laelia coenosa* depending on the growing seasons.

4 Discussion

This study revealed the effects of an invasive *Spartina* on insect species and related the changes in distributions and dietary breadth across two seasons in coastal wetlands. In our survey, the percentage of damaged leaves across the five sampling plots exceeded 60%, and in some cases, approached nearly 100% (Figure 6). This may significantly underestimate the true extent of leaf damage by herbivores, as it fails to include leaves that were entirely eaten or abscised prematurely due to heavy damage, particularly in *Phragmites* marshes. Our findings also indicated that *Laelia coenosa* larvae preferred *Phragmites* habitats over the invasive *Spartina* communities in summer, while the preference was reversed in autumn (Figure 4). The characteristics of leaf damaged and the spatial-temporal distribution pattern of the native insect *Laelia coenosa* exhibited similar patterns of change (Figure 5). Feeding experiments consistently showed that the dietary preference of *Laelia* larvae switched from *Phragmites australis* in summer to *Spartina alterniflora* in autumn (Figure 7).



From these findings, we consistently concluded that *Laelia coenosa* has recently expanded its habitat range, now inhabiting not only native *Phragmites* communities but also invasive *Spartina* communities in coastal wetlands.



Invasive plants can affect the spatial and temporal dynamics of native insect populations by disrupting a wide range of trophic interactions (Harvey et al., 2010a; Bezemer et al., 2014). Previous studies have consistently concluded that food source is a primary factor affecting the distribution and survival of herbivorous insects. For example, the invasive *Phragmites australis* offers a more favorable feeding habitat for the dominant grazers (e.g. *Physella gyrina* Say and *Fossaria* (Bakerlymnaea) *bulimoides* group), increasing their density along the southern shoreline of Lake Erie in the USA (Holomuzki and Klarer, 2010). The introduction of *Spartina* in salt marshes has also led to dietary shifts in crab species such as *Helice tientsinensis* and *Chiromantes dehaani* H. Milne Edwards (Qin et al., 2010). The non-native bryozoan *Membranipora membranacea* can serve as a new food source for the native nudibranch *Onchidoris muricata* in the summer and fall in the Gulf of Maine of the USA (Pratt and Grason, 2007). Additionally, invasive predators can disrupt food webs by forcing native predators to feed on suboptimal food sources, and reorganize the low-trophic-level communities, thereby causing significant disruption to native food web structures (Wainright et al., 2021). Thus, invasive species have the potential to alter the resource utilization patterns of native species, leading to both direct and indirect modifications in food web dynamics.

A wide variety of plant traits, such as carbon and nitrogen content, defensive metabolites, morphological characteristics, and phenological traits, are known to significantly influence the preferences for host plants and the associated distribution of herbivorous insects (Awmack and Leather, 2002; Salgado and Saastamoinen, 2019; Bovay et al., 2024). In general, larvae of the *Lepidoptera* order prefer leaves with high nitrogen and water content and low toughness (Peng et al., 2006; Ma et al., 2015). Native herbivores tend to prefer native plants, because exotic species may not provide a suitable diet (Tallamy and Shropshire, 2009). Previous studies have suggested native insect species (*Laelia coenosa*) prefer native *Spartina* in the USA to invasive *Spartina* in China through greenhouse experiments, due to differences in leaf nitrogen content and toughness rather than volatile compounds (Ma et al., 2015). Some studies suggested that the leaf total nitrogen of *Spartina* was significantly lower than that of *Phragmites* in summer in coastal wetlands (Jiang et al., 2009; Guo et al., 2023). In addition, some previous studies indicated that leaves of *Spartina* are more thickness and toughness than those of *Phragmites* in coastal wetlands (Hendricks et al., 2011; Guo et al., 2023). *Spartina* species, known for their salt-secreting capability, have leaves containing salt particles that can reduce the palatability of their diet for herbivorous insects (Smart and Barko, 1978; Smit et al., 2024). Therefore, insects *Laelia coenosa* tend to prefer feeding on native *Phragmites* over exotic species *Spartina* during the summer when food is abundant.

Furthermore, *Spartina* species have a longer growing season compared to the native *Phragmites* in China's salt marshes (Jiang et al., 2009; Wang et al., 2006). The growing season lengths for *Spartina* and *Phragmites* were 270 days and 220 days in the Yangtze Estuary of China, respectively (Liao et al., 2007). In autumn, *Spartina* exhibits higher leaf total nitrogen values and plant tissue water content than *Phragmites* (Wang et al., 2008; Jiang et al., 2009),

which tends to make it a more attractive food source for insects. In September, total plant C and N stock of *Spartina* stands in the Yangtze Estuary of China were 3.83 kg m⁻² and 57.21 g m⁻², respectively, while the values for *Phragmites* stands were significantly lower, at 0.89 kg m⁻² and 15.86 g m⁻², respectively (Liao et al., 2007). Consequently, the invasive *Spartina* creates a more palatable diet for insects, enhancing their density and effectively buffering against food deprivation stress in autumn in coastal wetlands. Similarly, many woody invasive plants in North America retained their leaves later in the autumn than native plants, resulting in extended leaf phenology. The extended leaf phenology of invasive species enhances their competitive advantage over native species by providing increased access to understory light (O'Connell and Savage, 2020). Therefore, there is a seasonal shift in insect habitat selection from *Phragmites* in summer to *Spartina* in autumn in coastal wetlands.

The invasive *Spartina*, characterized by its extended growing season, offers a dietary source and habitat for herbivorous insects in autumn. This additional resource may support an extra generation of insects in the fall and be advantageous for their overwintering, resulting in a shorter overwintering period and a higher survival rate of insects in spring. Consequently, this could lead to an increase in both the frequency and intensity of insect outbreaks in coastal wetlands. In turn, these outbreaks may facilitate further invasion of *Spartina* by causing significant damage to native species, as native insects could contribute to the decline of native species that otherwise might have competed with *Spartina*. Thus, the differences in damaging ability between the invasive and native plants by the native herbivorous may hinder the conservation and restoration of the invaded ecosystem. Looking ahead, additional research is necessary to validate these assumptions and to achieve a more comprehensive understanding of the impact of *Spartina* invasion on various insect behaviors, including oviposition preferences and the selection of overwintering sites.

5 Conclusions

In conclusion, our results suggest that the native insect *Laelia coenosa* preferentially consumes native *Phragmites* over invasive *Spartina* in summer, which may contribute to the decline of native *Phragmites*. Thus, the interaction between invasive *Spartina* and native insects appears to support the Enemy Release Hypothesis in summer. However, this pattern is not consistent in autumn. The invasive *Spartina* offers a dietary source and habitat for herbivorous insects *Laelia coenosa* in autumn with its extended growing season. These differences are anticipated to alter the trophic interactions within the invaded ecosystem, potentially aiding in the further spread of the exotic *Spartina* and hindering the reestablishment of native *Phragmites* populations. This finding helps explain the mixed results often observed in hypothesis tests and enhances our understanding of the mechanisms behind coastal invasions. Such insights will aid in understanding and predicting the success of invasive species in natural ecosystems.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

TX: Conceptualization, Data curation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. XM: Writing – original draft, Writing – review & editing. YL: Supervision, Writing – original draft, Writing – review & editing. HX: Writing – original draft, Writing – review & editing. SZ: Writing – original draft, Writing – review & editing. ZL: Conceptualization, Formal analysis, Funding acquisition, Investigation, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1478599/full#supplementary-material>

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