



Article

The Opposite of Biotic Resistance: Herbivory and Competition Suppress Regeneration of Native but Not Introduced Mangroves in Southern China

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Abstract: Mangrove forests are increasingly threatened by plant invasions worldwide, but some mangrove species are invasive and threaten salt marsh and native mangrove ecosystems. The southern coast of China is invaded by the cordgrass *Spartina alterniflora*, and the mangrove *Sonneratia apetala*, providing a model system for studying the processes and mechanisms through which non-native species establish and spread. We used a transplant experiment to test the overarching hypothesis that native herbivores and plants provided biotic resistance against invasion by *S. apetala*, and that the importance of these factors would vary geographically. Survival of transplanted mangrove seedlings was lower in Zhangjiang Estuary (23°55' N) than in Leizhou Bay (20°56' N), and varied with species and habitats. *S. apetala* had higher survival and growth rates than native mangroves at both sites, and *S. apetala* grew taller than the *S. alterniflora* canopy at Leizhou Bay in only two growing seasons. In contrast, native mangroves grew poorly in *S. alterniflora*. Grazing by rodents and insects suppressed the growth and survival of *Kandelia obovata* and *Avicennia marina* in Zhangjiang Estuary and Leizhou Bay, but had little effect on *S. apetala*. Competition with vegetation (*S. alterniflora* and native mangroves) exacerbated the reduced survival of native mangroves, and these effects varied across study sites. Low survival of non-native *S. apetala* in vegetated habitats at Zhangjiang Estuary was likely due to a synergistic effect of low winter temperatures and low light intensity. Escape from herbivory (the opposite to biotic resistance) and fast growth may drive the quick expansion of non-native *S. apetala* in China. Rapid encroachment of *S. apetala* may transform the native mangrove forests and monospecific intertidal *Spartina* grasslands into non-native mangrove forests in the southern coast of China.

Keywords: biological invasion; biotic resistance; mangroves; herbivory; competition; *Sonneratia apetala*; *Spartina alterniflora*; *Rattus losea*



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1. Introduction

Mangrove forests provide important ecosystem services [1,2], but presently they are severely degraded [3,4]. Human activities such as aquaculture, agriculture, and urban development have caused large-scale mangrove deforestation [5,6]. These direct human activities take place in the context of ongoing global changes, such as sea level rise, precipitation, and extreme temperature, that also impact the structure of mangrove communities, their biodiversity, and geomorphological setting [3,7–9]. In contrast to research on human impacts and global change, the role of plant invasions in the degradation of mangrove forests has received little attention [10,11].

Biological invasions are a well-known threat to natural ecosystems [12]. A recent literature survey found a total of 57 invasive plants in the world's mangrove forests [10].

Plant invasions in mangrove forests could affect sediment nitrogen stocks [11,13] and vegetation structure [14,15], composition, and diversity [10,16]. At the same time, mangroves can be invasive species encroaching into other ecosystems. For example, *Nypa fruticans* invaded native mangrove forests in western Africa, displacing native mangroves and forming dense monospecific stands [17]. In the United States, *Rhizophora mangle* has invaded Hawaii, where its detritus has a negative effect on faunal communities because of its high tannin content [18]. In the United States, Australasia, and South Africa, mangroves are encroaching into salt marsh habitats, changing microclimates [19,20], vegetation structure, and processes [8,21,22]. In comparison to the extensive research on how human activities and global change are affecting mangroves, there has been relatively little attention on the importance of invasions by non-native plants—whether into mangrove forests or by mangroves into other habitats.

The success of an invasive plant is dependent on multiple processes across a wide range of temporal and spatial scales [23,24]. A key hypothesis about invasions is the biotic resistance hypothesis, which postulates that resident species are able to hinder the establishment and spread of introduced species through negative biotic interactions such as herbivory and interspecific competition [25,26]. When studied, however, the effect of herbivores has been mixed: herbivores can promote [27], deter [28,29], or have no effect on the dominance of non-native plant species [30]. In the case of mangroves, many studies have focused on herbivory on propagules and seedlings of native species [31,32], but few studies have examined the role of herbivory in the invasion of non-native mangroves.

Competition with native species is another factor that could contribute to biotic resistance and limit invasion by non-native species [26]. Interspecific competition for limiting resources such as water, nutrients, and light may affect the establishment of non-native plants. Many studies have found that competition from native plants has a strong negative effect on non-native plants in grasslands [33], salt marshes [34], and forests [35]. However, although resident competitors can reduce the performance of individual non-native invaders, competition alone might not be enough to exert strong biotic control against a well-established invader [26]. In the case of mangroves, many studies have focused on competition among native species [36], and between natives and non-natives [14,37], but few studies have examined how herbivory and competition might interact to mediate the invasion by non-native mangroves.

Coastal habitats in China provide a model for studying the processes through which non-native species establish and spread, because intertidal habitats along almost the entire coastline have been heavily affected by two non-native plant species. The cordgrass *Spartina alterniflora* was deliberately introduced from the United States in 1979 with the goal of protecting the coast from erosion [38]. *S. alterniflora* has spread by planting and natural dispersal to cover intertidal mudflats along almost the entire Chinese coast [39]. Salt marsh species can be nurse plants to facilitate the survival of mangrove seedlings in harsh conditions [40,41]. Even though *S. alterniflora* temporarily facilitates the survival of native mangrove seedlings, it mostly competes with seedlings of native mangroves, slowing or preventing mangrove regeneration [11,14,37]. The mangrove *Sonneratia apetala* was introduced to China from Bangladesh in 1985 with the goal of revegetating degraded mangrove forests [42,43]. It has spread by planting and natural dispersal to dominate ~10% of the mangrove habitat in China, and now its introduced range encompasses more than 6 degrees of latitude from 19 to 25° N [44]. It dominates ~60% of the mangrove forests that have recently regenerated [4,45]. The widespread presence of these two non-native species provides an opportunity to study whether biotic resistance from native communities plays a role in limiting the spread of the non-natives and promoting the persistence of native mangrove forests.

The factors mediating the spread of *S. alterniflora* in China, and the consequences of this spread for native ecosystems, have been widely reviewed [29,38,46,47]. Here, we focus on the spread of *S. apetala*, and how its spread might be affected by native herbivores and competition from native mangroves and the pre-existing invasion of *S. alterniflora*. One factor

that might affect the spread of *S. apetala* is herbivory by native consumers. To our knowledge, however, no studies have found that herbivory alone can be sufficient to exclude non-native mangroves from invading a new habitat. However, herbivory might contribute to biotic resistance in combination with competition and abiotic stress [29,47]. Another factor that might affect the spread of *S. apetala* is competition with native mangroves, or with non-native *S. alterniflora*. A number of studies have documented the use of non-native *S. apetala* in mangrove afforestation projects, and its expansion on the Chinese coast [11,42,43]. We know less about how *S. apetala* interacts with native mangroves or non-native *S. alterniflora*, but the limited available evidence suggests that, once it escapes the canopy, *S. apetala* is competitively dominant over both native mangroves and *S. alterniflora* [37,43,48]. The ability of native consumers, native mangroves, and *S. alterniflora* to resist encroachment by *S. apetala* is likely to vary geographically, because competition intensity and herbivory rates may vary geographically, different mangrove species dominate different portions of the Chinese coastline, *S. alterniflora* productivity varies geographically [49], and *S. apetala* is a tropical species that is likely to be limited by cold stress at the high-latitude end of its range [9,11,43]. It is unknown how competition with native mangroves and herbivory by native herbivores might combine to provide biotic resistance against the early establishment and expansion of non-native *S. apetala*, and whether these interactions might vary geographically.

We conducted a transplant experiment with native and non-native mangroves at two sites in southern China to test three hypotheses about the abiotic and biotic factors affecting early establishment of two native mangroves, *Avicennia marina* and *Kandelia obovata*, and the non-native mangrove *S. apetala*. First, consumer pressure reduces the survival of mangrove seedlings, but affects the non-native species more than the native mangroves. Second, competition reduces mangrove establishment, but again affects the non-native species more than the native mangroves. Third, competition, herbivory, and mortality vary geographically as a function of climate, which native mangrove species is the local dominant, and the productivity of *S. alterniflora*. Based on our results, we discuss the prognosis for mangrove restoration and conservation in southern China.

2. Materials and Methods

2.1. Study Species

We studied two native and one non-native mangrove species. *K. obovata*, a native, is cold tolerant, and has a wide distribution along the southeast coast of China from 17 to 28° N [50]. *A. marina*, also native, is pantropical and has the broadest distribution, both latitudinally and longitudinally, of any mangrove species, extending to New Zealand (38° S) in the southern hemisphere and to China (26° N) in the northern hemisphere, with a high tolerance of hypersaline and inundation conditions [2]. *S. apetala* is native to southern India, Bangladesh, Sri Lanka, and Myanmar (21° N), and grows taller (to ~30 m) than either native species [51]. *S. apetala* was introduced to China from Bangladesh in 1985 and has been widely used in mangrove afforestation efforts since the 1990s because of its fast growth rate and tolerance to environmental stresses [42,45]. It has since become invasive, with effects on coastal geomorphology, hydrology, and plant composition [10,43].

All three mangroves overlap geographically with the salt marsh grass *S. alterniflora*, which is native to the Atlantic and Gulf Coasts of the United States. It has transformed open mudflats into monospecific, dense vegetation throughout its introduced range along the Chinese coast (19 to 40° N), and competes with native marsh plants and mangroves [14,38,46].

Intertidal vegetation in China is consumed by rats and insects. The distribution range of the native rat *Rattus losea* in southern China (18 to 30° N) overlaps broadly with that of mangrove forests. *R. losea* nests on mangrove canopies above the high-tide level, using leaves and branches of mangroves as construction material [52,53]. At sites invaded by *S. alterniflora*, rats build nests with leaves and stems of *S. alterniflora*, and feed on the ramets of *S. alterniflora* [29]. The most common leaf-chewing insects that consume mangroves in our study sites are *Cryptophlebia omebradelta* (Lepidoptera, Tortricidae), which consumes

K. obovata, *Oligochroa cantonella* (Lepidoptera, Pyralidae), which consumes *A. marina*, and *Orgyia postica* (Lepidoptera, Lymantriidae), which consumes *S. apetala* [54].

2.2. Study Sites

We worked at two study sites (Figure 1), Zhangjiang Estuary near the county of Yunxiao, Fujian Province (23°55' N, 117°26' E), and Leizhou Bay in the city of Leizhou, Guangdong Province (20°56' N, 110°10' E). Both sites are tidal wetlands with semi-diurnal tides where mangroves and *S. alterniflora* occur sympatrically. Zhangjiang Estuary is well within the geographic range of *K. obovata*, but is close to the northern distribution limits of *A. marina* and *S. apetala* [55]. Leizhou Bay is near the southern distribution limit of *K. obovata* but well within the geographic ranges of *A. marina* and *S. apetala*.

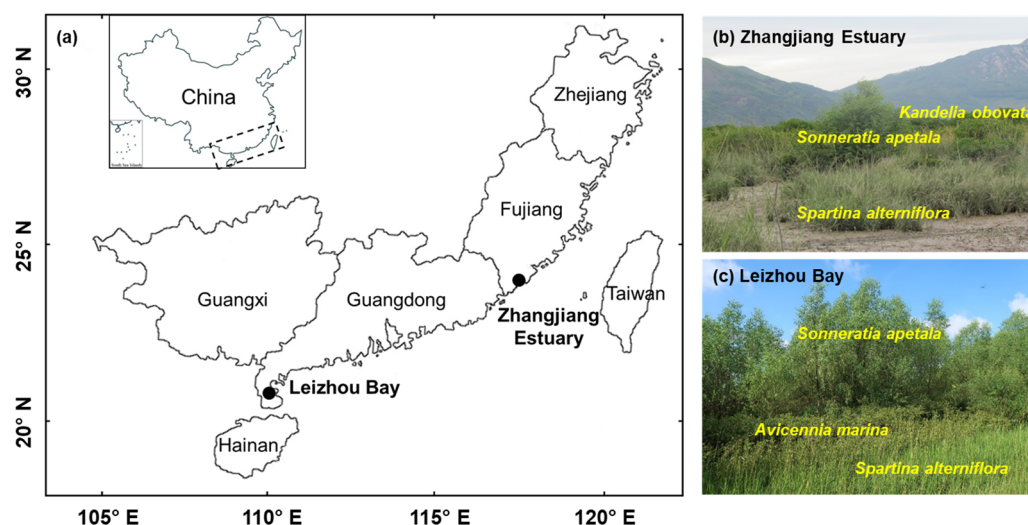


Figure 1. The study sites. (a) Map of southern China, showing the locations of the two study sites. Photographs of vegetation at (b) Zhangjiang Estuary, showing an individual *Sonneratia apetala* plant (~3 years old) growing amid native mangroves and *Spartina alterniflora*, and (c) Leizhou Bay, showing a large stand of *Sonneratia apetala* plants (4~5 years old and reproductive) encroaching upon native mangroves, with *Spartina alterniflora* in the forefront of the photograph.

The annual average temperature at Zhangjiang Estuary is 21.4 °C, with the highest monthly temperature of 29.5 °C in August and the lowest monthly temperature of 13.3 °C in January. The average annual precipitation is 1308 mm, most of which occurs from April to September. We worked at a mesohaline site along the estuary where the water column salinity averages 18 PSU, and the mean tide range is 2.32 m. Nitrogen content in the sediment averages 0.12% [49,55]. Vegetation at the site is dominated by the mangrove *K. obovata*, which grows up to 7 m tall in the upper intertidal, with patches of vigorous *A. marina* (3~4 m tall) and abundant and vigorous stands of *S. alterniflora* at intermediate intertidal elevations (Figure 1b, Supplementary Table S1). *S. alterniflora* was first present in the 1990s [14] and has not completely colonized all the available habitat, so there are some patches of open mudflat scattered throughout the coalescing stand of *S. alterniflora* [56]. *S. apetala* was planted on the coast near the mouth of the estuary in 2006 and has since spread into the estuary. We first noticed it at the mesohaline site in 2010 [37].

Leizhou Bay is near the current southern limit of *S. alterniflora* in China [57]. The average temperature at Leizhou Bay is 23.1 °C, with the highest monthly temperature of 32.8 °C in July and the lowest monthly temperature of 16.5 °C in January. The average annual precipitation is 1646 mm, most of which occurs from May to September. The water column salinity averages 22 PSU, and the mean tide range is 2.49 m. Nitrogen content in the sediment averages 0.04% [49]. The vegetation is dominated by the non-native mangrove *S. apetala*, which was planted in 1995 [43], with stands of short

(1~3 m tall) *A. marina* and patches of short (~3 m tall) *K. obovata* interspersed throughout (Figure 1c, Supplementary Table S1). A large stand and multiple smaller patches of low-stature *S. alterniflora* occur at intermediate elevations, and a large mudflat at lower elevations. *S. alterniflora* was first present at this site in 2006 [57].

2.3. Transplant Experiment to Evaluate Early Establishment of Mangroves

At both sites, we transplanted three species of mangrove (*K. obovata*, *A. marina*, *S. apetala*) into three habitats (native mangroves, *S. alterniflora*, and unvegetated mudflat). The nature of the habitats differed between the two sites. At Zhangjiang Estuary, the mangrove habitat was dominated by *K. obovata*, and the *S. alterniflora* habitat supported vigorous growth (height, 189 ± 4 cm (mean \pm SE), aboveground biomass, 2592 ± 186 g m⁻²). At Leizhou Bay, the mangrove habitat was dominated by native *A. marina*, and the *S. alterniflora* habitat was less productive (height, 102 ± 13 cm (mean \pm SE), aboveground biomass, 1297 ± 91 g m⁻²). We established six 2 m \times 2 m plots in each habitat at each site—plots within a habitat were at least 5 m apart, and the three groups of plots were ~40 m apart. At each site, the mudflat plots were lowest in elevation and the mangrove plots were highest in elevation, with a total elevational range of ~20 cm. Since we worked in the existing habitats at each site, it was not possible to intersperse plots representing different habitats, or to standardize elevation.

We transplanted three seedlings of each mangrove species into each plot on 24 March 2018 in Leizhou Bay and 4 April 2018 in Zhangjiang Estuary. The three species differ in propagule phenology, *K. obovata* is viviparous, *A. marina* is cryptoviviparous, and *S. apetala* is non-viviparous, but we chose to transplant them on the same dates so that they would experience the same abiotic conditions and in order to standardize the initial size. Propagules of *K. obovata* were collected from trees near the site in spring, were 20.1 ± 0.5 cm (mean \pm SE) in length, and were collected and planted on the same day. Seedlings of *A. marina* and *S. apetala* were purchased from a commercial nursery (propagules of these two species matured in autumn, then were cultivated in the nursery, which was located in the intertidal habitat and near to our study site), and were ~6 months old when planted. *A. marina* seedlings were 20.1 ± 1.5 cm (mean \pm SE) tall, and *S. apetala* seedlings were 14.5 ± 0.3 cm (mean \pm SE) tall when planted. Both had a root ball of ~6 cm \times 6 cm \times 10 cm when planted. We monitored seedling survival every month, and measured the height of each surviving seedling at the end of the second growing season in October 2019. Seedlings that died were omitted from analyses of height. For each species, we averaged plant height, relative growth rate, calculated as $[\text{Ln}(\text{final size}) - \text{Ln}(\text{initial size})] / (t_1 - t_0)$, where t_0 and t_1 are the time in months when the experiment started and ended within each plot, and used plots as the unit of replication. Data on mangrove performance were analyzed using three-way ANOVA, with site, species, and habitat as fixed factors. Due to the high mortality of some species in some habitats, we used individual one-way ANOVA and Tukey's HSD comparisons to compare the relative growth rate and height of surviving mangrove seedlings among species for each habitat at each site for which we had sufficient replication.

2.4. Effects of Herbivory

One cause of mortality to seedlings was herbivory. We measured herbivory by rodents (visible chewing damage to the stem) every month, and calculated the percentage of seedlings damaged by rodents in each plot over the course of the experiment. If the mangrove stem was grazed completely through, and the plant died within a month, we attributed mortality to rodent grazing. We measured herbivory by leaf-chewing insects (percent of leaves with any chewing damage) in September 2018, at the end of the growing season. We did not measure insect herbivory in 2019 because many of the mangrove seedlings had died, so the data were less informative. We averaged the percentage of leaves grazed by insects across the live seedlings in each plot. If insects fed on >90% of the leaves on a plant, and the plant subsequently died, we attributed mortality to insect

herbivory. Data on herbivory to mangroves were analyzed using three-way ANOVA, with site, species, and habitat as fixed factors.

2.5. Abiotic Factors

To characterize the abiotic conditions in each treatment at each site, we measured sediment water content and porewater salinity every two months between March 2018 and October 2019. Water content was measured gravimetrically by taking sediment samples (0 to 10 cm depth) from each plot and weighing them before and after drying. Porewater salinity was measured by rehydrating the dried sediment samples in a known volume of fresh water, measuring the salinity of the supernatant, and back-calculating to the original porewater salinity [58].

We measured light availability daily for two weeks every two months between March 2018 and October 2019. Light availability was measured using HOBO loggers (Pendant temp/light UA-002-64) deployed 30 cm above the sediment surface that logged Lux every 10 minutes ($n = 3$ per habitat type). For light availability, we averaged data from 11 a.m. to 2 p.m. on each day, deleting observations where the sensor was submerged at high tide. We monitored nighttime air temperature from December 2018 to February 2019, focusing on the winter temperatures because mangrove survival is related to winter minimum temperatures, with steep threshold responses that vary among species [8]. Nighttime air temperature was measured using HOBO loggers (Pendant temp UA-001-64) tied to PVC pipes at 30 cm above the sediment surface. We excluded daytime temperatures as direct solar insolation may lead to erroneous readings on unshielded HOBO loggers [20], and in any case, we were interested in minimum temperatures, which occurred at night. Hence, we calculated nightly (7 p.m.–7 a.m.) minimum temperatures from December 2018 to February 2019 for each habitat at each site. Abiotic data were analyzed using two-way ANOVA, with site and habitat as fixed factors.

2.6. Relative Importance of Biotic and Abiotic Factors

In order to determine the relative importance of the different biotic (mortality assigned to herbivory by rodents and insects) and abiotic (sediment water content, sediment porewater salinity, light intensity, temperature of the coldest month) factors on survival of the three mangrove species across the two sites (Leizhou Bay and Zhangjiang Estuary), we used a best subsets linear regression (Supplementary Table S2) to obtain the best regression models for variation in survival for each species. All analyses were performed using R (version 3.5.2) [59].

3. Results

3.1. Transplant Experiment to Evaluate Early Establishment of Mangroves

Final survival differed among species, habitats, and sites (Figure 2, Supplementary Table S3). *K. obovata* survived well at Leizhou Bay, especially in the mangrove and mudflat habitats, but had very low survival in Zhangjiang Estuary. *A. marina* survived well in the mudflat in Zhangjiang Estuary, but had very low survival in the mangrove (*K. obovata*) habitat at Zhangjiang Estuary and in the cordgrass habitat at Leizhou Bay. *S. apetala* survived well in all habitats at Leizhou Bay, but poorly in the mangrove (*K. obovata*) and cordgrass habitat at Zhangjiang Estuary.

For surviving plants, relative growth rates of *S. apetala* were higher than those of the two native mangroves in all habitats at both sites (Figure 3a,b, Supplementary Table S4). As a result, *S. apetala* grew taller than the *S. alterniflora* canopy in the cordgrass habitat at Leizhou Bay over only two growing seasons (Figure 3c,d, Supplementary Table S5).

3.2. Effects of Herbivory

The percentage of stems grazed by rodents differed among species, habitats, and sites (Figure 4, Supplementary Table S6). Rodent grazing was high (>70%) for *K. obovata* in all habitats in Zhangjiang Estuary, moderate for *K. obovata* in all habitats in Leizhou Bay, and

high (100%) for *A. marina* in the mudflat at Zhangjiang Estuary. Rodent grazing was low or zero for *S. apetala* in all habitats at both sites. Almost all (67~100%, depending on the site and habitat) of the *K. obovata* grazed by rodents died, but almost all of the *A. marina* grazed by rodents survived (Supplementary Figure S1, Table S7). Almost all of the rodent grazing occurred in December 2018–January 2019 at Zhangjiang Estuary and in April 2018 and April 2019 at Leizhou Bay (data not shown).

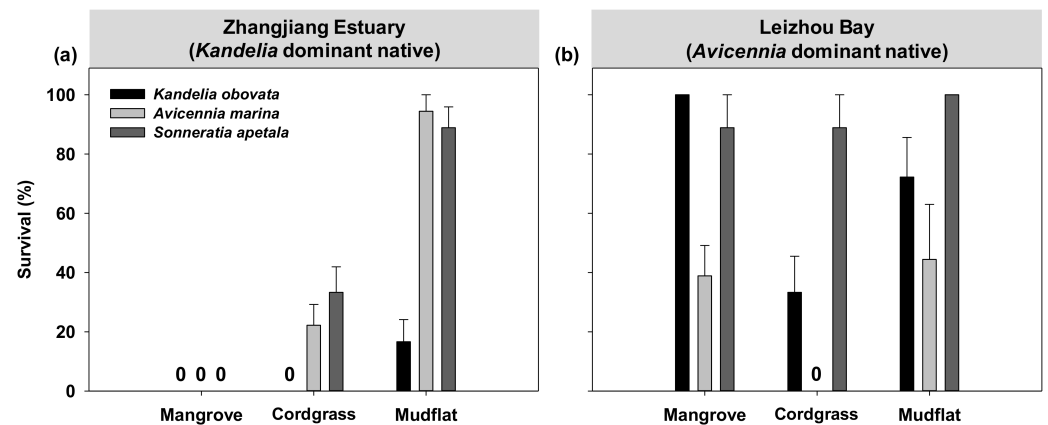


Figure 2. Seedling survival over two growing seasons in three habitats in (a) Zhangjiang Estuary and (b) Leizhou Bay. Data are means + SE ($n = 6$ per treatment). All main effects (site, species, habitat) and all two-way interactions affected mangrove survival (Supplementary Table S3).

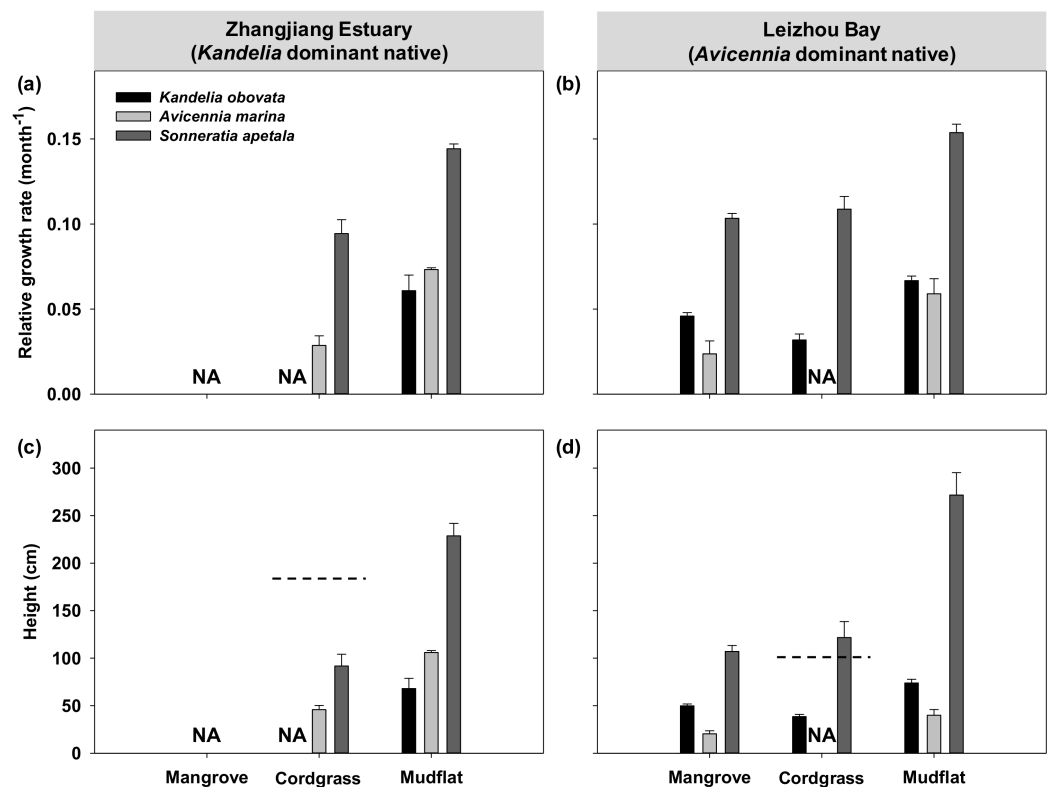


Figure 3. Relative growth rate (a,b) and height (c,d) of surviving seedlings at the end of two growing seasons in three habitats in Zhangjiang Estuary and Leizhou Bay. Data are means + SE ($n = 3$ –6 per treatment). NA = data not available because all the seedlings died. The dashed lines indicate the height of the *Spartina alterniflora* canopy at each site. Growth rates and height were different among species in each habitat at each site (Supplementary Tables S2 and S3) except for the mangrove habitat in Zhangjiang Estuary, where all seedlings died.

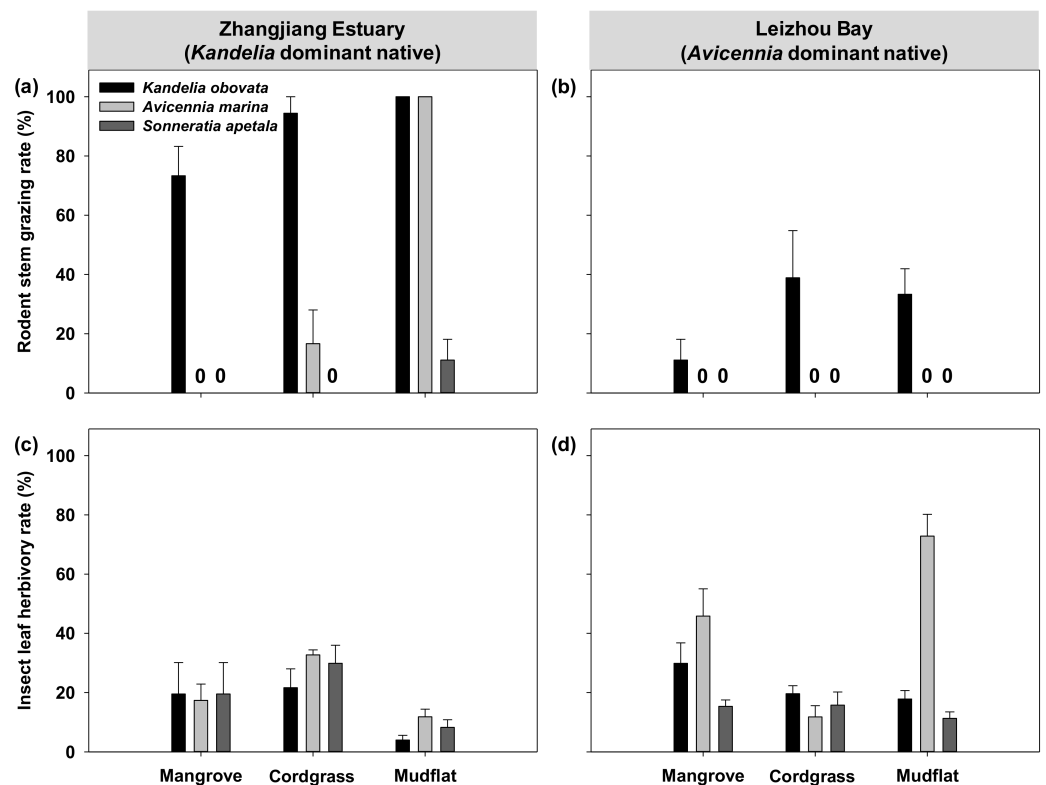


Figure 4. Percentage of stems grazed by rodents in three habitats in (a) Zhangjiang Estuary and (b) Leizhou Bay, and percentage of leaves grazed by insects in three habitats in (c) Zhangjiang Estuary and (d) Leizhou Bay. Data are means + SE ($n = 6$ per treatment). All the main effects (site, species, habitat) interacted to affect grazing by both rodents and insects (Supplementary Table S6).

The percentage of leaves grazed by insects differed among species and sites, but did not differ among habitats (Figure 4, Supplementary Table S6). Herbivory rates were higher for *A. marina* than for the other two mangrove species, especially at the Leizhou Bay site. All of the *K. obovata* and all of the *S. apetala* grazed by insects survived, but 38–100% of the *A. marina* grazed by insects at Leizhou Bay died (Supplementary Figure S1, Table S7).

3.3. Effects of Abiotic Factors

The major abiotic difference between habitats was light intensity (Table 1, Supplementary Table S8). Light intensity was highest in the unvegetated mudflat habitat, intermediate in the cordgrass habitat, and lowest in the mangroves, and was lower at Zhangjiang Estuary than at Leizhou Bay, especially in the vegetated habitats. The temperature of the coldest month was higher at Leizhou Estuary, but did not differ among habitats. Sediment water content was highest at Zhangjiang Estuary, and differed slightly among habitats. Porewater salinity was highest at Leizhou Bay, but did not differ among habitats. We saw no evidence of plants dying from stress due to sediment water content (drought or flooding), which in any case did not differ greatly among habitats or sites.

3.4. Effects of Competition

The pattern of residual mortality was consistent due to competition from other species (Supplementary Figure S1, Table S7). For mangroves that were not heavily grazed by rodents or insects, mortality was high for all three species in the mangrove habitat in Zhangjiang Estuary, and moderate for *A. marina* in the mangrove habitat in Leizhou Bay (Supplementary Figure S1). In the absence of other obvious causes, we assumed that this mortality was due to competition with existing adult mangroves for light or nutrients. Mortality was also high for all three species in the cordgrass habitat in Zhangjiang Estuary, where none of the mangrove species outgrew the *S. alterniflora* canopy, and for *K. obovata* and

A. marina in the cordgrass habitat in Leizhou Bay, where these two species did not outgrow the *S. alterniflora* canopy but *S. apetala* did. In the absence of other obvious causes, we assumed that this mortality was due to competition with *S. alterniflora* for light or nutrients.

Table 1. Abiotic factors in three habitats in Zhangjiang Estuary and Leizhou Bay. Data are means \pm SE (light intensity and air temperature of the coldest month: $n = 3$ per habitat at each site, sediment water content and sediment porewater salinity: $n = 35\sim 60$ per habitat at each site). Tukey's HSD significances (at the level of $p < 0.05$) are shown by different letters.

Source of Variance	Light Intensity ($\times 10^3$ Lux)	Temperature of the Coldest Month ($^{\circ}\text{C}$)	Sediment Water Content (%)	Sediment Porewater Salinity (PSU)
Zhangjiang Estuary				
Mangrove	7.0 \pm 1.1 e	12.3 \pm 0.1 b	49.0 \pm 0.2 a	18.9 \pm 1.0 ab
Cordgrass	25.7 \pm 4.3 d	12.3 \pm 0.1 b	52.0 \pm 0.5 a	17.6 \pm 0.8 b
Mudflat	83.9 \pm 1.3 b	12.1 \pm 0.2 b	51.7 \pm 0.4 a	18.4 \pm 0.9 ab
Leizhou Bay				
Mangrove	37.7 \pm 2.9 d	16.3 \pm 0.3 a	34.1 \pm 0.8 c	21.6 \pm 1.0 a
Cordgrass	57.6 \pm 4.8 c	16.4 \pm 0.1 a	40.7 \pm 1.1 b	21.8 \pm 0.8 a
Mudflat	105.0 \pm 4.8 a	16.6 \pm 0.0 a	28.2 \pm 0.5 d	19.1 \pm 0.8 ab

3.5. Relative Importance of Biotic and Abiotic Factors

The best regression models indicated that, for *K. obovata*, rodent herbivory, sediment porewater salinity, and light intensity were strong predictors of survival across both study sites, with rodent herbivory being the strongest driver (Table 2). For *A. marina*, rodent herbivory, insect herbivory, light intensity, and temperature were strong predictors for survival across both study sites, with light intensity being the strongest driver. In this model, higher temperatures were associated with lower survival, which is biologically implausible unless it reflects some other factor (perhaps increased herbivory or competition) that was not fully described by other variables in the regression model. For *S. apetala*, light intensity and temperature were strong predictors for survival across both study sites, with light intensity being the strongest driver. Overall, herbivory by rodents and insects was important for the two native mangroves, but not for the non-native *S. apetala*. Light intensity was important for both native and non-native mangroves.

Table 2. Results of the best multiple regression models for survival of three mangrove species across both sites. Significant p -values ($p < 0.05$) are in bold. The best models were chosen based on R^2 and Mallow's Cp and included some variables that were not statistically significant. Other reasonable models are shown in Supplementary Table S2.

Species	Variable	Coef.	SE	t	p
<i>Kandelia obovata</i> (Mallow's Cp = 5.49, Adj R^2 = 0.82)	Rodent	−0.91	0.07	−9.62	<0.0001
	Sediment porewater salinity	−0.08	0.09	−0.89	0.38
	Light intensity	0.12	0.08	1.51	0.14
<i>Avicennia marina</i> (Mallow's Cp = 3.75, Adj R^2 = 0.54)	Rodent	−0.18	0.12	−1.49	0.14
	Insect	−0.33	0.14	−2.39	0.02
	Light intensity	0.81	0.13	6.34	<0.0001
	Temperature	−0.36	0.14	−2.48	0.02
<i>Sonneratia apetala</i> (Mallow's Cp = 5.36, Adj R^2 = 0.72)	Light intensity	0.001	0.0001	5.09	<0.0001
	Temperature	7.48	2.14	3.48	0.001

4. Discussion

Our results indicate that establishment of native mangrove seedlings on the southern coast of China is limited by herbivory and competition. Worldwide, some communities have “biotic resistance” to non-native species, where natives suppress the non-native species. We found the opposite: native mangrove seedlings suffered strong herbivory and competition, however, the non-native mangrove *S. apetala* was less affected. In particular,

we found that the non-native mangrove *S. apetala* can survive and outcompete invasive *S. alterniflora* over only two growing seasons in Leizhou Bay, but that both native mangroves survived poorly in the *Spartina* stands. Escape from herbivory and fast growth may drive the quick expansion of non-native *S. apetala* in China. As a result, it is likely that the coastal plant community will be increasingly dominated by non-native *S. apetala*.

4.1. Herbivory by Rodents and Insects Mediates Mangrove Establishment

Mangroves often suffer extensive mortality due to consumers at the propagule [60,61] and seedling [31,32] stages. Adult mangroves also experience considerable herbivory at times [62,63], but this is rarely severe enough to cause mortality or change plant species composition. This is consistent with results from other plant species: in general, juvenile stages are more vulnerable to consumers than are adults [64]. We found that grazing by the native rodent *R. losea* and insects strongly suppressed native mangrove growth and survival at the sites we studied. In particular, grazing by rodents especially affected *K. obovata* in Zhangjiang Estuary, where it was the dominant native mangrove. Grazing by insects especially affected *A. marina* in Leizhou Bay, where it was the dominant native mangrove.

Herbivores can have strong deleterious effects on plant growth, reproduction, and survival [65,66]. A number of herbivore taxa are known to affect the distribution and abundance of intertidal plants, with most research focusing on crabs, insects, birds, and large mammals in salt marshes [62,67]. Historically, small mammal herbivores were thought to play a minor role in structuring saltmarsh plant communities [68,69], but a number of exceptions are known. For example, herbivory by meadow voles (*Microtus pennsylvanicus*) and deer mice (*Peromyscus leucopus*) influences plant species interactions in New England [70], and grazing by the introduced rodent nutria, *Myocastor coypus*, affects the distribution and productivity of intertidal plants in Louisiana [71]. Here, we show that small mammal grazing plays an important role in the early establishment of mangroves at two study sites in southern China (Supplementary Figure S2).

We observed grazing by *R. losea* on mangrove seedlings at two sites that were 820 km apart in southern China, indicating that herbivory by rodents on mangroves is widespread. *R. losea* is widely distributed in southeast China, where it causes significant damage to crops [53]. It was previously known to nest in mangrove canopies above the high-tide level, using leaves and branches of mangrove plants as construction materials [52]. Now that the introduced *S. alterniflora* has become widespread along the Chinese coast, *R. losea* preferentially builds its nests with leaves and stems of *S. alterniflora* along the mangrove–*S. alterniflora* ecotone [29]. We did note, however, that rat nests were more common at Zhangjiang Estuary, where *S. alterniflora* stands were widespread and vigorous, than at Leizhou Bay, where *S. alterniflora* stands were smaller and shoots were shorter (authors' personal observations). Consistent with this, grazing by rats on mangrove seedlings was greater at Zhangjiang Estuary than at Leizhou Bay. *R. losea* preferred to feed on native versus non-native mangrove species. In particular, rodent grazing heavily suppressed the survival of native *K. obovata*, because rodents fed both on the tips of newly planted propagules and on the stems of growing seedlings. *A. marina* was less affected, because rodents only grazed the more tender, upper stems of the plants, and not the tougher, main stem, which allowed the mangroves to resprout after grazing (Supplementary Figure S3). In addition, the fact that seedlings of *A. marina* possessed a 6 cm × 6 cm × 10 cm root ball at the start of the experiment might have helped them recover from grazing compared to *K. obovata*, which did not have a root ball at the beginning of the experiment; however, it would not explain the differences in grazing location. Rodents largely avoided the non-native *S. apetala* seedlings. The proximate reasons why *S. apetala* is mostly avoided by the rodents are not known, but the result is that rodent grazing suppresses regeneration of the native mangrove species, but not the non-native species.

Both the native and non-native mangroves suffered some insect herbivory in our study (Supplementary Figure S4); however, insect folivory was highest on *A. marina* at the lower-latitude site of Leizhou Bay, where it was the dominant native species. This latitu-

dinal pattern was consistent with general biogeography theory, predicting that herbivory pressure increases with decreasing latitude, and data from both salt marshes and mangroves showing that herbivory is higher at lower latitudes [63,72,73]. Leaves of *A. marina* have a higher nitrogen content and lower tannin content than leaves of many other mangrove species [2,50], which may explain why this species was preferentially grazed by insects. In contrast, leaves of *S. apetala* have a higher tannin content than leaves of native mangroves [74], which may explain why the non-native species was avoided.

These results are consistent with the “enemy release hypothesis” [25] for *S. apetala*—that it has escaped its native herbivores in the introduced range, and that this loss of herbivory is one factor that contributes to its success. We did not directly compare herbivory on *S. apetala* between the native and introduced ranges, so we cannot directly evaluate this hypothesis, but it is known that *S. apetala* suffers some herbivory by *Orgyia osseata* and *Streblote siva* in its native range [75], and we observed little to no herbivory on it in China.

4.2. Competition from Native Mangroves and Non-Native Cordgrass Mediates Mangrove Establishment

In addition to herbivory, mangrove seedlings were strongly affected by competition. Mangrove seedlings, similar to small plants in general, face intense competition for light from their taller neighbors [76]. None of the mangrove seedlings that we planted in stands of *K. obovata* (e.g., mangrove stands at Zhangjiang Estuary) survived, likely because this habitat had the lowest light availability (10% of ambient light) due to shading by large *K. obovata* trees (Supplementary Table S2). Survival gradually increased in other habitats with more light availability. We note that these plants may have also been competing for sediment nutrients, which we did not measure. Regardless, competition seems to be strong for mangrove seedlings, such as those studied here, but weak once mangroves outgrow the canopy of their neighbors [77] (authors’ personal observation).

We found that the non-native grass *S. alterniflora* strongly suppressed the growth and survival of mangrove seedlings. This result is consistent with the general finding that invasive non-native species often have strong competitive impacts on native species [26]. *S. alterniflora* coexists with mangroves in parts of its native range in the United States and in parts of its introduced range in China. In both cases, a number of studies have shown that it competes with mangrove seedlings. For example, in its native range, *S. alterniflora* impedes the growth of black mangrove (*A. germinans*) seedlings [78,79]. Similarly, in China, *S. alterniflora* significantly reduces the survival and growth of native mangrove seedlings [14,37]. Consistent with these past results, *S. alterniflora* strongly suppressed regeneration of the two native mangroves at the two sites we studied in China [14,37,57]. As with herbivory, however, the effect on *S. apetala* was weaker.

Overall, survival of the non-native mangrove *S. apetala* was higher than that of native mangroves. *S. apetala* mortality from abiotic factors and competition, however, was higher than that of the native mangroves at the high-latitude site (Zhangjiang Estuary), likely because *S. apetala* has a tropical distribution in its native range and is therefore sensitive to low temperatures in its introduced range in China [42,51]. The average low temperature during winter in Zhangjiang Estuary was <12.5 °C (average of nighttime temperatures over the coldest month), which is similar to the temperature limit of 13.6 °C (average of 24 h temperatures over the coldest month) reported for *S. apetala* in its native range [75]. Lower survival of non-native *S. apetala* in vegetated habitats likely occurred because plants were simultaneously suffering from low temperatures and low light intensity.

We noted a synergistic interaction between grazing and light availability in suppressing the establishment of native mangroves. When grazing and shading were both present, as in the mangrove understory and the *S. alterniflora* habitat, establishment of native mangroves was very poor. In contrast, the non-native mangrove *S. apetala* was able to establish in mangrove (Leizhou Bay) and *S. alterniflora* habitats in both sites. This synergistic interaction between herbivory and competition for light is in broad agreement with a growing body of literature showing that consumer pressure can interact synergistically with environmental stressors [29,47,62]. Our findings highlight the importance of considering multiple

factors that may covary when assessing the strength of biotic resistance mechanisms, especially considering that herbivory and competition are universal processes that operate across ecosystems and that naturally interact with each other [80].

4.3. Novel Interaction between Non-Native Species in Southern China

China has the largest *S. alterniflora* invasion in the world [39]. *S. alterniflora* has aggressively invaded mudflats and disturbed stands of native mangroves along the southern coasts of China during the last two decades [38,45], forming a mangrove–salt marsh ecotone across more than 9° of latitude. *S. alterniflora* competes with seedlings of native mangroves such that native mangroves can rarely regenerate in *Spartina* stands [11,14,37]. At the same time, however, *S. alterniflora* cannot invade intact stands of native mangroves [29,47], so both the non-native grass and the native mangroves can coexist in the absence of disturbance. The non-native mangrove *S. apetala*, however, alters this outcome. *S. apetala* grows rapidly and can outcompete both the invasive grass *S. alterniflora* and native scrub mangroves over two or three growing seasons [37,43,48]. As a result, *S. apetala* can be used to control the *S. alterniflora* invasion [48], but the end result is to replace one non-native species with another, and to replace native mangroves with a non-native mangrove. *S. apetala* had a higher growth rate than the native mangroves—this rapid growth rate is why this species was deliberately introduced into China for afforestation projects [42,45]. Although *S. apetala* was attractive to managers because its rapid growth led to impressive “afforestation” statistics, its introduction to China is likely to transform the native mangroves and intertidal *S. alterniflora* grasslands into low-diversity stands of non-native mangrove across the entire intertidal area. Our results suggest that coastal managers should avoid planting non-native *S. apetala* as a strategy either for restoration or for controlling the *Spartina* invasion.

5. Conclusions

Our study was the first, to our knowledge, to look at the role of mammal and insect herbivores in mediating the early establishment of both native and non-native mangrove species. Meanwhile, we considered how the vigorous invasion of *S. alterniflora* influenced the establishment of both native and non-native mangrove seedlings. Our findings showed that successful establishment of *S. apetala* was facilitated by release from natural enemies (the opposite of biotic resistance) and by fast growth that allowed it to outcompete neighboring plants. Our results provide new insights into how herbivory, competition, and abiotic factors interact to mediate the establishment of native and non-native mangroves, and also help forecast the future of coastal ecosystems in southern China.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13020192/s1>, Figure S1: Causes of mortality of seedlings of the three mangrove species. Figure S2: The native rat *Rattus losea* and its nest in Zhangjiang Estuary and in Leizhou Bay. Figure S3: Native mangrove seedlings that were grazed by rodents. Figure S4: Native and non-native mangrove leaves grazed by insects. Table S1: Density and vegetation structure of two native mangrove forests and *Spartina alterniflora* in Zhangjiang Estuary and Leizhou Bay. Table S2: Results of the best subset linear regression using up to six independent variables to predict survival of *Kandelia obovata*, *Avicennia marina*, and *Sonneratia apetala* in Leizhou Bay and Zhangjiang Estuary. Tables S3–S5: Summary of ANOVA tables examining the effects of site, species, habitat, and the interaction between them on plant survival, relative growth rate, and height in Zhangjiang Estuary and Leizhou Bay. Tables S6–S8: Summary of ANOVA tables examining the effects of site, species, habitat, and the interaction between them on the rodent stem grazing rate, the insect leaf herbivory rate, mortality by rodents, and competition and abiotic factors in Zhangjiang Estuary and Leizhou Bay.

Author Contributions: S.C.P. and Y.Z. designed the experiment and supervised the study; D.P., J.W., and Y.Z. conducted the experiment; D.P. and Y.Z. analyzed the data. All authors have read and agreed to the published version of the manuscript.

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