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INTRODUCTION

Collection: Invasion of Spartina Alterniflora in Coastal China

Lessons from the invasion of *Spartina alterniflora* in coastal China

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Biological invasions are a growing global problem and tightly linked to the future well-being of humanity and the ecosystem health of our planet. The Millennium Ecosystem Assessment identified invasive species as one of five key factors directly affecting global biodiversity and ecosystem services (UNEP, 2006). The vexing problem of species invasions poses both basic and applied opportunities for ecologists. Thus, studies of invasion ecology have both advanced our understanding of multiple fundamental questions in ecology and evolutionary biology, and contributed to the management of biological invasions.

Coastal wetlands, which have the greatest ecosystem services per unit area of any ecosystem type (Costanza et al., 1997), are not immune to the challenge of invasive species (Gedan et al., 2009). *Spartina alterniflora*, native to the East and Gulf Coasts of North America, exemplifies these threats: it has spread to coastal and estuarine wetlands globally, causing considerable ecological and economic damage (Strong & Ayres, 2013). *S. alterniflora* was intentionally introduced to China in 1979 from three U.S. states (North Carolina, Georgia, and Florida) to promote sedimentation, control soil erosion, and protect embankments (Li et al., 2009). Over four decades, it spread to become the most dominant salt marsh plant along China's 18,000-km coastline (Figure 1), currently accounting for more than 60% of salt marsh area in China (Li et al., 2022). The widespread, well-documented and rapid invasion of *S. alterniflora* along the coast of China provides unique opportunities for studying the causes and consequences of plant invasions. This collection brings together 15 studies published in ESA journals that provide general insights into the ecology of *S. alterniflora* invasions in China and identifies avenues for future research on invasion biology. These studies consider the invasive effects on biodiversity and ecosystem functioning, the pre-adaptation and phenotypic plasticity of plant traits in response to environmental changes, the effects of human and native biotic factors on invasiveness of *S. alterniflora*, and the invasibility of native communities.

Spartina alterniflora is a poignant example of an invasive plant, both because of its rapid and extensive spread, and because of the harm done to native ecosystems and human economies (Li et al., 2009; Liu et al., 2016).

FIGURE 1 *Spartina alterniflora* is already the most dominant plant in China's coastal wetlands. Here it is seen sweeping through the mudflats and salt marshes of the Yellow River Delta (credit: Qiang He).

S. alterniflora has reduced biodiversity in China's coast by displacing native salt marsh plants, encroaching into mangrove gaps, and transforming mudflat habitats into salt marshes (Li et al., 2022; Zhang et al., 2012). *S. alterniflora* has homogenized soil communities (Zhang et al., 2019), has a higher leaf litter decomposition rate than the native *Phragmites australis* across a range of latitude (Cheng et al., 2022), and has driven losses in habitat and food resources of migratory birds (Gan et al., 2010). Its spread has destroyed aquaculture industries that were based on farming mudflat species such as razor clams.

In order to spread widely across latitude, invasive plant species need to match their phenotype to a wide range of abiotic conditions. This can occur through multiple introductions from a range of source populations or through a single introduction followed by phenotypic plasticity or rapid evolution. In a 4-year field survey, Chen et al. (2021) found a high degree of plasticity in flowering phenology of *S. alterniflora*, with plants flowering later at mid-latitude sites with intermediate temperatures and wide tidal ranges. Consistent with life-history theory, plants flowered later under conditions favoring vigorous growth. Selection for earlier flowering associated with limited growth periods of plants at high and low latitudes suggests that *S. alterniflora* has already colonized much of the geographic range favorable to it on the east coast of Asia. To understand variation of plant traits with latitude, Liu et al. (2017) used common gardens at low, medium, and high latitudes to study *S. alterniflora* populations collected from 10 sites along China's east coast. There was no evidence for genetic variation in vegetative growth with latitude, which indicates great plasticity in vegetative growth. However, there was evidence for genetically based latitudinal clines in sexual reproduction, especially in common gardens located at high latitudes, indicating a provenance-by-environment interaction. Therefore, the rapid spread and high performance of *S. alterniflora* in China were likely due to pre-adaptation and phenotypic plasticity, followed by rapid evolution.

A variety of other mechanisms further mediate the spread and impact of *S. alterniflora*. Coastal wetlands are characterized by variable physical environments, intense biotic interactions, and strong anthropogenic impacts—each of which can contribute to invasion success. Li et al. (2014) found that propagule pressure, competition, disturbance, and herbivory could jointly mediate the dynamics of mangroves being invaded by *S. alterniflora*. The combination of competition and herbivory eliminated *S. alterniflora* from intact mangroves. In the presence of disturbances, however, *S. alterniflora* survived in mangrove gaps and intertidal mudflats, inhibiting mangrove recruitment to these areas. Further work showed that grazing by native herbivores enhanced the resistance of mangrove forests to *S. alterniflora* invasion in southern China (Zhang et al., 2018). Similarly, Ning et al. (2019) found that disturbance caused by human ditching created windows of opportunity for *S. alterniflora* invasion in northern China, but that native herbivores enhanced the resistance of salt marshes to *S. alterniflora* invasion. These studies suggest that, although superior competitive ability is an important factor promoting plant invasions, a variety of ecological interactions can mediate invasiveness of exotic plants in specific environments.

Anthropogenic eutrophication often accelerates plant invasions, because invasive plants are generally more efficient in utilizing nutrients than are native plants (Liao et al., 2008). Many estuarine wetlands in China receive high nutrient loads from adjacent agriculture and aquaculture and incomplete sewage treatment. Xu et al. (2020) found that human-mediated eutrophication was the major factor driving geographic variation in productivity of invasive *S. alterniflora* salt marshes, challenging classic patterns in which geographic productivity patterns are primarily controlled by temperature (Kirwan et al., 2009). In China, eutrophication will likely continue to increase, and is likely to aggravate the invasion of *S. alterniflora*. In a long-term field experiment (*Spartina* Invasion and Nitrogen Enrichment [SINE] experiment) in the Yangtze estuary, one of the most eutrophic estuaries in China, researchers from Fudan University found that the light use plasticity of *S. alterniflora* was enhanced under N enrichment, which facilitated the coexistence of conspecifics of varying sizes, thereby increasing growth and invasiveness of *S. alterniflora* by alleviating intraspecific competition (Xu, Zhou, et al., 2022). In addition, the negative effects of herbivory under ambient N were shifted to positive effects under N enrichment, with herbivory stimulating complementary increases in density and aboveground biomass (Xu, Zhang, et al., 2022).

Because coastal wetlands occur at the edges of land and ocean, soils in coastal wetlands can vary in salinity from fresh to highly saline. This variation in soil salinity is a key factor affecting plant competition. *S. alterniflora* is more tolerant of salt stress than is native *P. australis* in China (Tang et al., 2014). As a result, *S. alterniflora* not only out-competed the native plants, but also spread to areas that were unsuitable for most native plants. *P. australis*, which has a narrow salinity niche, persisted only in low-salinity habitats. Tang et al. (2018) further found that the nature of competition between *S. alterniflora* and *P. australis* changed along the salinity gradient. As salt stress increased, the dominant driver of the growth of native *P. australis* shifted from competition to stress, whereas competition was always important for the growth of the salt-tolerant invader. Zhang et al. (2012) found that *S. alterniflora* could gradually replace mangroves in intermediate salinity regions of Chinese southern estuaries. However, *S. alterniflora* was significantly inhibited by salt barrens in high marsh areas (Qi et al., 2017). The general lesson here is that, even for a highly tolerant and plastic invader, there are limits to habitat suitability, and competition with natives may play out differently depending on habitat type and abiotic tolerances of different native species.

Together, these recent studies of the *S. alterniflora* invasion in China serve as a model providing insights for future research in invasion ecology. Invasion ecology has shifted from describing patterns to exploring mechanisms, and so requires a mechanistic understanding of vegetation dynamics, biotic interactions, and environmental adaptations related to plant invasions. Because of their ability to adapt quickly to novel environments, widespread invasive plants are ideal subjects for ecological and evolutionary studies. The adaptive responses of invasive plants to novel environments are associated with corresponding changes at the genomic, transcriptome, and metabolome levels; however, these molecular-level regulatory mechanisms and their associations with plant traits and biotic interactions remain under-explored (Mounger et al., 2021). Meanwhile, *S. alterniflora* invasion can change arthropod assemblages and trophic interactions, but these changes could be reversed by the restoration of the native *P. australis* following removal of the invader (Jiang et al., 2022). It is not clear whether the restoration of native plants can achieve the restoration of the original biota and ecosystem functions. Finally, the lessons learned from the case of *S. alterniflora* invasions in China provide a sharp warning regarding the risks of future coastal invaders, given that other risky exotic plants (e.g., the exotic mangroves *Sonneratia apetala* and *Laguncularia racemosa*) are being used in wetland afforestation projects in China. More broadly, plant invasions are globally ongoing and ubiquitous. This case study with *Spartina* illustrates how comprehensive studies of plant invasions with other species in other geographic regions have the potential to richly inform both basic ecological and evolutionary science, and management and conservation strategies.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

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REFERENCES

Chen, X., W. Liu, S. C. Pennings, and Y. Zhang. 2021. "Plasticity and Selection Drive Hump-Shaped Latitudinal Patterns of Flowering Phenology in an Invasive Intertidal Plant." *Ecology* 102: e03311.

Cheng, C., Z. X. Liu, Y. Z. Zhang, B. Li, and J. H. Wu. 2022. "Leaf Litter Decomposition and its Drivers Differ between an Invasive and a Native Plant: Management Implications." *Ecological Applications*: e2739. https://doi.org/10.1002/eap.2739.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, et al. 1997. "The Value of the World's Ecosystem Services and Natural Capital." *Nature* 387: 253–60.

Gan, X., C. Choi, Y. Wang, Z. Ma, J. Chen, and B. Li. 2010. "Alteration of Habitat Structure and Food Resources by Invasive Smooth Cordgrass Affects Habitat Use by Wintering Saltmarsh Birds at Chongming Dongtan, East China." *The Auk* 127: 317–27.

Gedan, K. B., B. R. Silliman, and M. D. Bertness. 2009. "Centuries of Human-Driven Change in Salt Marsh Ecosystems." *Annual Review of Marine Science* 1: 117–41.

Jiang, J. J., Y. J. Zhao, Y. L. Guo, L. Gao, C. L. Richards, E. Siemann, J. H. Wu, B. Li, and R. T. Ju. 2022. "Restoration of Native Saltmarshes Can Reverse Arthropod Assemblages and Trophic Interactions Changed by a Plant Invasion." *Ecological Applications*: e2740. https://doi.org/10.1002/eap.2740.

Kirwan, M. L., G. R. Guntenspergen, and J. T. Morris. 2009. "Latitudinal Trends in *Spartina Alterniflora* Productivity and the Response of Coastal Marshes to Global Change." *Global Change Biology* 15: 1982–9.

Li, B., C. H. Liao, X. D. Zhang, H. L. Chen, Q. Wang, Z. Y. Chen, X. J. Gan, et al. 2009. "*Spartina* alterniflora Invasions in the Yangtze River Estuary, China: An Overview of Current Status and Ecosystem Effects." *Ecological Engineering* 35: 511–20.

Li, B., Z. Ma, J. Wu, and R. Ju. 2022. *Plant Invasion Ecology: The Case of Spartina alterniflora in China*. Beijing: Higher Education Press.

Li, Z., W. Wang, and Y. Zhang. 2014. "Recruitment and Herbivory Affect Spread of Invasive *Spartina alterniflora* in China." *Ecology* 95: 1972–80.

Liao, C., R. Peng, Y. Luo, X. Zhou, X. Wu, C. Fang, J. Chen, and B. Li. 2008. "Altered Ecosystem Carbon and Nitrogen Cycles by Plant Invasion: A Meta-Analysis." *New Phytologist* 177: 706–14.

Liu, W., K. Maung-Douglass, D. R. Strong, S. C. Pennings, and Y. Zhang. 2016. "Geographical Variation in Vegetative Growth and Sexual Reproduction of the Invasive *Spartina alterniflora* in China." *Journal of Ecology* 104: 173–81.

Liu, W., D. R. Strong, S. C. Pennings, and Y. Zhang. 2017. "Provenance-by-Environment Interaction of Reproductive Traits in the Invasion of *Spartina alterniflora* in China." *Ecology* 98: 1591–9.

Mounger, J., M. Ainouche, O. Bossdorf, A. Cavé-Radet, B. Li, M. Parepa, A. Salmon, J. Yang, and C. Richards. 2021. "Epigenetics and the Success of Invasive Plants." *Philosophical Transactions of the Royal Society B* 376: 20200117.

Ning, Z., T. Xie, Z. Liu, J. Bai, and B. Cui. 2019. "Native Herbivores Enhance the Resistance of an Anthropogenically Disturbed Salt Marsh to *Spartina alterniflora* Invasion." *Ecosphere* 10: e02565.

Qi, M., T. Sun, H. Zhang, M. Zhu, W. Yang, D. Shao, and A. Voinov. 2017. "Maintenance of Salt Barrens Inhibited Landward Invasion of Spartina Species in Salt Marshes." *Ecosphere* 8: e01982.

Strong, D. R., and D. R. Ayres. 2013. "Ecological and Evolutionary Misadventures of *Spartina*." *Annual Review of Ecology, Evolution, and Systematics* 44: 389–410.

Tang, L., Y. Gao, B. Li, Q. Wang, C.-H. Wang, and B. Zhao. 2014. "*Spartina alterniflora* with High Tolerance to Salt Stress Changes Vegetation Pattern by Outcompeting Native Species." *Ecosphere* 5: art116.

Tang, L., A. A. Wolf, Y. Gao, and C. H. Wang. 2018. "Photosynthetic Tolerance to Non-resource Stress Influences Competition Importance and Intensity in an Invaded Estuary." *Ecology* 99: 1327–37.

UNEP (United Nations Environment Programme). 2006. *Marine and Coastal Ecosystems and Human Well-Being: A Synthesis Report Based on the Findings of the Millennium Ecosystem Assessment*. Nairobi: UNEP.

Xu, X., H. Liu, Y. Liu, C. Zhou, L. Pan, C. Fang, M. Nie, and B. Li. 2020. "Human Eutrophication Drives Biogeographic Salt Marsh Productivity Patterns in China." *Ecological Applications* 30: e02045.

Xu, X., C. Zhou, Q. He, S. Qiu, Y. Zhang, J. Yang, B. Li, and M. Nie. 2022. "Phenotypic Plasticity of Light Use Favors a Plant Invader in Nitrogen-Enriched Ecosystems." *Ecology* 103: e3665.

Xu, X., Y. Zhang, S. Li, H. Chen, M. Liu, B. Li, and M. Nie. 2022. "Native Herbivores Indirectly Facilitate the Growth of Invasive *Spartina* in a Eutrophic Salt Marsh." *Ecology* 103: e3610.

Zhang, Y., G. Huang, W. Wang, L. Chen, and G. Lin. 2012. "Interactions between Mangroves and Exotic *Spartina* in an

Anthropogenically Disturbed Estuary in Southern China." *Ecology* 93: 588–97.

Zhang, Y., H. Meng, Y. Wang, and Q. He. 2018. "Herbivory Enhances the Resistance of Mangrove Forest to Cordgrass Invasion." *Ecology* 99: 1382–90.

Zhang, Y., S. C. Pennings, B. Li, and J. Wu. 2019. "Biotic Homogenization of Wetland Nematode Communities by Exotic *Spartina alterniflora* in China." *Ecology* 100: e02596.

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