



A plant invader declines through its modification to habitats: A case study of a 16-year chronosequence of *Spartina alterniflora* invasion in a salt marsh

Long Tang^{a,b}, Yang Gao^c, Cheng-huan Wang^d, Bin Zhao^b, Bo Li^{b,*}

^a School of Human Settlements and Civil Engineering, Xi'an Jiaotong University, Xi'an, Shaanxi Province, China

^b Coastal Ecosystems Research Station of the Yangtze River estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, Shanghai, China

^c Institute of Water Resources and Hydro-electric Engineering, Xi'an University of Technology, Xi'an, Shaanxi Province, China

^d School of Life Sciences, Shanghai Key Laboratory of Urbanization and Ecological Restoration, East China Normal University, Shanghai, China

ARTICLE INFO

Article history:

Received 30 March 2012
Received in revised form 13 July 2012
Accepted 10 August 2012
Available online 6 October 2012

Keywords:

Chongming Dongtan
Feedbacks
Inundation time
Invasion dynamics
Plant invasions
Population decline
Spartina alterniflora
Standing litter
Time-dependence

ABSTRACT

Many invaders can substantially modify the habitats that they invade, but the long-term effects of these changes on the invaders themselves remain uncertain. *Spartina alterniflora*, an aggressive invasive plant of coastal wetlands, can reduce the tidal inundation time and accumulate standing litter by sediment trapping and by high production. A 16-year chronosequence of *S. alterniflora* invasion in Dongtan marsh in Yangtze River estuary, China revealed that *S. alterniflora* had a 5-year enhancement followed by a longer decline. Steady decreases in the tidal inundation time and increases in the standing litter per unit living mass were observed. A controlled experiment showed that the growth of *S. alterniflora* was significantly limited by the decrease in the inundation time and by the standing litter. These results indicate that the changes in habitats caused by invaders can limit the invaders over time because the accumulation of habitat changes creates certain habitat properties that exceed the optimal range for invaders. These findings highlight the importance of the impacts of invasion on the long-term dynamics of invasive populations.

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1. Introduction

Understanding invasion dynamics and mechanisms can contribute to the management of invasions (Taylor and Hastings, 2004; Strayer et al., 2006). Many studies have focused on the limiting factors that no longer restrain invasive species in invaded habitats. However, substantial changes in invaded habitats are often induced by the invaders themselves through ecosystem engineering effects (Crooks, 2002; Strayer et al., 2006; Cui et al., 2011). It is likely that these changes will influence invasive populations because the performance of all species is habitat-dependent.

The feedback between invaders and invaded habitats may need to be understood over long time scales. Invaders often affect invaded habitats in three primary ways (Crooks, 2002). First, invaders can change resource availability. For example, invasive cordgrasses (*Spartina* spp.) have converted the soil properties by trapping sediment (Chung, 2006; Li et al., 2009; Wan et al., 2009). Second, invaders can change nitrogen processes. Certain invasive

plants are nitrogen fixers and have altered nitrogen cycling (Crooks, 2002; Strayer et al., 2006). Third, invaders can change the disturbance regime of ecosystems that they invade (Crooks, 2002; Strayer et al., 2006). These environmental effects are often slow, can be cumulative and take many years to develop (Strayer et al., 2006). For example, it often requires decades for a shift in plant species to change soil characteristics (Crooks, 2002; Chung, 2006). Therefore, studying the long-term feedback between invaders and their habitats can contribute to the understanding of invasion dynamics and mechanisms.

The long-term effects of the changes in habitats induced by invaders on the invaders themselves are still uncertain in many cases. Most studies of the effects of invaders are of short duration, and the results of these studies have often indicated that the changes in habitats induced by invaders can favour the invaders themselves (Strayer et al., 2006; Zhao et al., 2009). For example, *Tamarix* spp. can inhibit native competitors by decreasing the channel width, blocking water flows and deepening the water table (Crooks, 2002). However, it is not quite clear whether the habitats in which these hydrological changes accumulate are suitable for invasive species. A few recent studies have shown that certain invaders were limited by changed habitats over time (Lankau

* Corresponding author. Tel.: +86 21 65642178; fax: +86 21 65642178.
E-mail address: bool@fudan.edu.cn (B. Li).

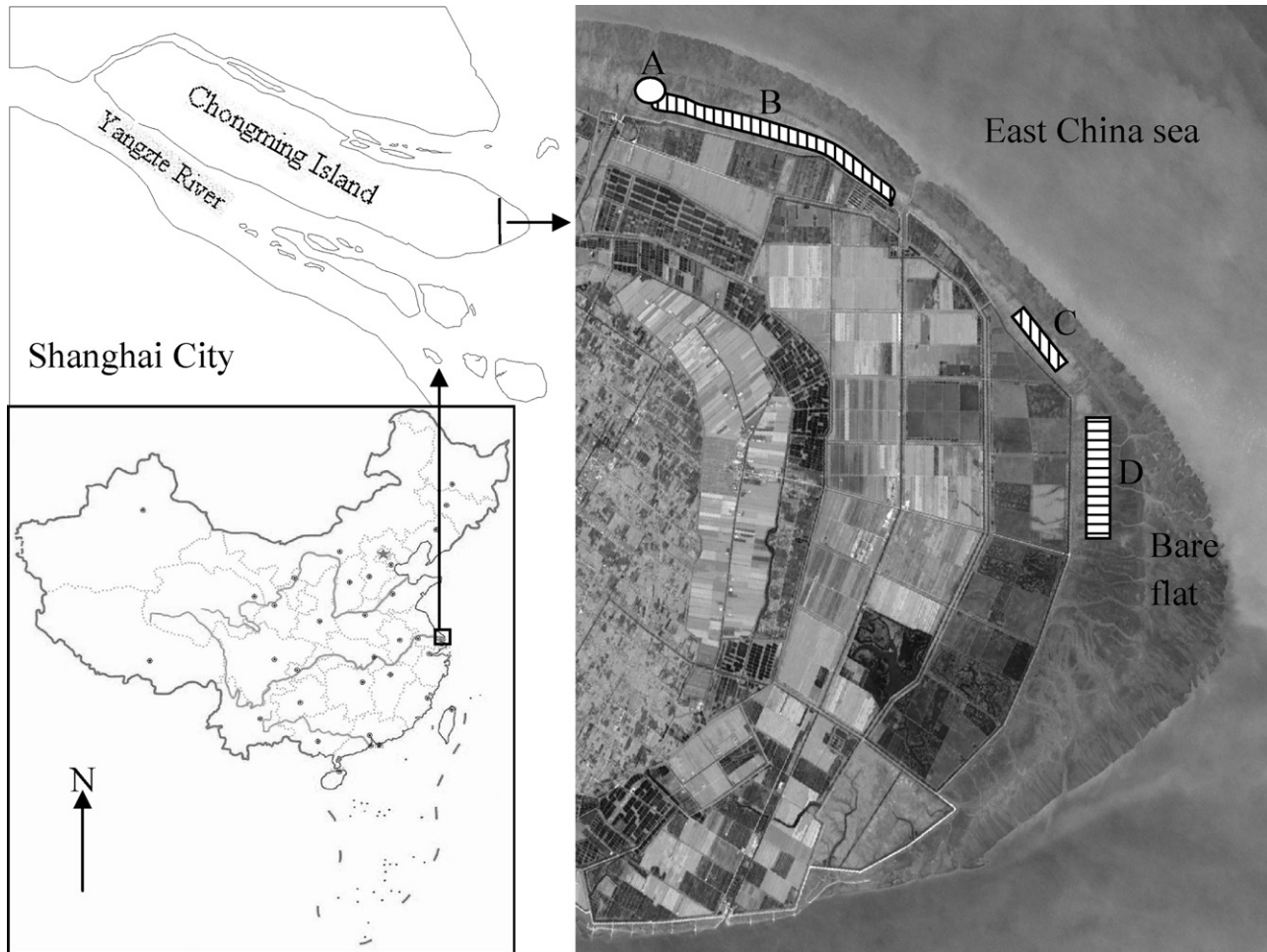


Fig. 1. Sketch map of the zones representing the different growth times of *Spartina alterniflora* in Dongtan. (A) The zone where *S. alterniflora* was first found in 1995; (B) and (C) Beibaxiao and Dongwangsha, where *S. alterniflora* was planted in 2001; (D) Buyuguang, where *S. alterniflora* was planted in 2003.

et al., 2009; Diez et al., 2010). For example, invasive *Alliaria petiolata* declines when it has extirpated native plants because toxic allelochemicals require resources to produce but are ineffective in intraspecific competition (Lankau et al., 2009). Thus, an interesting question arises: will invaders change their invaded habitats to maintain their dominant status or to limit their own growth over time?

Invasive *Spartina alterniflora* L. has invaded many marshes worldwide. This invader elevates the marsh height by continuously trapping sediments and then reduces the tidal inundation time (Crooks, 2002; Cuddington and Hastings, 2004; Chung, 2006; Li et al., 2009). Simultaneously, invasive *S. alterniflora* accumulates much standing litter through high production and then creates a new aboveground structure in the invaded habitats (Crooks, 2002; Chung, 2006; Li et al., 2009). A decrease in inundation time can change the input of water, dissolved inorganic N and salt ions from tidal subsidies (Li et al., 2009; Peng, 2010), and the standing litter can change the environmental conditions (Wang et al., 2006). Therefore, it is likely that these changes induced by *S. alterniflora* will influence the invader's own long-term performance.

We used space-for-time substitution to examine the long-term changes in *S. alterniflora* populations and sought to understand how the changes in tidal inundation time and the accumulation of standing litter affect the performance of this invasive plant. Our goal was

to highlight the importance of changes in invaded habitats induced by invaders on invasion dynamics.

2. Methods

Experiments were conducted in the Shanghai Chongming Dongtan National Nature Reserve, located on Chongming Island, Shanghai (31°25'–31°38'N, 121°50'–122°05'E) (Fig. 1). *S. alterniflora* was first found in Dongtan in 1995 and was planted in the north of Dongtan in 2001 and 2003 (Chen et al., 2004) (Fig. 1). Currently, this invasive plant is rapidly expanding into new areas. Four *S. alterniflora* populations, with estimated ages of 1, 5, 7, and 16 years, were present in 2008.

To test the changes in the performance of *S. alterniflora*, the tidal inundation time and the mass of the standing litter with time, we randomly set 10 quadrats (1 m × 1 m) in each zone to correspond to the different invasion times represented by the four populations. During early November 2008, we harvested the aboveground mass by clipping and measured the tidal inundation time.

To test the effects of the tidal inundation time and the standing litter on the performance of *S. alterniflora*, an experiment was conducted during mid-January 2009. Based on the inundation times determined in 2008, the zones inundated for 28.5 ± 4.1 (mean \pm SE) h during 15 days (a tidal cycle) were categorised as long-inundation habitats. This duration was significantly longer

than that of the zones categorised as short-inundation habitats (14.8 ± 3.9 h/15 days) (ANOVA; $P < 0.01$). We randomly set 10 plots ($10 \text{ m} \times 10 \text{ m}$) in each of these two types of habitats. Two quadrats ($3 \text{ m} \times 3 \text{ m}$) were placed in each plot. The aboveground mass was removed by clipping in one quadrat, whereas the other quadrat served as control. In early November 2009, we measured the performance of *S. alterniflora* in the core area ($1 \text{ m} \times 1 \text{ m}$) of each quadrat.

We measured the canopy height of *S. alterniflora* and then harvested the aboveground mass. Living ramets and flowering ramets in each quadrat were counted to calculate the density and the flowering rate. Ten ramets were randomly sampled to measure the basal diameter, and five flowering ramets were randomly sampled to measure the florets and fruit on each spike to estimate the seed-setting rate. These data were averaged within each quadrat as a replicate. The standing litter and living materials were then oven dried at 80°C to constant weight and weighed.

The tidal inundation time was estimated with a gypsum dissolution technique. A cube of gypsum ($2 \text{ cm} \times 2 \text{ cm} \times 2 \text{ cm}$) was oven dried at 120°C to constant weight and weighed. The cube was then packed in a nylon net. The parcel was attached to one end of an iron wire, and the other end of the wire was inserted into the soil under the *S. alterniflora* canopy. The cube was covered with a PVC pipe (diameter $10 \text{ cm} \times$ length 35 cm), which was inserted into the soil. The side with one hole was turned to face the tide and was covered with a cap. After 15 days, the cube was dried at 120°C to constant weight and weighed. The tidal inundation time was estimated by the dissolution curve of the gypsum cube in sea water, which was obtained in the laboratory ($y = 24.991x$; y is the inundation time (hours) and x is the decrease in the weight of the gypsum (g); linear fit, $n = 5$, $R^2 = 0.999$, $P < 0.001$). One gypsum cube with a pipe was placed in each quadrat.

The ratio of standing litter (RL) was used to assess the standing litter per unit mass of the living ramets of *S. alterniflora*. The RL was defined as follows:

$$RL = \frac{M_S}{M_L} \times 100\%,$$

where M_S and M_L represent the mass of the standing litter and the living ramets in each quadrat, respectively.

The mean ratio of change (MRC) was used to assess the rate of change in the study habitats. The MRC was defined as follows:

$$MRC = \left| \frac{H_N - H_T}{H_T} \right| \times 100\%,$$

where H_T and H_N represent the average tidal inundation times of two consecutive age groups, which are calculated respectively by $(H_5 - H_1)/H_1 \times 100\%$, $(H_7 - H_5)/H_5 \times 100\%$ and $(H_{16} - H_7)/H_7 \times 100\%$. The RL values for each age group can also be substituted for the H variables in this equation.

A one-way ANOVA was used to test the differences in the performance of *S. alterniflora*, including dry biomass, canopy height, basal diameter, flowering rate and seed-setting rate, the differences in the tidal inundation time, the differences in the mass of the standing litter and the differences in the RL among the four different-aged populations. A Tukey test was used as the *post hoc* test. A two-way nested ANOVA was used to test the effects of the tidal inundation time and the standing litter on the performance of *S. alterniflora*, with standing litter nested within tidal inundation time.

3. Results

In the 16-year chronosequence of the invasion, *S. alterniflora* had a temporary enhancement and then declined. The dry biomass and density both attained their maximum values in the 5-year-old population (all $p < 0.05$, Fig. 2I and II). The flowering rate

and the seed-setting rate did not differ significantly between the 1- and 5-year-old populations, but these ratios were both significantly higher than those of the 7- and 16-year-old populations (all $p < 0.05$, Fig. 2V and VI).

With the increasing growth of *S. alterniflora*, the tidal inundation time decreased significantly ($p < 0.05$, Fig. 3I). Although the standing litter mass did not differ significantly among these populations ($p > 0.05$, Fig. 3II), the ratio of standing litter (RL) increased significantly with the age of the population ($p < 0.05$, Fig. 3III). Furthermore, the changes in the habitats were initially slow, then acute, and then long-term chronic (Fig. 3). The mean ratios of decrease in the tidal inundation time (MRC-inundation) were 15%, 33% and 31% in 3–5 years, 5–7 years and 7–16 years, respectively. The corresponding mean ratios of increase in the standing litter per unit mass of the living ramets (MRC-RL) were 4%, 33% and 13%, respectively.

Both the short inundation and the standing litter had significant inhibitory effects on the growth of *S. alterniflora* (all $p < 0.05$) (Fig. 4I and II), and short inundation also inhibited reproduction of *S. alterniflora* (all $p < 0.05$) (Fig. 4V and VI).

4. Discussion

It is not surprising that invaders form dense stands after a few years. However, declines in invasive species are noteworthy because similar declines also occur in other species (Simberloff and Gibbons, 2004; Banasiak and Meiners, 2009; Phillips, 2009; Yao et al., 2010). The performance of *S. alterniflora* across a 16-year chronosequence declined soon after the plant formed dense stands (Fig. 2). Not only invasive plants but also invasive animals decline over time. For example, invasive toads on the leading edge of an invasion show dispersal traits, including larger body sizes, longer legs and greater activity compared to those in the interior of the invaded area (Phillips, 2009).

The decline of invaders after an initial success can be attributed to the development of limiting factors, such as introductions of competitors or pathogens (Simberloff and Gibbons, 2004; Banasiak and Meiners, 2009; Lankau et al., 2009; Diez et al., 2010). In this study, we have also found negative feedback from changes in the abiotic habitats induced by the invaders themselves. Dense stands of *S. alterniflora* can markedly reduce the tidal inundation time by raising the marsh elevation through trapping large quantities of sediment, and change the characteristics of light and space by producing massive amounts of standing litter (Figs. 2 and 3). Consequently, the properties of the habitat exceed the optimal range for the invader. These changes are accompanied by large decreases in resources such as light, space and inputs of water, dissolved inorganic N and salt ions from tidal subsidies (Peng, 2010). The trapped sediments and the standing litter were accumulated over time (Fig. 3). Moreover, standing litter could trap sediments, and longer inundation time might favour standing litter to retain. Thus, invasive *S. alterniflora* creates unsuitable habitats for itself, consequently reducing its growth.

The feedbacks between invaders and their habitats typically vary over time and might not be seen during the initial phase of the invasion. Because the *S. alterniflora* populations younger than 4 years had a low density and biomass (Fig. 2I and II), it did not produce large amounts of standing litter (Fig. 3II) and trapped sediments slowly (Chung, 2006). Therefore, the habitat of *S. alterniflora* was changed little during the early period of the invasion (Fig. 3). After the *S. alterniflora* populations begin to flourish, the habitats are markedly changed by the dense stands of the invader (Figs. 2 and 3). Subsequently, *S. alterniflora* began to decline (Fig. 2). This decline indicated that the habitats had become unsuitable for

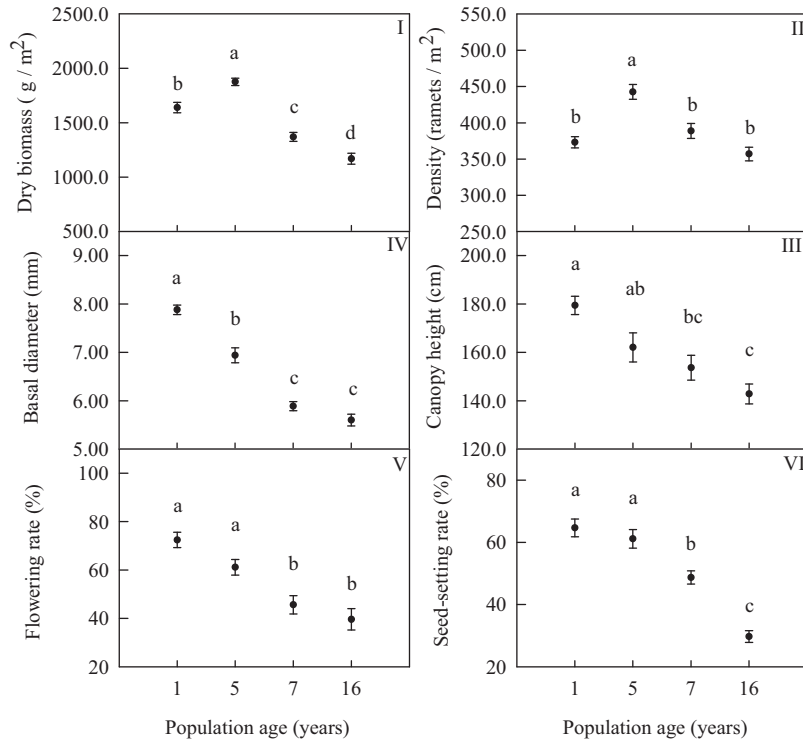


Fig. 2. Changes in performance of *Spartina alterniflora* along with population age. The different letters indicate significant differences at $p < 0.05$.

S. alterniflora during the late stage of the invasion. Low performance of old populations and poor input from tide to altered habitats can be responsible for decrease in the rate of change in the habitats as the invader declined (Figs. 2 and 3). In the study, the old populations had poor production of standing litter due to their low biomass, and received little input of the sediments from the tide water which is reduced by the increasing elevation. The case of *S. alterniflora* confirms that the negative feedback between invaders and habitat changes occurs if the habitats can no longer be changed effectively by the invaders.

Our results suggested that any advantage enjoyed by the invader may attenuate over time at least in the case of *S. alterniflora*. Certain studies have shown that changes in habitats induced by invaders have positive effects (Cuddington and Hastings, 2004; Zhao et al., 2009), which may occur during the early stage of an invasion. It is probable that founder stands of *S. alterniflora* are most likely to flourish in the changed habitats, where the competitive ability of natives such as *Scirpus mariqueter* and *Scirpus triquete* is

reduced because these natives are more sensitive than the invader to the decrease in light, space and the inputs of nutrients from tidal subsidies (Zhao et al., 2009). These considerations imply that *S. alterniflora* can be limited over time because it has reduced the tidal inundation time and has accumulated standing litter so that the amounts of these resources decrease steadily (Peng, 2010). Of course, other untested mechanisms are also possible, which might be related to soil processes.

The studies of the long-term feedback between invaders and their habitats can contribute to evaluating management approaches for well-established invaders and can serve to identify which new invaders should be targeted for early eradication (Strayer et al., 2006). The decline of invasive populations can attenuate the invasiveness of the populations (Lankau et al., 2009). In *S. alterniflora*, the expansion of old populations will decrease due to low vegetative growth, small individual size and poor sexual reproduction. Similarly, old populations of invasive *A. petiolata* have low levels of allelochemicals (Lankau et al., 2009). Therefore, the

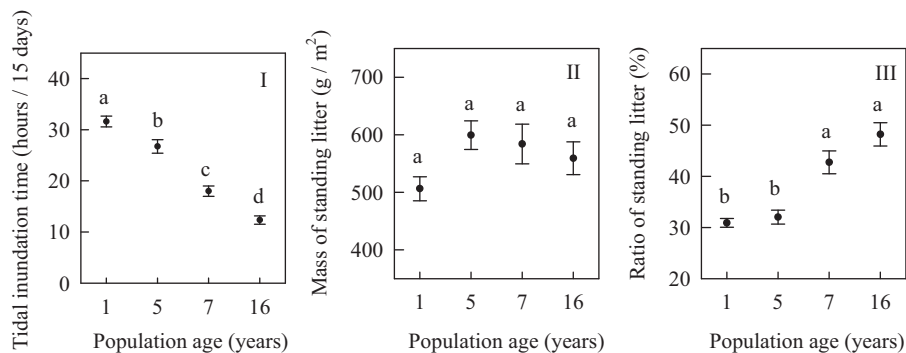


Fig. 3. Changes in tidal inundation time, mass of standing litter and ratio of standing litter along with *Spartina alterniflora* age. The different letters indicate significant differences at $p < 0.05$.

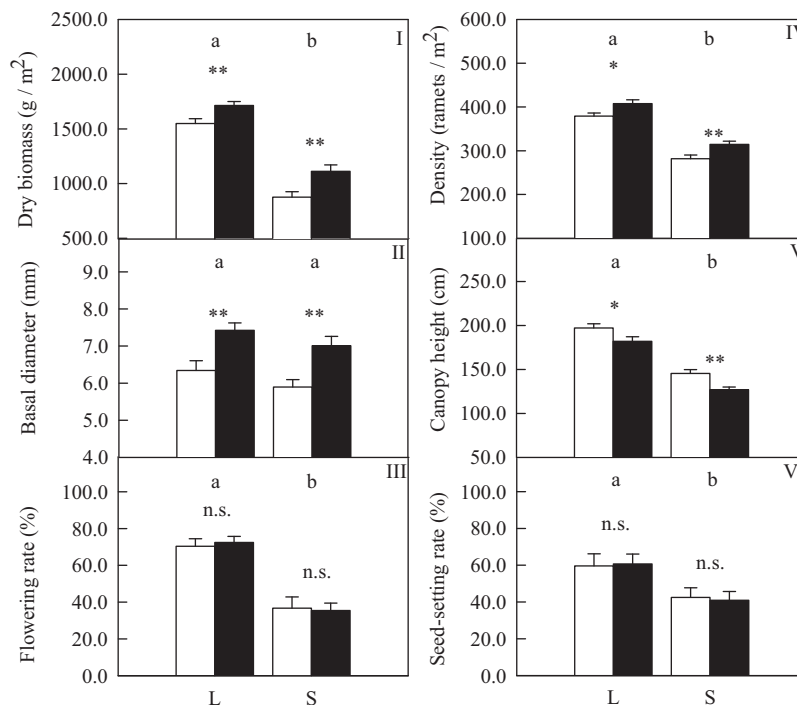


Fig. 4. Effects of tidal inundation time and standing litter on the performance of *Spartina alterniflora*. L and S represent long (28.5 ± 4.1 h/15 days) and short (14.8 ± 2.9 h/15 days) tidal inundation times, respectively; (□) and (■) represent control and removed standing litter, respectively; The letters and asterisks indicate the significant differences within the inundation time groups, and the asterisks indicate the significant differences between the control and removed standing litter at $p < 0.05$ (** $p < 0.01$).

eradication of young populations takes precedence over the management of mature ones (Taylor and Hastings, 2004).

By investigating *S. alterniflora* populations of different ages, we have found long-term decline of this species following a temporary period of flourishing. This pattern can be attributed to the accumulation of changes in the habitat and the development of negative feedback between the plant and its environment. These findings show that the changes in habitats induced by the invaders themselves can substantially influence the long-term dynamics of invasive populations.

It is not yet clear whether other invaders can degrade their habitats over time. Moreover, it is not yet known whether the declining invaders will be replaced by native competitors or will regain their dominant status by adapting their strategies or through the recovery of degraded habitats. Understanding additional long-term biological invasions offers a useful approach to these questions.

Acknowledgements

This research was funded by the National Natural Science Foundation (Grant Nos.: 31100301, 31100317 and 30930019), and Science and Technology Commission of Shanghai Municipality (Grant Nos.: 10JC1400700 and 12XD1400500). We thank Chongming Dongtan National Natural Reserve and the students in our laboratory for their assistance with field sampling.

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