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Patterns of Alien Plant Invasion across Coastal Bay Areas in Southern China

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ABSTRACT

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An understanding of the ways in which levels of invasions by alien species are correlated with environmental factors is helpful to manage the negative impacts of these invasive species. Two tropical coastal areas in South China, Shenzhen Bay and Leizhou Bay, are national nature reserves, but they are threatened by invasive plants. Here, we investigated the level of invasion by exotic plants at both bays, and its relationship with selected environmental factors. We found a total of 34 invasive plant species, 18 of which were present at both bays; among these, 15 species were in terrestrial areas, three were at the ecotone, and one was in the mangroves. The two bays had a similar degree of invasion but were dominated by different species. Three invasive species (*Ipomoea purpurea*, *Wedelia trilobata*, and *Panicum repens*) were abundant at both bays, and only one species, *Sonneratia apetala*, was present in the mangroves. The number of alien species increased from mangrove to ecotone to terrestrial areas in both bays, while, in proportion, ecotone supported the most alien species in Shenzhen Bay. The relationships between plant invasion and habitat features depended on the variables that were used to measure the degree of invasions. In general, the occurrence of alien species was positively correlated with soil organic carbon and total N content but negatively correlated with the leaf area index and soil salinity. The biomass of alien plants was, on the other hand, positively correlated with total N and soil water content in the soil, and the density of alien plants was not correlated with habitat characteristics. Most of the alien plants originated from tropical America, but a few were from Africa and south Asia. We recommend restoration efforts that include removal of alien species, soil improvement, and the planting of native species.

ADDITIONAL INDEX WORDS: *Alien species, mangroves, coastal zone, China, Guangdong, Shenzhen Bay.*

INTRODUCTION

Mangroves are unique ecosystems found only in tropical and subtropical coastal mud flats, and they are able to provide important ecosystem goods and services (Weinstein *et al.*, 2007). Critical mangrove ecosystem services include supporting coastal food webs, protection of biodiversity and shorelines, mitigation of inland effects of storms, and reduction of pollution. Unfortunately, these important ecosystems have suffered from severe habitat loss and degradation, as well as increasing biological invasions (Sobrino *et al.*, 2002). Estuaries and coasts are particularly susceptible to invasion by nonnative species, because shipping and aquaculture frequently introduce new species (Williams and Grosholz, 2008).

In the past two decades, a large amount of research has been carried out on biological invasions, examining, among other topics, invasion patterns, processes, and impacts (Davis, 2009; Fridley, Brown, and Bruno, 2004; Kueffer, 2010; Novoa *et al.*, 2012; Simberloff *et al.*, 2013). Collectively, these studies showed that invasive alien species have changed ecosystem composition, structure, function, and dynamics. Some of the researches have focused on invasions in estuarine and coastal environments and their abiotic related mechanisms (Carboni, Santoro, and Acosta, 2011; Gonzalez-Moreno *et al.*, 2013; Lortie and Cushman, 2007; Santoro *et al.*, 2012; Sobrino *et al.*, 2002; Von Holle and Motzkin, 2007). However, few have reported on the invasion patterns and the relationships between plant invasions and environmental factors in mangrove ecosystems (Kueffer *et al.*, 2010; Williams and Grosholz, 2008). The mangrove ecosystem, with its ecological and socioeconomic importance, deserves more attention in this regard (Fourqurean *et al.*, 2010).

In south China, Leizhou Bay and Shenzhen Bay, located in Zhanjiang City and Shenzhen City, respectively, were important mangrove habitats along the Chinese coasts. To protect mangrove forests, local governments created nature reserves in the 1980s in both bays. They were later upgraded to national nature reserves. Prior to the establishment of natural reserves, both bays had been subject to land reclamation and fish/shrimp farming, which caused severe habitat loss and degradation

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(Ren *et al*., 2007, 2011). In addition, both bays have been major seaports in southern China, with Shenzhen Bay having greater economic activity and a larger human population than Leizhou Bay. As a consequence, the number of alien plants in these areas has been continuously on the rise (Ren *et al*., 2008, 2011).

In this study, we surveyed the alien invasive plants in the two bays to gain new insight into the current pattern of plant invasion, how future invasions might be prevented, and how the habitats might be protected and sustainably developed. We addressed the following three questions: (1) What are the levels of invasion and the identity of the invasive species in the two bays (2) What are the spatial patterns of invasive plants along the sea-to-land gradient from seaward to landward? (3) What factors are associated with plant invasion in these coastal zones? Since existing studies suggested that ecosystem edges and ecotones are in general more susceptible to invasions than the interiors of ecosystems (Davis, 2009), we hypothesized that invasion in ecotones would have the highest level of invasion along the sea-to-land environmental gradient. Because different community variables may have different responses to environmental conditions and thus give different indications in the degree of invasion (Guo and Symstad, 2008), we measured the species richness, density, and biomass of invasive plants, in both absolute and proportional terms to make comparisons.

MATERIALS AND METHODS

Study Sites

The study sites are located in the coastal areas in Leizhou Bay and Shenzhen Bay in Guangdong Province, South China (Figure 1). Both bays are in the lower subtropical maritime monsoon climatic zone in East Asia. Leizhou Bay, 20 km from Zhanjiang City (20°30′ N, 109°03′ E), has about 2 km^2 of mangroves dominated by *Avicennia marina, Aegiceras corniculatum*, *Rhizophora stylosa*, and *Kandelia candel*. The annual average temperature is 22.9 °C (28.4 °C in July and 15.5 °C in January), and the annual precipitation is 1711 mm (about 73% in the rainy season, April–October, and 27% in the dry season). The annual average evaporation is 1700–2000 mm (Ren *et al*., 2008).

Shenzhen Bay, located outside of Shenzhen City, on the east coast of the Pearl River Estuary (about 22°30′–22°39′ N, 113°53′–114°05′ E), has more than 3 km^2 of mangroves dominated by *Bruguiera gymnorrhiza*, *Kandelia candel*, *Aegiceras corniculatum*, *Avicennia marina*, and *Acanthus ilicifolius*. The annual average temperature is 22.4 °C (28.2 °C in July and 14.1 °C in January). The annual average rainfall is 1700–1900 mm (about 70% in the rainy season, April–October, and 30% in the dry season). The annual average evaporation is 1500–1800 mm (Ren *et al*., 2011).

Vegetation and Soil

In July 2009, we established seven transects (10 m wide) across the whole land–sea interface zone in each bay (Figure 1). Each transect was $\leq$300 m long, and the distance between two transects was at least 300 m. Different numbers of 10 m $\times$ 10 m quadrats were placed along each transect depending on the transect length. The number of quadrats was three to five for the mangrove community, 15–20 for the terrestrial community, and one for the ecotone between the mangrove and the terrestrial communities. For each of the three types of communities, *i.e*. the mangrove, the ecotone, and the terrestrial, one quadrat from each of the seven transects was selected for among-community comparisons and statistical analyses on the total number of species, density, and the Shannon-Wiener index. Selection of quadrats was random except for those located in the ecotones. Since there were only seven quadrats in the ecotone at each bay, all were selected.

In each selected 10 m $\times$ 10 m quadrat, we recorded the number of native and invasive species. The height, diameter at breast height (DBH; trees only), basal diameter (mangrove plants only), crown size, and growth status (living or dead) of each individual were also recorded. Using the classification of China's list of invasive plants, we designated all plants in the quadrats as invasive or native species (CAS Academic Divisions, 2009; Li and Xie, 2002; SEPA, 2007). *Sonneratia apetala* was recently listed as an invasive species in the mangrove forests (Ren *et al*., 2009). We visually estimated the coverage of invasive plants in the quadrats on a scale of 1 to 5. In addition, in order to provide a background comparison of the overall diversity of the two bays, we calculated the Shannon-Wiener index for each bay using R Language 2.11.0 (Magurran, 1988). The formula was: $H = -\sum P_i \ln P_i$, where P_i was the relative abundance of i species at each quadrat, and H described the species richness and the equitability of individual distribution within species. The larger the value of H, the greater was the diversity.

To estimate the biomass in the terrestrial and ecotone quadrats, we harvested all plants (later divided into invasive alien species and native species) in a 5 m $\times$ 5 m (for terrestrial) or 2.5 m $\times$ 2.5 m (for ecotone) subquadrat located in each selected 10 m $\times$ 10 m quadrat in the two communities. The fresh materials were weighed in the field and then oven dried to constant mass at 75 °C in the laboratory for determination of dry weight. Mangrove biomass was estimated based on tree height, DBH, or basal diameter (Ren *et al*., 2010).

To characterize the dimensionless quantity of plant canopies, we calculated the leaf area index, which was defined as the one-sided green leaf area per unit ground surface area (Ren *et al*., 2008). The leaf area index for each quadrat in each transect was recorded on cloudy days with a CI-110 canopy analyzer; five measurements were taken for each quadrat on each date. Furthermore, three soil cores (3.7 cm diameter and 30 cm depth) were randomly taken from each of the 10 m $\times$ 10 m quadrats when the tide was low, and then pooled to form one soil sample per quadrat. Soil water content was measured by comparing the mass of a subsample before and after oven-drying at 105 °C. Soil salinity was measured with an optical refractometer, and temperature and pH were measured with an auto-thermometer and a pH meter (Ren *et al*., 2007). Soil subsamples were air-dried and then sieved for nutrient analysis. Soil organic matter, total N, total P, and total K were determined according to Wartel, Barusseau, and Cornand (1995; see also Institute of Soil Science, Chinese Academy of Sciences, 1978).

Statistical Analysis

We used the coverage of 18 invasive plant species that were common to both bays to construct a vegetation matrix

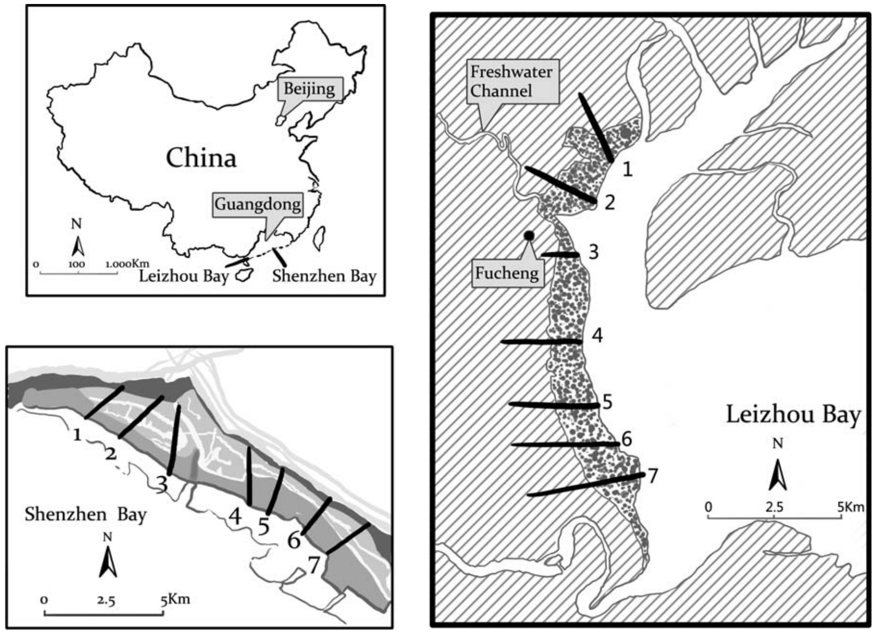

Figure 1. Locations of the two study sites, *i.e.* Shenzhen Bay and Leizhou Bay, in southern China. Each site had seven transects.

containing plant data from all quadrats. We also built a data matrix for the nine abiotic variables characterizing each quadrate. Then, canonical correspondence analysis (CCA) was used to examine the relationships between vegetation and abiotic variables with PC-ORD4 for Windows (Lachance and Lavoie, 2008; Økland, 1990).

Since abiotic factors are likely to play a crucial role in modifying the density, species richness, and biomass of native and exotic species in plant communities (Lortie and Cushman, 2007; Santoro *et al.*, 2012), we carried out multiple stepwise regression analyses to determine relationships between the density, species richness, and biomass of invasive plants and selected environmental factors. The absolute values of the density, species richness, biomass, and environmental factors were used. The analyses were performed with SPSS 13.0 software package (SPSS, Inc., Chicago, Illinois).

RESULTS

Degree of Invasion in the Two Bays

Shenzhen Bay contained 103 vascular plant species belonging to 45 families (Table 1); these included five mangroves species and 27 invasive plant species (Figures 2a and b). The average Shannon-Wiener index was 1.03 ± 0.41. Leizhou Bay contained 86 vascular plant species belonging to 36 families (Table 1); these included eight mangrove species and 31 invasive plant species (Figures 2a and b). The average Shannon-Wiener index was 0.98 ± 0.30. There were 71 plant species that were common to both bays, including 18 invasive plant species. The number of alien invasive species in both bays was smallest in the mangrove area, intermediate in the ecotone area, and largest in the terrestrial area; of the 18 invasive species that were common to both bays, 1, 3, and 15 grew in mangrove, ecotone, and terrestrial quadrats, respectively (Table 1).

Many of the invasive species in terrestrial areas were found at both bays, and the same was true for invasive species in ecotone areas (Table 1). These species belonged to the Asteraceae (six species), Poaceae (four species), Amaranthaceae (two species), Fabaceae (two species), and Euphorbiaceae (two species). Most species of invasive alien plants originated from tropical America (28 species), and others were from Africa (three species) and South Asia (two species) (Table 1). In contrast, *Sonneratia apetala*, an introduced mangrove species in the family of Sonneratiaceae, was the only invasive plant that was found in the secondary mangrove forests in both bays (Table 1).

The ecotone at Shenzhen Bay contained the alien invasive species *Mikania micrantha*, *Ipomoea purpurea*, *Wedelia trilobata* (L.) Hithc., and *Panicum repens* L. (Table 1). Among these, the vine *M. micrantha* had damaged the mangrove forest by forming dense mats over the mangroves and other plants. Three of the four invasive species found in the ecotone of Shenzhen Bay were also found in the ecotone at Leizhou Bay, *i.e. I. purpurea*, *W. trilobata*, and *P. repens*. While *M. micrantha* was not found in the Leizhou Bay, *Spartina alterniflora* Lossel (Table 1), a species not found in Shenzhen Bay, was present in the ecotone of Leizhou Bay. *Spartina alterniflora* was a recent invader that appeared to be spreading rapidly.

Invasive plants in the terrestrial quadrats included 22 herbaceous species, six vines, and five shrubs (Table 1). Three of the five species found in the ecotone were vines, and the other two were herbs. The only invasive species found in the mangroves was a tree.

Table 1. *Alien invasive plants in Shenzhen Bay and Leizhou Bay, south China.*

Species	Family	Life-Forms	Origin	Degree of Invasion[a] Shenzhen Bay	Leizhou Bay	Serial Number of Species[b]
Terrestrial						
Alternanthera philoxeroides (Mart.) Griseb	Amaranthaceae	Herb	South America	4	2	S1
Chenopodium ambrosioides L.	Chenopodiaceae	Herb	Brazil	2	3	S2
Amaranthus viridis L.	Amaranthaceae	Herb	Tropics of Africa	2		
Anredera cordifolia (Tenore) Steenis	Basellaceae	Liana	South America		3	
Leucaena leucocephala (Lam.) de Wit.	Fabaceae	Tree	Tropics of America	4		
Euphorbia hirta L.	Euphorbiaceae	Herb	Tropics of America	4	2	S3
Ricinus communis L.	Euphorbiaceae	Shrub	East Africa		5	
Malvastrum coromandelianum (L.) Garcke	Malvaceae	Herb	America		1	
Passiflora foetida L.	Passifloraceae	Liana	Neotropical	2	1	S4
Lantana camara L.	Verbenaceae	Shrub	Tropics of America	3	1	S5
Stachytarpheta jamaicensis (L.) Vahl.	Verbenaceae	Herb	Central and South America		4	
Ipomoea cairica (L.) Sweet	Convolvulaceae	Liana	Africa	1		
Waltheria indica L.	Sterculiaceae	Shrub	Tropics of America		4	
Datura stramonium L.	Solanaceae	Shrub	Central America		1	
Solanum capsicoides All.	Solanaceae	Shrub	Brazil	1		
Erigeron annuus (L.) Pers.	Asteraceae	Herb	America	2		
Eupatorium catarium Veldkamp	Asteraceae	Herb	South America		2	
Eupatorium ororatum L.	Asteraceae	Herb	Central America		3	
Galinsoga parviflora Cav.	Asteraceae	Herb	South America	3	2	S6
Parthenium hysterophorus L.	Asteraceae	Herb	Tropics of America		3	
Wedelia trilobata (L.) Hithc.	Asteraceae	Liana	Tropics of America	2	3	S7
Paspalum conjugatum Bergius	Poaceae	Herb	Tropics of America	5	5	S8
Abutilon theophrasti	Malvaceae	Herb	Brazil		2	
Sesbania cannabina	Fabaceae	Herb	Australia, Tropics of Asia	3		
Aster subulatus	Asteraceae	Herb	Central America	5	5	S9
Rhynchelytrum repens	Poaceae	Herb	South Africa	3	4	S10
Erigeron canadensis L	Asteraceae	Herb	North America	5	3	S11
Mikania micrantha	Asteraceae	Liana	Central America	3		
Axonopus compressus	Poaceae	Herb	Tropics of America		5	
Spermacoce latifolia	Rubiaceae	Herb	South America	1	4	S12
Phytolacca americana	Phytolaccaceae	Herb	India	1	5	S13
Bidens pilosa Linn.	Asteraceae	Herb	Tropics of America	3	1	S14
Xanthium spinosum L.	Asteraceae	Herb	South America	2	1	S15
Ecotone						
Ipomoea purpurea	Convolvulaceae	Liana	Tropics of America	4	3	S16
Wedelia trilobata (L.) Hithc.	Asteraceae	Liana	Tropics of America	3	3	S7
Panicum repens L.	Poaceae	Herb	Brazil	3	3	S17
Spartina alterniflora Lossel.	Poaceae	Herb	America		1	
Mikania micrantha	Asteraceae	Liana	Central America	3		
Mangvore						
Sonneratia apetala	Sonneratiaceae	Tree	Bangladesh	2	2	S18
Total				27	31	18

[a] Invasion was rated on a scale from 1 to 5 (low to high) based on visual assessment of coverage.
[b] Blank cells mean that the species does not occur in both bays.

In both bays, the invasive species with large coverage (with a high invasiveness rating) included *Paspalum conjugatum* Bergius, *Aster subulatus*, *Rhynchelytrum repens*, *Erigeron canadensis* L., *Alternanthera philoxeroides* (Mart.) Griseb, and *Euphorbia hirta* L. (Table 1).

In Shenzhen Bay, invasive plant species accounted for 24.7, 44.4, and 20.0% of the species in terrestrial, ecotone, and mangrove areas, respectively (Figure 2c). Invasive species accounted for 85.9, 47.7, and 4.6% of the plant density and 79.4, 12.6, and 5.6% of the biomass in terrestrial, ecotone, and mangrove areas, respectively (Figures 2f and i).

In Leizhou Bay, invasive plant species accounted for 39.4, 33.3, and 12.5% of all species in the terrestrial, ecotone, and mangrove areas, respectively (Figure 2c). Invasive species represented 82.3, 11.5, and 9.2% of the plant density (number of individuals per unit area) and 81.8, 8.6, and 10.5% of the biomass in terrestrial, ecotone, and mangrove areas, respectively (Figures 2f and i).

Comparison of the Habitats between the Two Bays

At both bays, the leaf area index (LAI) was relatively low, and LAI declined from mangrove to ecotone to terrestrial areas (Table 2). The soil bulk density values were large, and soil nutrient contents were low at both bays. The values for other soil physical and chemical properties were also relatively low at both bays (Table 2).

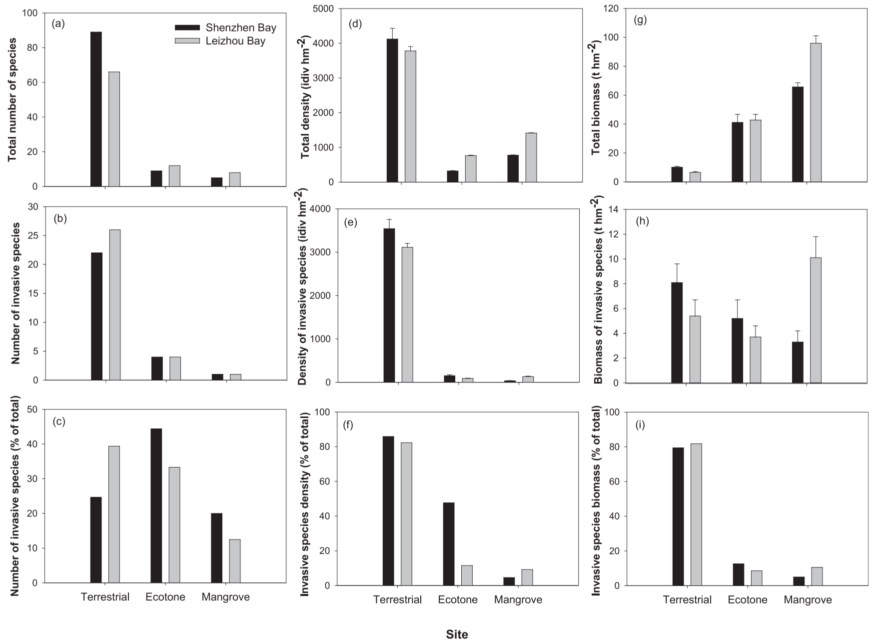

Figure 2. Number of species (a, b, c), density (d, e, f), and biomass (g, h, i) of all plants, native or invasive, at Shenzhen and Leizhou Bays in southern China. Error bars are standard errors. Sample sizes are seven quadrats for each plant community type at each site.

The Relationship between Invasive Plants and Environmental Factors

According to CCA for data from terrestrial areas, invasive alien species composition was positively correlated with soil bulk density, soil organic carbon, and total N content and was negatively correlated with LAI and salinity (Figure 3). Inferring from the species where they were distributed, in ecotone areas, invasive species composition was positively correlated with LAI. In mangrove areas, invasive species composition was positively correlated with soil organic carbon, total N, and pH (Figure 3).

Multiple stepwise regression indicated that among the environmental factors studied, the biomass of invasive plants was strongly and positively related with total N and soil water content (SWC; $y = -0.142 + 0.012\ \mathrm{N} + 0.006\ \mathrm{SWC}$; $r = 0.497$, $p = 0.01$), while soil bulk density was strongly and negatively correlated with the biomass of invasive plants ($r = 0.422$, $p = 0.005$). The soil bulk density (SD) and soil water content were strongly and positively correlated with the richness of invasive plants ($y = 0.351 + 0.126\ \mathrm{SD} + 0.010\ \mathrm{SWC}$; $r = 0.473$, $p = 0.01$). The density of invasive plants was not correlated with the habitat characteristics of the terrestrial, ecotone, or mangrove areas.

DISCUSSION

Patterns of Alien Invasive Plants in the Mangrove Coastal Ecosystems in Southern China

Both Leizhou Bay and Shenzhen Bay are located in the tropics, with similar climates and soil, and they support mangrove forests naturally. They both have a long history of aquaculture and port trade, which have resulted in habitat loss and degradation. The degraded habitats have made it difficult for native plants to reestablish and have allowed some pre-adapted alien plants to invade (Ren *et al.*, 2007, 2011). Most of them are native to tropical America, perhaps from regions with similar climates to southern China.

In our study areas, the nonnative mangrove, *S. apetala*, was introduced for rehabilitation of the mangrove forests in Leizhou Bay and Shenzhen Bay in the 1990s, after trials of planting native mangrove species in the degraded and barren mud flats failed (Zan *et al.*, 2003). *Sonneratia apetala* can reproduce sexually and has great dispersal power, and it appears to be a superior competitor to established native species. Therefore, *S. apetala* has invaded both bays and has impacted the structure and function of the mangrove ecosystems (Ren *et al.*, 2009; Zan *et al.*, 2003). There are other nonnative introduced mangrove species causing environmental problems in other regions of the world, such as Bangladesh (Biswas *et al.*, 2007) and south Florida and Hawaii in the United States (Fourqurean *et al.*, 2010).

The invasive plants identified in this study share some traits. In both bays, the dominant invasive plants belong to large families such as Compositae, Gramineae, Amaranthaceae, Leguminosae, and Euphorbiaceae. These families are widely distributed around the world, and many of their species show strong environmental adaptability and strong invasiveness. Also, these perennial evergreen herbs, shrubs, and lianas produce many seeds, they flower throughout the year, and many have both sexual and asexual reproductive systems (Ng and Corlett, 2002). Although the invasive species in this study share traits, they are also quite diverse. They include both

Table 2. *Habitat characteristics of Shenzhen Bay and Leizhou Bay.*[a]

Characteristics	Shenzhen Bay			Leizhou Bay		
	Terrestrial	Ecotone	Mangrove	Terrestrial	Ecotone	Mangrove
Leaf area index	1.1 ± 0.2	1.5 ± 0.2	1.9 ± 0.2	0.8 ± 0.3	1.6 ± 0.2	2.0 ± 0.2
pH	3.91 ± 0.05	4.56 ± 0.05	6.04 ± 0.03	4.22 ± 0.06	4.85 ± 0.03	6.83 ± 0.02
Salinity (%)	10.2 ± 0.3	18.6 ± 0.6	25.6 ± 1.6	10.4 ± 0.3	18.1 ± 1.9	19.7 ± 0.9
Soil bulk density (g cm^{-3})	1.72 ± 0.31	1.29 ± 0.09	0.58 ± 0.05	1.66 ± 0.12	1.41 ± 0.11	0.67 ± 0.03
Soil water content (%)	9.8 ± 1.4	32.2 ± 1.6	72.5 ± 5.1	10.2 ± 1.1	29.8 ± 2.7	73.8 ± 3.4
Soil organic carbon (%)	6.5 ± 0.6	10.2 ± 0.3	28.4 ± 1.1	5.6 ± 1.2	11.3 ± 0.9	21.1 ± 2.1
Total N (%)	0.61 ± 0.08	0.91 ± 0.11	1.31 ± 0.05	0.57 ± 0.07	0.75 ± 0.05	1.06 ± 0.05
Available P (%)	0.78 ± 0.08	0.78 ± 0.02	0.87 ± 0.11	0.41 ± 0.06	0.39 ± 0.03	0.36 ± 0.03
Total K (%)	21.11 ± 1.14	23.19 ± 2.31	23.21 ± 1.95	22.23 ± 4.12	22.31 ± 2.35	24.45 ± 2.11

[a] Values are means ± standard error. For soil properties, soil was sampled from 0 to 30 cm depth.

light-demanding as well as shade-tolerant species. Life-forms varied from vines to mat-forming herbs, tall herbs, grasses, ruderal and understory subshrubs, shrubs, small trees, and tall trees. They also have different habitat preferences, growth rates, and dispersal modes. The observed diversity of invaders is in line with the recent argument that invasive species cannot be characterized by a universal set of traits (Daehler, 1998; di Castri, 1989; Kueffer and Daehler, 2009; Thompson, Hodgson, and Rich, 1995).

Did Ecotones Have the Highest Degree of Invasion?

Generally, ecosystem edges and ecotones are more susceptible to invasion than the interiors of ecosystems (Davis, 2009). Results from our study, however, offered limited support to this hypothesis, as different community variables (number of species *vs*. density *vs*. biomass) indicated different invasion patterns. In general, the number of invasive species indicates the introduction effort and also future potential invasions, but the biomass that truly reflects the amount of resources used (Guo and Symstad, 2008).

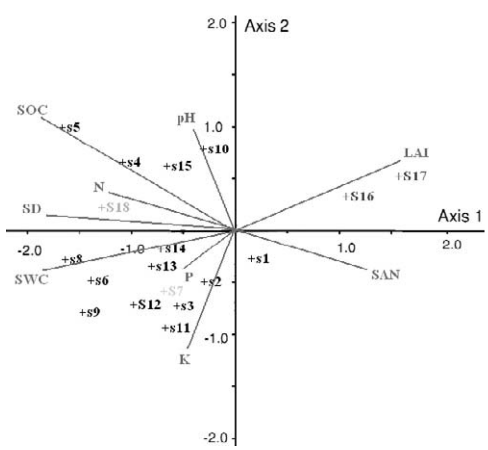

Figure 3. Canonical correspondence analysis ordination diagram of the 18 common species at Shenzhen and Leizhou Bays in southern China and nine environmental factors sampled in the 316 quadrats at the same sites. LAI = leaf area index, pH = pH value, SAN = salinity, SD = soil bulk density, SWC = soil water content, SOC = soil organic matter, N = total N, P = total P, K = total K. Black-colored codes are plants found in the terrestrial community, green are in the mangrove community, blue are in the ecotone, and pink are in both the terrestrial community and the ecotone. Species codes can be found in Table 1.

Similarly, different measures of the same variable (*i.e*. absolute value *vs*. proportion) also showed different patterns in our study. Specifically, species number and density of invasive plants increased from the mangrove forest to the ecotone to the terrestrial area; the percentage of species that were invasive did not follow this trend. Particularly, the proportion of invasive species at the ecotone was even higher than at the other two habitat types at Shenzhen Bay. Nevertheless, we believed that the proportion values (%) were a more accurate indication of invasion patterns because they took into consideration the fact that different habitats had varied levels of resource availability. The environmental degradation and habitat homogenization, and loss of biodiversity and ecological memory (*sensu* Sun *et al*., 2013) may result in an increased probability of invasion at the seaward end of the sea-to-land gradient.

Invasion is a complex process, and many abiotic and biotic factors may affect invader performance in coastal ecosystems (Carboni, Santoro, and Acosta, 2011; Davis, 2009). Abiotic, biotic, and historical land use affected levels of nonnative species richness, whereas nonnative cover was largely associated with abiotic conditions, particularly soil characteristics (Von Holle and Motzkin, 2007). Local abiotic factors likely play a crucial role in modifying the relative abundance of native and exotic species in plant communities (Lortie and Cushman, 2007). In the current study, the occurrences of specific invasive species in different communities (terrestrial, ecotone, and mangrove) were related to different ecological conditions, defined by the soil (such as soil bulk density, soil organic carbon, total N, and salinity) and light factors. The physical and chemical properties of the soil of the terrestrial, ecotone, and mangrove areas were degraded relative to those of largely undisturbed mangrove ecosystems at the Xiaoliang Long-Term Research Station, also in southern China (Ren *et al*., 2007). Long-term habitat change, especially soil degradation, may have increased the vulnerability of the two studied bay areas to plant invasions. The richness and biomass of invasive plants were strongly and positively related with soil bulk density, while the density of invasive plants was positively correlated with soil nutrients (total N). That means soil nutrients may not determine whether an area is invaded, but they may affect the growth of invasive species after invasion. Of course, besides soil properties, a successful invasion depends on other factors (e.g., the interactions between invaders and native species; Carboni *et al*., 2013; Kueffer *et al*., 2010).

Control of Invasion and Ecological Restoration in Both Bays

The Shannon-Wiener index values of relatively undisturbed mangrove and terrestrial forest in the region (good reference sites) are 1.38 and 4.12, respectively (Ren *et al*., 2007, 2008). The low Shannon-Wiener index and the dominance of invasive species seen in these two study sites suggests that we have a long way to go in restoring the two studied bays to a desirable state.

Two invasive species detected in this study are particularly damaging to the recovery of native ecosystem. One is *S. alterniflora* (salt-marsh cordgrass), which is native to North America. It can form dense single-dominant communities that completely change coastal habitats. It is listed as one of the world's most invasive species (IUCN, 2001). *Spartina alterniflora* should be removed from coastal areas in south China as soon as possible to prevent its spread. The second species, *M. micrantha*, was introduced to Shenzhen Bay about 10 years ago. This species can exert large impacts on habitats for native plants and birds by smothering the canopy of native trees and mangroves, which can lead to death of even large trees. Although considerable human and financial resources have been directed toward eradication of these and other invasive species in south China, the efforts have failed. Future efforts should be focused on minimizing their spread and impacts.

Morais *et al*. (2012) reported that the invasive species *Acacia longifolia* in sand dune habitats was favored in competition with natives under high salinity. However, He, Cui, and An (2012) indicated that physical stress rather than plant interactions limited cordgrass invasions. Native mangroves survive in habitats with seawater. The introduced *S. apetala* can grow in saline environments and is strongly competitive and dispersive (Bantilan-Smith *et al*., 2009; Ewel and Putz, 2004). In our view, *S. apetala* should not be a component of restored coastal nature reserves and should be removed. *S. apetala*, however, could be used as a nurse plant during the early rehabilitation of severely degraded, barren flats. The species must be closely monitored and controlled, however, so that it would not spread into nearby habitats. They should be removed once native species begin to establish.

Current Chinese laws prohibit cutting and planting in core zones of nature reserves, yet invasive plants are already present in the core zones of both bays. Effective control of these invasive plants in the core zones entails not only improvement of soil conditions for native plants, but also have exemption to the current law such that planting natives trees, shrubs, and herbaceous species can be allowed. In other words, we should control invasive plants in coastal areas by restoring native communities. Nature reserve authorities need to have their staffs, farmers, and the general public educated regarding the processes, patterns, and consequences of alien species invasions. Stakeholders should also be encouraged to participate in preventing invasions by alien plants and in restoring the ecosystem. Finally, actions to prevent new invasions by alien plants should be conducted on landscape scale, which includes the management of invaded habitats, as well as their neighboring areas, which may contribute invasive propagules or exert other negative influence.

CONCLUSIONS

Although national nature reserves have been established in Shenzhen Bay and Leizhou Bay, both bays are seriously invaded by alien plants. Degradation of the whole coastal ecosystem has reached such levels that invasive species have been able to invade the terrestrial areas, ecotones, and mangroves, with the terrestrial areas having higher richness, density and abundance of invasive plants. Invasion was positively correlated with soil organic carbon and total N content. Considering that soil nutrient levels may not determine whether an area is invaded but may affect the growth of invasive species after invasion, we recommend that the nature preserve administrations adopt comprehensive management programs to control the invasive plants and to prevent further invasion. Effective restoration efforts are needed along the gradient from terrestrial to mangrove areas. This may include soil improvement, invasive species removal and control, and the planting of native species. At the same time, both nature reserves should educate the public about invasive plants and should encourage citizens to participate in ecosystem protection and restoration.

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