RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

The effect of *Spartina alterniflora* eradication on waterbirds and benthic organisms

Chenxue Lyu[1], Shen Zhang[2], Xiaotong Ren[3], Mengling Liu[4], Kar-Sin K. Leung[5], Tao He[6], Qing Chen[7], Chi-Yeung Choi[1,8,9,10]

There has been an increasing number of coastal restoration projects to eradicate Smooth cordgrass (*Spartina alterniflora*) and restore bare tidal flats to conserve waterbirds. However, the evidence for the assumed benefits to waterbirds and benthic organisms after such restoration efforts remains limited. We evaluated the impact of *S. alterniflora* eradication on waterbirds and benthic organisms in southern China. We deployed time-lapse cameras and satellite trackers to quantify and compare the occurrence frequency and habitat use of birds in different habitats. We compared the density and biomass of benthic organisms collected in bare tidal flats and areas where *S. alterniflora* had been eradicated. We found that almost all waterbirds, except gulls, avoided areas where *S. alterniflora* was present. Once *S. alterniflora* was eradicated, the species richness and species-level diversity of shorebirds and waterbirds did not differ significantly from those of the bare tidal flats. At least 9 out of 14 tracked individual shorebirds used areas where *S. alterniflora* had been eradicated, with Common Redshank (*Tringa totanus*) demonstrating a clear preference for such habitat. The density and biomass of benthos in deeper sediments (5–20 cm below the surface) were significantly lower in areas where *S. alterniflora* had been eradicated than in bare tidal flats, indicating that the food resources for birds may take longer than 1 year to recover. This research demonstrates that the eradication of *S. alterniflora* is important for the restoration of waterbird habitats, and such efforts should be made in areas that are important to waterbirds.

Key words: invasive species, shorebird, Smooth cordgrass, tidal flat, wader, Zhanjiang National Mangrove Nature Reserve

Implications for Practice

- Restoration of bare tidal flats through eradicating invasive saltmarsh *Spartina alterniflora* can benefit waterbirds within a few months by providing open areas for waterbirds to forage.
- The impact of such restoration on benthic organisms, in terms of density and biomass, is less clear and they may take longer than 1 year to recover.
- Initiating projects to restore bare tidal flats by eradicating or controlling the spread of exotic saltmarsh plants and mangroves may be an important way to conserve migratory waterbirds globally.

Introduction

China's intertidal wetlands, positioned along the East Asian-Australasian Flyway (EAAF), are critically important for migratory waterbirds during migration stopover and wintering periods (Xia et al. 2017; Choi et al. 2020). Studies have shown that China's coastal wetlands support more than 200 species of waterbirds, including critically endangered species such as Spoon-billed Sandpiper (*Calidris pygmaea*) (Peng et al. 2017; Wang et al. 2018; Fan et al. 2021). However, 28–38% of coastal wetland areas in China were lost from the 1970s to 2018 (Song et al. 2020; Wang et al. 2021).

Author contributions: C-YC conceived and designed the research; all authors conducted the fieldwork and laboratory work; SZ mapped the habitat types; CL, C-YC conducted the analysis and led the writing of the manuscript with input from all authors.

[1]School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen, China
[2]Shanshui Conservation Center, Beijing, China
[3]Institute of Ecology, College of Urban and Environmental Sciences, Peking University, 100871, Beijing, China
[4]Marine Environmental Monitoring Center of Guangxi, Beihai, Guangxi, China
[5]Hong Kong Waterbirds Ringing Group, Mai Po Nature Reserve, Hong Kong, China
[6]Guangdong Zhanjiang Mangrove National Nature Reserve, Guangdong, China
[7]Shenzhen Mangrove Wetlands Conservation Foundation, Shenzhen, China
[8]Division of Natural and Applied Sciences, Duke Kunshan University, 215316, Kunshan, Jiangsu, China
[9]Environmental Research Center, Duke Kunshan University, 215316, Kunshan, Jiangsu, China
[10]Address correspondence to C.-Y. Choi, email choimo@yahoo.com

doi: 10.1111/rec.14023
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14023/suppinfo

The reclamation of tidal flats and the invasion of Smooth cordgrass (*Spartina alterniflora*) have substantially reduced the habitat available for waterbirds (Gan et al. 2009; Jackson et al. 2021), contributing to a rapid decline in coastal waterbird populations. For example, the population of endangered Great Knot (*Calidris tenuirostris*) declined at an average rate of 5.1% per year, and the endangered Far Eastern Curlew (*Numenius madagascariensis*) declined with an average rate of 5.8% per year from 1993 to 2012 (Studds et al. 2017; World Conservation Union 2021).

To prevent coastal erosion, protect seawalls and achieve a higher rate of terrestrial land expansion, *S. alterniflora* was introduced to China in 1979 (Chung 1993). It has spread rapidly throughout coastal China and is now distributed along all the coastal provinces and municipalities in the mainland (Zuo et al. 2012; Mao et al. 2019; Meng et al. 2020), including many important waterbird sites (Jackson et al. 2021). Other countries and regions also face this problem, including New Zealand, Korea, and the west coast of North America (Strong & Ayres 2013; Kim et al. 2015). *S. alterniflora* is a perennial rhizomatous grass and its invasion has triggered considerable changes to intertidal wetland ecosystems. *S. alterniflora* competes with mangroves (Shen et al. 2022), and the dense *S. alterniflora* patches are not favorable habitat for shorebirds, as dense vegetation makes it difficult for shorebirds to forage and avoid predators (Gan et al. 2009). For this reason, many managers have taken actions to control the spread of and remove *S. alterniflora* to restore waterbird habitats (Zhou et al. 2015; Zhao et al. 2020). However, the assumed benefits of *S. alterniflora* eradication to waterbirds have not been quantified in China. With the increasing number of *S. alterniflora* eradication projects initiated to protect migratory waterbirds and restore tidal flat ecosystems in China (Li & Zhang 2008; Tang et al. 2021), evaluating the assumed benefits on migratory waterbirds and tidal flat wetland ecosystems has become particularly urgent. The varied outcomes from different eradication methods will also provide managers with insights into the best approach to suit their needs.

Benthic organisms are an important source of food for many waterbirds and form an important part of a tidal flat ecosystem. Studies have shown that invasion by *S. alterniflora* replaces the native saltmarsh community and covers open intertidal flats, thereby changing the composition of benthic organisms (Chen et al. 2007). The change in vegetation structure, soil characteristics, hydrology, or biotic interactions could also impact the composition of benthic organisms (Gao et al. 2018). The extensive root system of *S. alterniflora* makes it difficult for benthic organisms to form burrows (Zhao et al. 2014; Lu et al. 2022), thereby impacting the food source for waterbirds (Mao et al. 2019). Experiments in northeast England and Washington restored the bare surfaces of silt and sand in areas cleared of Common Cordgrass (*Spartina anglica*) by using herbicide, turning the areas into a habitat suitable for benthic organisms and attracting waterbirds to re-use these wetlands (Evans 1986; Patten & O'Casey 2007). Therefore, comparing the density and biomass of benthic organisms between *S. alterniflora* eradicated areas and bare tidal flat areas (where *S. alterniflora* was absent) can improve our understanding of the effects of *S. alterniflora* eradication on benthic communities, and it may explain the distribution of waterbirds across these habitats (Robichaud et al. 2022).

In this study, we assess the effect of the eradication of *S. alterniflora* on benthic organisms and waterbirds by comparing areas where *S. alterniflora* had been eradicated, untreated areas where it was still present, and natural bare tidal flat areas at the Guangdong Zhanjiang Mangrove National Nature Reserve (ZMNNR) in South China. We predict that areas with *S. alterniflora* present will have lower waterbird occurrence than areas where *S. alterniflora* has been eradicated. In addition, the frequency of waterbird occurrence, benthic density, and benthic biomass will not differ significantly between natural bare tidal flats and areas where *S. alterniflora* has been eradicated.

Methods

Study Area

Guangdong ZMNNR is located in Guangdong province in south China (20.2350°–21.5708°N, 109.6725°–110.5053°E). It is a subtropical area with a mild climate; the average annual temperature is 22.3°C and the average annual rainfall is 1,400 mm (Gao et al. 2009; Lu et al. 2015). The total area of the reserve is 20,300 ha, dominated by mangroves and bare tidal flats. There are more than 9,000 ha of mangrove forests, of which the main species are Black Mangrove (*Bruguiera gymnorrhiza*), Red Mangrove (*Rhizophora mucronata*), Narrow-leaved Kandelia (*Kandelia candel*), River Mangrove (*Aegiceras corniculatum*), and White Mangrove (*Avicennia marina*). It is an important migratory stopover, wintering, and breeding site for threatened waterbirds on the southern coast of China. There have been 194 species of birds recorded in the reserve in total, of which 59 are waterbirds (Zhang et al. 2008). Between December 2015 and January 2021, up to 38 critically endangered Spoon-billed Sandpipers (Martinez & Allcock 2016; Leung et al. 2022) were recorded on the tidal flats of the ZMNNR during the winter. It is the site with the largest number of overwintering Spoon-billed Sandpipers in China, reflecting the importance of ZMNNR in the conservation of threatened waterbirds. In 2002, ZMNNR was designated as a Ramsar site, a wetland site of international importance, because of its importance for waterbirds and mangroves (Wetlands-International 2017). However, the exotic *Spartina alterniflora* was found in the reserve around 2006 and spread quickly along the coast, with a total area of more than 18.5 ha (Chen unpublished data; Guo et al. 2018) by 2018. In our study, we chose the Fucheng area of ZMNNR as our study area due to the presence of high numbers of waterbirds, especially the critically endangered Spoon-billed Sandpipers, compared to other parts of the ZMNNR, and it was the primary area for a *Spartina* eradication project (Fig. 1; Zou et al. 2008; Choi et al. 2020). This area has a tidal range of 4.7 m (National Marine Data and Information

Figure 1. The study area (Fucheng) in relation to Leizhou Peninsula, Guangdong.

Service 2019) and about 2,700 ha of bare tidal flats at low tide (Murray et al. 2022).

ZMNNR managers recognized the negative impact of *S. alterniflora* on the wetland ecosystem and initiated an eradication project between November 2019 and July 2020. A total of 18 ha of *S. alterniflora* was planned for eradication at Fucheng. In November 2019, managers removed 14 ha of *S. alterniflora* to the north of Fucheng by digging up the surface layer (including all the rhizome layer) and then burying that at a depth of 1.5 m, using an excavator (Fig. S1). This process created a relatively soft layer of sediments near the surface, as the excavator mostly worked its way backwards and, therefore, did not cause sediment compaction to the eradicated area. From 8 May, 2020 to 19 July, 2020, an additional 4 ha of *S. alterniflora* was removed to the south of Fucheng with the support of Shenzhen Mangrove Wetlands Conservation Foundation, by cutting the stems, breaking the roots with an excavator, and covering the patch (to 30 cm beyond the edge) with two-layer black plastic shade-cloth (permeable to water and air) to prevent regeneration and seed germination. The shade cloths were all present in their covering plots until they were removed in July 2021 after checking the *S. alterniflora* roots, and the recurrence rate (seedlings or regrowth from rhizomes) was under 5%. *S. alterniflora* under mangroves were removed by manual digging of the surface rhizomes. Despite the eradication treatment, a few patches of *S. alterniflora* remained in the middle part of the study area (2.71 ha) (Fig. S2). This study compared usage by waterbirds and the abundance of benthic organisms in three types of habitats: natural bare tidal flats, areas with *S. alterniflora* present, and areas where *S. alterniflora* had been eradicated.

Sampling Methods

Waterbird Habitat Use—Time-Lapse Cameras. Waterbird habitat sampling was carried out over two winters. In the first winter (December 2019), eight paired quadrats (10 m × 10 m) were set up; each pair comprised an experimental quadrat where *S. alterniflora* was present (the height of *S. alterniflora* was 70–100 cm) and a control quadrat on the nearby bare tidal flat. In the second winter (December 2020), 12 paired quadrats (10 m × 10 m) were set up, each pair comprising an experimental quadrat either with *S. alterniflora* present ($n = 7$) or with *S. alterniflora* eradicated ($n = 5$), and a corresponding control quadrat on nearby bare tidal flat; the distances between the two paired quadrats were less than 300 m (63.2 ± 58.9 m; mean ± SD) and their relative elevations on the tidal flat were roughly the same, giving them similar inundation and exposure duration (see the details in Figs. S3 & S4).

A time-lapse camera (Brinno BCC2000 and F1.2 18–55 mm lens) was installed next to each quadrat, with an angle that allowed a complete view of the quadrat area to monitor the use by birds during the recording time (Fig. S5). A short bamboo pole was installed at each corner of the quadrat to allow identification of the quadrat boundary from the photo. Whenever possible, these cameras were installed before the quadrats were exposed by the falling tide (before birds arrived) and retrieved after the quadrats were covered by the rising tide (after birds left) to minimize potential disturbance to birds. Recording times for each pair of quadrats were kept as close as possible by installing and retrieving cameras in both control and treatment plots of the same pair before moving on to the next.

The daily recording time at each pair of quadrats was at least 3 hours (the maximum was 8 hours and 50 minutes) and a photo was taken every 10 seconds (the total sampled time was 756 hours and 47 minutes). All birds walking in the quadrats captured in the photos were recorded and identified to species level whenever possible. More than 10% of the birds were identified to species level, 26% were identified to at least genus level, about one-third to at least family level, more than 95% to at least order level, and only 4% of the birds were unidentified due to the poor image quality, light, weather, and other factors.

In this research, we defined shorebirds as species belonging to the order Charadriiformes (except gulls), waterbirds as birds from orders Charadriiformes and Ciconiiformes, and all birds as all kinds of birds present in the quadrats (Table 1). We selected only waterbirds that walked within the sample quadrat and combined that information with recording time, using the Margalef formula (Margalef 1956) to calculate species richness per hour (Equation 1) and the Shannon–Wiener index (Shannon 1948) to calculate the diversity index (Equation 2). The diversity index was calculated in order-level, family-level, genus-level, and species-level diversity indices according to different identification results. We also calculated bird occurrence frequency (the number of birds that appeared in the quadrat per hour).

$$d = (S-1)/\ln n \tag{1}$$

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i) \tag{2}$$

Among these indices, d is the Margalef diversity index per hour, S is the total number of species per hour in the sample, n is the total number of individuals per hour in the sample, H' is the Shannon–Wiener diversity index, and p_i is the ratio of the number of individuals in the i-th species to the total number of individuals.

All analysis were conducted in R 4.0.3 (R Core Team 2020). We first compared the occurrence frequency of shorebirds, gulls, and terns (including Saunders's Gull [*Saundersilarus saundersi*]; Black-headed Gull [*Chroicocephalus ridibundus*]; Caspian Tern [*Sterna caspia*], and Gull-billed Tern [*Gelochelidon nilotica*]), waterbirds, and all birds in the paired quadrats (treatment vs. control). We used the Wilcoxon signed-rank test to compare the indices (Margalef diversity index and Shannon–Wiener diversity index) of shorebirds between the treatment and control groups over two years because the raw and transformed data did not meet the assumption of a normal distribution for parametric tests (Kühnast & Neuhäuser 2008; Fagerland 2012). We plot the corresponding figures using the ggplot2 (Wickham 2016) package. Results are reported as mean ± SD. The results were considered statistically significant when p-value was less than 0.05.

Waterbird Habitat Use—Satellite Trackers. During the two winters, shorebirds were captured using mist nets at night. They were then ringed and fitted with solar GPS-GSM (global positioning system-global system for mobile communications) or GPS-Bluetooth trackers. The tracker models included Druid Debut Nano (2.8–3.8 g), Druid Mini (6.3 g), and Global Messenger HQBG0804 (5.2 g). The reported GPS circular error of probability (50%) for Nano is 2.5 m while Mini is 5 m. All trackers and harnesses used weighed less than 5% of the bird's body weight, with an overall average of 3.2 ± 0.7% ($n = 16$). Trackers were fitted to waterbirds either with leg-loop harnesses or by a glue-on method (Thaxter et al. 2014; Chan et al. 2016; Chang et al. 2020). Trackers could record about 100 GPS location fixes daily when the charging conditions were good (e.g. sunny and the solar panel was not obscured). Data were uploaded to a cloud database for storage through a Bluetooth receiver or GSM network. The retrieved location data were then used to quantify the habitat use of the tracked individuals in the study area. We marked the boundary of the study area by generating a minimum convex polygon based on all location fixes to quantify the habitat used by tracked birds.

Based on our experiences in the field in two winters, as well as satellite imagery (see details below), we then categorized our study area into six habitat types at a resolution of 30 m: (1) open sea or shallow water from dataset FROM-GLC10, 2017 v 0.1.3 (Gong et al. 2019); (2) farmland from dataset FROM-GLC10, 2017 v 0.1.3, (Gong et al. 2019); (3) aquaculture fishpond by visual interpretation using sentinel-2 L1C scene S2A_MSIL1C_20201208T031121_N0209_R075_T49QDD_20201208T051809.SAFE (United-States-Geological-Survey 2021); (4) mangrove by visual interpretation using the same image as fishpond; (5) *S. alterniflora* present or eradicated area mapped using drone imagery from ZMNNR, and (6) bare tidal flats in years 2014–2016 using satellite images (Murray et al. 2019) and extracted for our analysis (Table S2). All data were integrated, visually checked, and refined, then down-scaled to 30-m resolution to meet the coarsest dataset; all other types of habitats were defined as non-habitat as waterbirds rarely used these areas. The habitat map was then reprojected to CGCS2000/Gauss-Kruger zone 19 (EPSG:4497). After the creation of the habitat map, all location fixes were overlayed onto the map to determine the habitat type for each fix point. We then summarized the habitat composition used by each bird. Finally, we examined habitat preference using Bailey intervals (Cherry 1996). We filtered out consecutive location fixes that were less than 30 minutes apart (Sanzenbacher & Haig 2002) or with a speed faster than 5 km/h when birds were likely to be in flight to minimize dependence between fixes and remove potential biases toward locations with good charging condition that increased recording frequency.

Benthic Sampling. Based on the preliminary tracking data and field observation, waterbirds tended to move between segregated parts of the coastline in our study area, and we divided the coastline into the north, middle, and south sections. These also corresponded to different methods for *S. alterniflora* eradication (northern sites by burial, middle and south sites by cutting). Within each section, we further divided the area into upper, middle, and lower tidal zones by dividing the width of the tidal flat (roughly the distance from the seawall to the lowest tide line during low spring tide, which was about 1.5 km) into

Table 1. The list of birds recorded in this study.

Item				Common Name	Scientific Name
1				Common Greenshank	*Tringa nebularia*
2				Common Redshank	*Tringa totanus*
3				Far Eastern Curlew	*Numenius madagascariensis*
4				Eurasian Whimbrel	*Numenius phaeopus*
5				Eurasian Curlew	*Numenius arquata*
6				Dunlin	*Calidris alpina*
7			Shorebirds	Grey Plover	*Pluvialis squatarola*
8				Kentish Plover	*Charadrius alexandrinus*
9	All birds	Waterbirds		Greater Sand Plover	*Charadrius leschenaultii*
10				Lesser Sand Plover	*Charadrius mongolus*
11				Saunders's Gull	*Saundersilarus saundersi*
12				Black-headed Gull	*Chroicocephalus ridibundus*
13				Caspian Tern	*Sterna caspia*
14				Gull-billed Tern	*Gelochelidon nilotica*
15				Chinese Pond-heron	*Ardeola bacchus*
16				Little Egret	*Egretta garzetta*
17				Cattle Egret	*Bubulcus ibis*
18				Long-tailed Shrike	*Lanius schach*
19				Common Kingfisher	*Alcedo atthis*
20				Yellow Bittern	*Ixobrychus sinensis*
21		Other birds		Barn Swallow	*Hirundo rustica*
22				Red-billed Starling	*Sturnus sericeus*
23				Pied Harrier	*Circus melanoleucos*
24				Black-winged Kite	*Elanus caeruleus*

three tidal zones with equal width. The upper tidal zone was dominated by vegetation (mangroves and *S. alterniflora*), while the middle and lower tidal zones were bare tidal flats. A stratified (by tidal zone) random sampling approach was used in our benthic sampling design as the inundation time (i.e. tidal zone) has a strong influence on the distribution of benthic organisms (Choi et al. 2014). Benthic samples were collected from the upper (*S. alterniflora* eradicated areas) and middle tidal zones. No samples were collected from the lower tidal zone due to the substantial difference in inundation time.

Within each section (north, middle, and south) and tidal zone (upper and middle), we randomly selected three sampling quadrats (3 m × 3 m) using ArcGIS ("Create random points tool") with the minimum distance between quadrats set at 100 m. The average distance between the seawall and quadrats in the upper tidal zone was 169.5 m, and the average distance between the seawall and quadrats in the middle tidal zone was 591.5 m. *S. alterniflora* eradicated areas were located mainly at the lower edges of the upper tidal zone, which reduced the difference in inundation time between benthic samples collected in *S. alterniflora* eradicated areas and those in the bare tidal flats of the middle tidal zone, making a comparison reasonable. The impact of different tidal zones was kept to the minimum because the average distance between quadrats in *S. alterniflora* eradicated areas in the upper tidal zone and bare tidal flats in the middle tidal zone to the seawall was about 400 m.

Three core subsamples were randomly collected from each quadrat. Each core subsample (diameter 15.5 cm, area 0.075 m^2, and 20 cm deep) was divided into the top 5 cm and bottom 15 cm (5–20 cm). These two depths were sampled because shorebird species differ in their bill lengths and potentially exploit different depths of the benthos (Fitter & Cramp 1980; Piersma et al. 1993). All core samples were washed in situ through a 0.5 mm sieve. The benthic organisms were stored in 95% ethanol, and in the laboratory, all organisms were identified to the finest practicable taxonomic level using a dissecting microscope. We also recorded measurements from each organism, including body length, width, and height, for biomass estimation. Benthic samples were collected in December 2020 (13 months after *S. alterniflora* eradication by burying in the north section, 5 months after *S. alterniflora* eradication by cutting in the middle and south sections) with 17 quadrats and 51 core subsamples collected. The quadrats in the upper tidal zone were all located in areas where *S. alterniflora* had been eradicated (Fig. S6). The three core subsamples within each quadrat and depth class were combined in the analysis.

Based on the body measurement data, the ash-free dry mass of each benthic organism was estimated using standard conversion equations for the most closely related taxon (Rogers 2006; Choi 2015; Table S1). Measurements were still taken and recorded for the broken benthic organisms collected, with biomass estimated using the most closely related taxon and the size measured. The total biomass was divided by the surface area of the corer to obtain the total biomass per unit area, which was separated into the top layer biomass (top 5 cm), the bottom layer biomass (5–20 cm), and the combined biomass (0–20 cm). As the raw and transformed data did not meet the assumption for a normal distribution, we used the Wilcoxon signed-rank test in R to compare the biomass and density of benthic organisms between paired plots in different habitats, namely areas where *S. alterniflora* had been eradicated and paired nearby bare tidal flats.

Results

Waterbird Habitat Use—Time-Lapse Cameras

The Frequency of Occurrence of Birds in Different Habitat Types. Based on the two-winter data, the occurrence frequencies of shorebirds, waterbirds, and all birds were significantly higher in the bare tidal flats than in paired areas where *Spartina alterniflora* was present ($p < 0.01$), but there was not such a difference for gulls (Table S3; Figs. S7 & S8). The occurrence frequency of shorebirds was also significantly higher in the bare tidal flats than in areas where *S. alterniflora* had been eradicated. Although the occurrence frequency of shorebirds (2.17 ± 3.38 per hour, $n = 43$), waterbirds (3.40 ± 3.87 per hour, $n = 43$), and all birds (3.54 ± 3.96 per hour, $n = 43$) in the *S. alterniflora* eradicated areas were not as high as that in the bare tidal flats (shorebirds: 6.51 ± 8.09 per hour, $n = 43$; waterbirds: 6.80 ± 8.35 per hour, $n = 43$; all birds: 6.89 ± 8.43 per hour, $n = 43$), the occurrence frequencies were still substantially higher than the areas with *S. alterniflora* present (shorebirds: 0.07 ± 0.19 per hour, $n = 41$; waterbirds: 0.18 ± 0.58 per hour, $n = 41$; all birds: 0.15 ± 0.31 per hour, $n = 41$). The occurrence frequency of gulls was also higher in areas where *S. alterniflora* had been eradicated than in those where *S. alterniflora* was present (from 0 to 0.24 ± 0.53 per hour).

The Species Richness and Diversity Indices of Waterbirds in Different Habitat Types. We found that species richness and nearly all diversity indices were significantly higher in the bare tidal flats than in areas with *S. alterniflora* present, except for the order-level diversity index (Table S3; Fig. 2A & 2B), indicating that *S. alterniflora* had an adverse effect on the bird species richness and diversity. For the comparison between areas where *S. alterniflora* had been eradicated and bare tidal flats, the species richness, order-level, family-level, genera-level, and species-level diversity indices were not significantly different (Table S3; Fig. 2C & 2D).

Species richness and species-level diversity of shorebirds were generally higher in the areas where *S. alterniflora* had been eradicated compared to areas where *S. alterniflora* was present (species richness: 0.05 ± 0.07 vs. 0, species-level diversity: 0.06 ± 0.13 vs. 0) (Fig. 2).

Waterbird Habitat Use—Satellite Trackers

In 2020, a total of 16 birds were tracked, comprising nine Common Redshank (*Tringa totanus*), two Red Knot (*Calidris canutus*), two Gray Plover (*Pluvialis squatarola*), one Saunders's Gull and two Greater Sand Plover (*Charadrius leschenaultii*), however no data were received from two

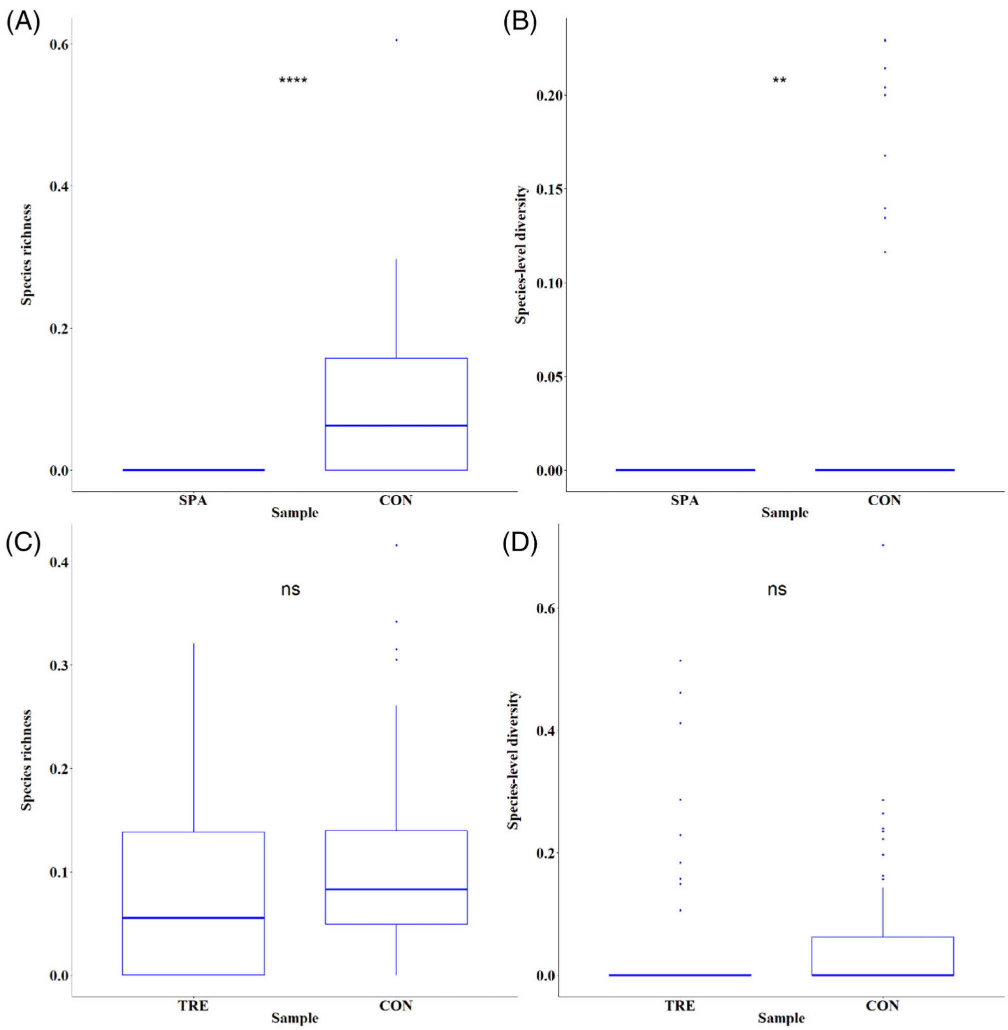

Figure 2. The species richness and diversity indices of shorebirds for different experimental groups: (A) is the species richness and (B) is species-level diversity for *Spartina alterniflora* present areas (SPA) and bare tidal flats (CON). (C) and (D) are the species richness and species-level diversity for *S. alterniflora* eradicated areas (TRE) and bare tidal flats (CON). Asterisks denote p less than 0.05, while "ns" denotes p greater than 0.05.

Common Redshanks, possibly due to the individuals leaving the area after release, tracker failure or death. Over 26,600 location fixes were obtained (1904 $\pm$ 2,456 per individual bird [$n = 14$]). The overall average tracking duration per tracked bird was almost 2 months (56.79 $\pm$ 52.78 days, $n = 14$).

From the tracking data, some individuals, including Common Redshank, were detected using *S. alterniflora* eradicated areas (Fig. S9). More than 5% of all Common Redshank fixes were recorded from such areas, although these areas accounted for only 0.09% of the total study area, or 0.63% of all intertidal areas (mangrove and bare tidal flats) (Fig. 3). Six of seven tracked Common Redshanks used areas where *S. alterniflora* had been eradicated, with one individual using these areas in 15% of its location fixes. Moreover, there appear to be some differences in the habitat use patterns between species, with Common Redshank often using vegetated areas (mangrove, 15.29 $\pm$ 14.68%, $n = 7$), while other species rarely used vegetated areas (mangrove, 0.29 $\pm$ 0.45%, $n = 7$). Most of the *S. alterniflora* eradicated areas were located next to or close (range: 0–300 m) to mangroves, which may be one reason that Common Redshank (6.86 $\pm$ 4.26%, $n = 7$) used *S. alterniflora* eradicated habitat substantially more than other species (0.71 $\pm$ 0.88%, $n = 7$) (Table 2).

The observations described above were confirmed in the Bailey intervals analysis (Table 3). Common Redshank used bare tidal flats, mangroves, and *S. alterniflora* eradicated habitats more than expected and fishponds in proportion to their availability; for other waterbirds, bare tidal flats and fishponds were used more than expected, and *S. alterniflora* eradicated habitat was used in proportion to its availability. The tracked shorebirds generally preferred bare tidal flats, mangroves, fishponds, and *S. alterniflora* eradicated habitats while avoiding sea or shallow water and farmland.

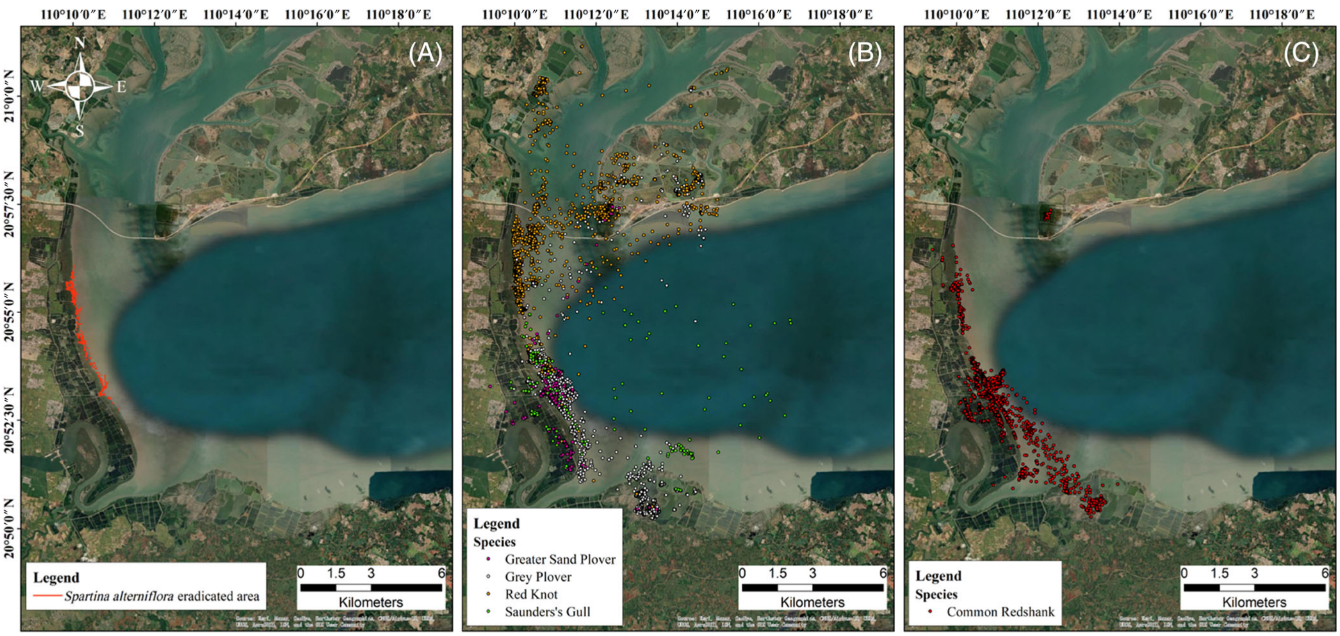

Figure 3. Locations of tagged waterbirds: (A) was the distribution of *Spartina alterniflora* eradicated areas (provided by Guangdong Zhanjiang Mangrove National Natural Nature Reserve); in (B), white circles denote location fixes from Gray Plovers, pink denotes Greater Sand Plovers, orange denotes Red Knots and green denotes Saunders's Gull; in (C), red circles denote location fixes from Common Redshank.

Table 2. The composition (in percentage) of different habitat types used by tracked birds with all location fixes was used.

Species	*Bird identities*	*Bare tidal flat*	*Fishpond*	*Mangrove*	Spartina alterniflora *eradicated*	*Sea or shallow water*	*Farmland*	*Total number of location fixes*
Common Redshank	CORE_00	59	30	2	9	1	0	174
Common Redshank	CORE_01	42	13	38	5	2	0	5,050
Common Redshank	CORE_02	44	19	32	5	1	0	2,762
Common Redshank	CORE_03	61	17	12	8	2	0	4,573
Common Redshank	CORE_18	67	33	0	0	0	0	6
Common Redshank	CORE_22	46	15	23	15	0	0	13
Common Redshank	CORE_35	81	13	0	6	0	0	32
Gray Plover	GRPL_01	25	71	1	0	4	0	137
Gray Plover	GRPL_23	51	45	0	1	3	0	6,479
Greater Sand Plover	GSPL_00	59	39	0	2	0	0	286
Greater Sand Plover	GSPL_01	68	29	0	0	2	1	702
Red Knot	REKN_40	12	67	0	0	21	0	57
Red Knot	REKN_65	23	48	0	0	29	0	6,206
Saunders's Gull	SAGU_23	44	30	1	2	23	0	176

Density and Biomass of Benthic Organisms

In December 2020, we collected benthic samples from 18 quadrats (three cores per quadrat) with a total of 816 individual organisms from at least 63 species, dominated by gastropod and polychaete (Table S4). The overall average densities of benthic invertebrates in the top layer (top 5 cm) and bottom layer (5–20 cm) were 459.30 ± 559.25 /m^2 and 305.22 ± 556.11/m^2, respectively. *Pirenella asiatica* (class: Gastropoda) was the most abundant species overall and accounted for more than 35% of the total number of individuals. This species was more abundant in the upper tidal zone (24 ± 64.37/m^2) than in the middle tidal flat (8.56 ± 21.78/m^2).

The effects of *S. alterniflora* eradication treatments on the biomass of benthic organisms were complicated. The top layer in areas where *S. alterniflora* had been eradicated had a significantly higher biomass ($p < 0.01$) than bare tidal flats, while in the bottom layers, the bare tidal flats had a significantly higher biomass ($p < 0.01$) (Fig. 4). The biomass totals in combined layers were not significantly different between the two habitat types. For benthic organism density in the bottom and combined layers, the bare tidal flats were significantly higher ($p < 0.01$ for both) than the *S. alterniflora* eradication areas, but there was no significant difference in the top layer. After considering different

Table 3. Percentage (%) of habitat availability and actual habitat usage by waterbirds and Bailey's 95% confidence interval (CI). Consecutive location fixes collected within 30 minutes were excluded. Habitat type with % available less than that in Bailey's 95% CI indicated that such habitat type was used more than expected, and vice versa. Habitat type with % available that falls into the range of Bailey's 95% CI indicated that such habitat type was used in proportion to its availability.

		Bailey's 95% CI for percentage of usage and results					
Habitat type	*% Habitat available*	*Common Redshank* (n = *6)*		*Other waterbirds* (n = *6)*		*Combined (n = 12)*	
Bare tidal flat	0.1148	(0.5922, 0.6966)	Prefer	(0.3191, 0.4246)	Prefer	(0.4702, 0.547)	Prefer
Fishpond	0.2139	(0.1468, 0.2324)		(0.3081, 0.4129)	Prefer	(0.2402, 0.3088)	Prefer
Mangrove	0.0246	(0.0693, 0.1353)	Prefer	(0.0029, 0.0095)	Avoid	(0.0346, 0.0686)	Prefer
Spartina alterniflora eradicated	0.0009	(0.0326, 0.0833)	Prefer	(0.0029, 0.014)		(0.0173, 0.0437)	Prefer
Sea or shallow water	0.5689	(0.0027, 0.0277)	Avoid	(0.2155, 0.3116)	Avoid	(0.1115, 0.1646)	Avoid
Farmland	0.0769	(0.0029, 0.0084)	Avoid	(0.0029, 0.0139)	Avoid	(0.0014, 0.007)	Avoid

eradication methods, findings were consistent with the combined results except that differences between habitats were nonsignificant for the top-layer benthic biomass when *S. alterniflora* was eradicated via the burial method, and differences between habitats were nonsignificant for the benthic biomass and total density in the bottom layer when *S. alte*rniflora was removed by the cutting and shade-cloth method (Figs. S10 & S11, Table S5). Overall, these results demonstrated that the density and biomass of benthic organisms in the bottom layer were often lower in *S. alterniflora* eradicated areas than on bare tidal flats.

Discussion

Our research shows that the eradication of *Spartina alterniflora* is an effective means of restoring waterbird habitats. Almost all waterbirds demonstrated an avoidance of areas where *S. alterniflora* was present. Once *S. alterniflora* was removed, the species richness and species-level diversity of shorebirds and waterbirds had no significant difference from that of the bare tidal flats. Tracking data also showed that waterbirds used, and some even preferred, areas where *S. alterniflora* was eradicated. Nonetheless, the density and biomass of benthic organisms (in the bottom 5–20 cm) as food for waterbirds tended to be significantly lower in *S. alterniflora* eradicated area than in bare tidal flats.

Many studies have shown that the abundance and diversity of waterbirds are negatively related to the height of vegetation (Colwell & Dodd 1995; Shepherd & Lank 2004). *S. alterniflora* grows very densely and the density in Leizhou was about 100–250 shoots/m^2, with a height range of 100–150 cm (Liu et al. 2016). Tall vegetation creates a barrier to the foraging of waterbirds and makes predator avoidance more difficult; as a result, waterbirds are reluctant to move into the *S. alterniflora* area (Gan et al. 2009). For most waterbirds, *S. alterniflora* restricts their activities and food availability, so the spread of *S. alterniflora* has a negative impact on waterbird abundance and diversity (Gan et al. 2009). In Yancheng, Jiangsu, China, due to the invasion of *S. alterniflora*, Red-crowned Cranes (*Grus japonensis*) have lost 80% of their suitable habitat, and their abundances have fallen sharply (Okoye et al. 2020). In the United Kingdom, the abundance of Dunlin (*Calidris alpina*) wintering in the British Isles was reduced sharply in areas where *Spartina anglica* had expanded (Goss-Custard & Moser 1988).

In this study, the eradication of *S. alterniflora* is an effective means to restore habitats for waterbirds. The species richness and diversity of shorebirds and waterbirds in bare tidal flats were significantly higher than in areas where *S. alterniflora* was present, while no significant difference was found in these indices between bare tidal flats and areas where *S. alterniflora* had been eradicated, indicating that the latter has been restored to serve a similar function as bare tidal flats for shorebirds and waterbirds. Chen's study in Zhanjiang showed a similar pattern, as the species richness, diversity index, and Pielou's evenness for avifauna were significantly lower in areas with *S. alterniflora* than in unvegetated shoals (Chen et al. 2018*a*). Our work also indicated that the species richness, abundance, frequency of occurrence, and species-level diversity of shorebirds were substantially higher in areas where *S. alterniflora* had been eradicated than in areas where *S. alterniflora* was present.

In England, waterbirds, particularly Common Redshank, fed more on intertidal areas cleared of *S. anglica* than on areas with it (Evans 1986). The same pattern was found with our tracked Common Redshanks. This is consistent with another study from the United States that showed a higher abundance of waterbirds in *S. alterniflora* eradicated area than in *S. alterniflora* untreated area (Patten & O'Casey 2007). Together, these studies suggest that the abundance of waterbirds will increase after the eradication of *S. alterniflora*. Given its rapid expansion along the coastal tidal flats in East Asia, especially in important waterbird sites along the China and Korea coasts (Kim et al. 2015; Jackson et al. 2021), it is critically important for local managers to control and eradicate *S. alterniflora* to improve the habitat availability for waterbirds.

There is little doubt that waterbirds will use eradicated areas, but different waterbird species may benefit differently from this process. In the case of our study area, it was clear that Common Redshanks, but not other waterbird species, prefer to forage at the mangrove edge and in *S. alterniflora* eradicated habitats. This may be related to the distribution of their main prey (decapods, isopods, and amphipods; Huang et al. 2022), hence, they probably benefit more from the eradication than other waterbird species.

As a key migratory stopover and wintering site for waterbirds, Fucheng in the ZMNNR has become one of the internationally important wetlands, supporting a variety of waterbirds, including

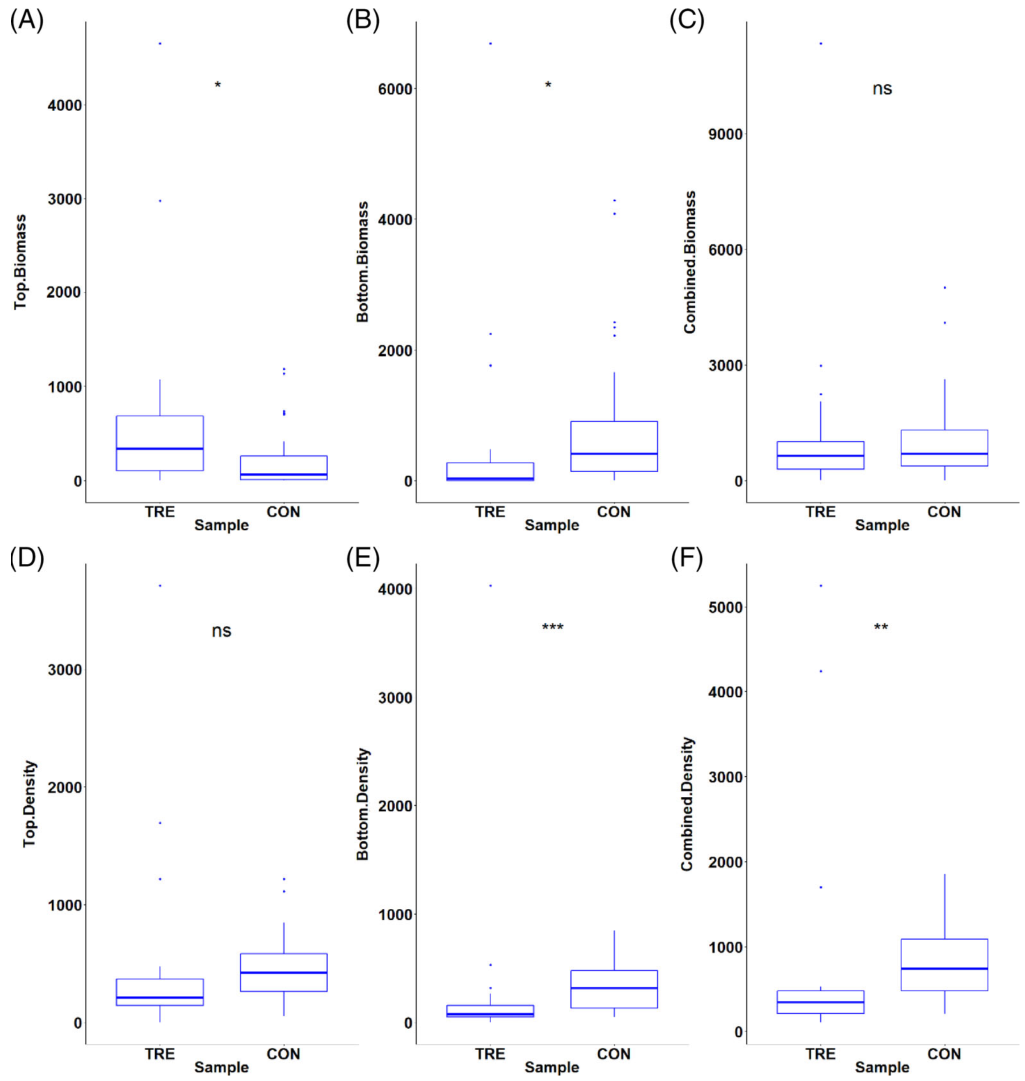

Figure 4. The biomass (grams per square meter) and density (number per square meter) of different layers (top [0–5 cm], bottom [5–20 cm], and combined layer) for *Spartina alterniflora* eradicated areas (TRE) and bare tidal flats (CON) in combined sections. Asterisks denote p less than 0.05, while "ns" denotes p greater than 0.05.

8% of the estimated world population of the critically endangered Spoon-billed Sandpiper—a flagship species for wetland conservation along the EAAF (Leung et al. 2022). Loss of waterbird habitats in ZMNNR will affect waterbird populations negatively along their migration routes. Our study shows that the eradication of *S. alterniflora* is an effective means to restore waterbird habitats. It is important to continue monitoring and controlling *S. alterniflora* in ZMNNR to ensure it will not reinvade the eradicated areas. It is also important to expand the studied species and locations to gain a more comprehensive understanding of the *S. alterniflora* eradication benefits to waterbird species.

One of the important drivers behind the differential distribution in waterbirds is the availability of food that a habitat can provide (Piersma et al. 1995). Waterbirds tend to choose wintering grounds with higher availability of food, higher energy content, and lower foraging costs (Piersma 2012). Benthic organisms are the vital energy sources of waterbirds (Duijns et al. 2013; Choi et al. 2017; Micael & Navedo 2018). In this study, the density of benthic organisms was lower in *S. alterniflora* eradicated areas compared to bare tidal flats at deeper depths (5–20 cm). As the differences in tidal inundation were not substantial, except the few days during neap tide cycle when *S. alterniflora* eradicated areas are exposed for longer while bare tidal flats may get inundated for longer, the observed differences could be caused by other factors (Choi et al. 2014): first is the effect of *S. alterniflora* eradication, as *S. alterniflora* was one of the primary food sources for macrobenthic fauna (Chen et al. 2018*b*); second, local people were farming shellfish by setting out shellfish seedlings on bare tidal flats and spraying pesticide to control other benthic predators (Peng et al. 2021); thirdly, the black shade-cloth used to cover *S. alterniflora* could form a barrier to sediments and benthic organism re-establishment, and the presence of dead *S. alterniflora* roots and shoots both above and belowground in some eradicated area could also hinder settlement by benthic organisms (Brusati & Grosholz 2006; Neira et al. 2006).

The use of black shade-cloth to cover *S. alterniflora* does not seem ideal. It may discourage vertical movement of benthic organisms, thereby changing the benthic communities and potentially affecting local people who collect natural benthic organisms for food; secondly, shade-cloth may also change the local topography over time, depending on its size and the strength of tidal current. Other approaches that do not involve black shade-cloth, such as herbicide use, are worth consideration. The density of benthic organisms in areas where *S. alterniflora* was eradicated did not recover to the level in bare tidal flats. It remains unclear how benthic communities will respond to the eradication process over time. A long-term monitoring effort is needed, lasting over 1 year after eradication. Our findings show that waterbirds returned and used *S. alterniflora* eradicated area very quickly. However, it is important to keep in mind that the bottom layer (5–20 cm) of eradicated areas is probably not providing as much food (i.e. benthic organisms) as the bottom layer of bare tidal flats, and this may impact the foraging of waterbirds that are capable of feeding on prey deep in the sediments (e.g. Eurasian Curlew [*Numenius arquata*], Bar-tailed Godwit [*Limosa lapponica*]). The patterns reported could be affected by the different inundation duration between eradicated areas (upper tidal zone) and bare tidal flats (middle tidal zone), as the former was exposed for about $78.49 \pm 6.81\%$ and the latter for $52.82 \pm 5.31\%$ ($n = 31$) of the time in the sampling month.

In short, the restoration of bare tidal flats through *S. alterniflora* eradication created foraging habitats for waterbirds, with species such as Common Redshank potentially benefiting more than other species do. However, areas where *S. alterniflora* was eradicated tended to have lower benthic organism density and biomass than bare tidal flats in the bottom layer, indicating that it may take longer for the benthic community to recover after restoration. These findings provided an example for evaluating the effectiveness of tidal flat restoration along the coast, and long-term monitoring is required to understand the long-term impact, especially on the change in benthic communities and thereby, food availability to waterbirds. There are some recommendations for relevant restoration effort: (1) design of monitoring work to assess effectiveness should be planned at an early stage, together with the eradication plan; (2) during the eradication work, ensure lucid communication between the eradication team and the monitoring team; (3) long-term monitoring lasting longer than a year is needed to assess the effectiveness of such eradication work. Finally, the removal of *S. alterniflora* is only the beginning of restoration. Taking the habitat preferences of different waterbirds into consideration and restoring the appropriate native plant or bare tidal flat to avoid habitat loss due to changes in vegetation type is an important step to follow, as well as an important way to conserve migratory waterbirds globally (Choi et al. 2022).

Acknowledgments

The funding support from Shenzhen Mangrove Wetlands Conservation Foundation and Shenzhen Science and Technology Program (JSGG20210802153535002, JCYJ20210324104205014) are gratefully acknowledged. We are in debt to Y. Ma, H. Peng, J. Xiong, H. Zeng, and the local volunteers for assisting with sample collection. We thank Y.-C. Lai, C.-H. Lin, C.-Y. Chiang, L. Xiang, W. Xue, and C. Cheng for helping with bird ringing and tagging activities. We thank L. Zhang's assistance with bird identification. We would also like to thank W. Chen for technical suggestions, L. Lin and Y. Xu for logistic support, Zhanjiang Mangrove National Nature Reserve for fieldwork facilitation, and L. Gibson for his comments on the earlier version of this manuscript. Data collected in this study will be available online after acceptance of the manuscript for publication.

LITERATURE CITED

Brusati ED, Grosholz ED (2006) Native and introduced ecosystem engineers produce contrasting effects on estuarine infaunal communities. Biological Invasions 8:683–695. https://doi.org/10.1007/s10530-005-2889-y

Chan YC, Brugge M, Tibbitts TL, Dekinga A, Porter R, Klaassen RHG, Piersma T (2016) Testing an attachment method for solar-powered tracking devices on a long-distance migrating shorebird. Journal of Ornithology 157:277–287. https://doi.org/10.1007/s10336-015-1276-4

Chang Q, Syroechkovskiy E, Anderson GQ, Aung PP, Beresford A, Brides K, et al. (2020) Post-breeding migration of adult Spoon-billed Sandpipers. Wader Study 127:200–209. https://doi.org/10.18194/ws.00201

Chen H, Li B, Hu J, Chen J, Wu J (2007) Effects of *Spartina alterniflora* invasion on benthic nematode communities in the Yangtze Estuary. Marine Ecology Progress Series 336:99–110. https://doi.org/10.3354/meps336099

Chen Q, Lin G, Ma K, Chen P (2018*a*) Determining the unsuitability of exotic cordgrass (*Spartina alterniflora*) for avifauna in a mangrove wetland ecosystem. Journal of Coastal Research 35:177–185. https://doi.org/10.2112/JCOASTRES-D-17-00203.1

Chen Q, Xu G, Zhang S, Ma K (2018*b*) Consumption of an exotic plant (*Spartina alterniflora*) by the macrobenthic fauna in a mangrove wetland at Zhanjiang, China. Wetlands 38:327–335. https://doi.org/10.1007/s13157-017-0970-9

Cherry S (1996) A comparison of confidence interval methods for habitat use-availability studies. Journal of Wildlife Management 60:653–658. https://doi.org/10.2307/3802084

Choi CY (2015) The northward migration stopover ecology of Bar-tailed godwits and great knots in the Yalu Jiang Estuary. PhD Dissertation. Massey University, Palmerston North, New Zealand

Choi CY, Battley PF, Potter MA, Ma ZJ, Liu W (2014) Factors affecting the distribution patterns of benthic invertebrates at a major shorebird staging site in the Yellow Sea, China. Wetlands 34:1085–1096. https://doi.org/10.1007/s13157-014-0568-4

Choi CY, Battley PF, Potter MA, Ma ZJ, Melville DS, Sukkaewmanee P (2017) How migratory shorebird species selectively exploit prey at a single-species-dominated staging site. The Auk 134:76–91. https://doi.org/10.1642/AUK-16-58.1

Choi CY, Li J, Xue WJ (2020) China coastal waterbird census report (Jan. 2012–Dec. 2019). Hong Kong Bird Watching Society, Hong Kong

Choi CY, Xiao H, Jia MM, Jackson M, Lai YC, Murray N, Fuller R (2022) An emerging coastal wetland management dilemma between mangrove expansion and shorebird conservation. Conservation Biology 36:e13905. https://doi.org/10.1111/cobi.13905

Chung CH (1993) Thirty years of ecological engineering with spartina plantations in China. Ecological Engineering 2:261–289. https://doi.org/10.1016/0925-8574(93)90019-C

Colwell MA, Dodd SL (1995) Waterbird communities and habitat relationships in coastal pastures of northern California. Conservation Biology 9:827–834. https://doi.org/10.1046/j.1523-1739.1995.09040827.x

Duijns S, Hidayati NA, Piersma T (2013) Bar-tailed godwits *Limosa l. lapponica* eat polychaete worms wherever they winter in Europe. Bird Study 60: 509–517. https://doi.org/10.1080/00063657.2013.836153

Evans P (1986) Use of the herbicide 'Dalapon' for control of spartina encroaching on intertidal mudflats: beneficial effects on shorebirds. Colonial Waterbirds 9:171–175. https://doi.org/10.2307/1521210

Fagerland MW (2012) T-tests, non-parametric tests, and large studies—a paradox of statistical practice? BMC Medical Research Methodology 12:78. https://doi.org/10.1186/1471-2288-12-78

Fan J, Wang X, Wu W, Chen W, Ma Q, Ma Z (2021) Function of restored wetlands for waterbird conservation in the Yellow Sea coast. Science of the Total Environment 756:144061. https://doi.org/10.1016/j.scitotenv.2020.144061

Fitter RS, Cramp S (1980) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palaearctic. Volume III. Wader to gulls. Oxford University Press, Oxford, England

Gan X, Cai Y, Choi CY, Ma ZJ, Chen J, Li B (2009) Potential impacts of invasive *Spartina alterniflora* on spring bird communities at Chongming Dongtan, a Chinese wetland of international importance. Estuarine, Coastal and Shelf Science 83:211–218. https://doi.org/10.1016/j.ecss.2009.03.026

Gao X, Han W, Liu S (2009) The mangrove and its conservation in Leizhou Peninsula, China. Journal of Forestry Research 20:174–178. https://doi.org/10.1007/s11676-009-0032-0

Gao X, Wang M, Wu H, Wang W, Tu Z (2018) Effects of *Spartina alterniflora* invasion on the diet of mangrove crabs (*Parasesarma plicata*) in the Zhangjiang Estuary, China. Journal of Coastal Research 34:106–113. https://doi.org/10.2112/JCOASTRES-D-17-00002.1

Gong P, Liu H, Zhang M, Li C, Wang J, Huang H, Song L (2019) Stable classification with limited sample: transferring a 30-m resolution sample set collected in 2015 to mapping 10-m resolution global land cover in 2017. Science Bulletin 64:370–373. https://doi.org/10.1016/j.scib.2019.03.002

Goss-Custard J, Moser M (1988) Rates of change in the numbers of Dunlin, *Calidris alpina*, wintering in British estuaries in relation to the spread of *Spartina anglica*. Journal of Applied Ecology 25:95–109. https://doi.org/10.2307/2403612

Guo X, Pan WS, Chen YC, Zhang W, He T, Liu YM, Zhang YH (2018) Invasion of *Spartina alterniflora* and protection of mangroves in Guangdong Zhanjiang mangrove National Nature Reserve and adjacent coastal area. Forestry and Environmental Science 34:58–63

Huang PY, Poon ESK, Chan LY, Chan DTC, Huynh S, So IWY, Sung YH, Sin SYW (2022) Dietary diversity of multiple shorebird species in an Asian subtropical wetland unveiled by DNA metabarcoding. Environmental DNA 4:1381–1396. https://doi.org/10.1002/edn3.350

Jackson MV, Fuller RA, Gan X, Li J, Mao D, Melville DS, Choi CY (2021) Dual threat of tidal flat loss and invasive *Spartina alterniflora* endanger important shorebird habitat in coastal mainland China. Journal of Environmental Management 278:111549. https://doi.org/10.1016/j.jenvman.2020.111549

Kim EK, Kil J, Joo YK, Jung YS (2015) Distribution and botanical characteristics of unrecorded alien weed *Spartina anglica* in Korea. Weed & Turfgrass Science 4:65–70. https://doi.org/10.5660/WTS.2015.4.1.65

Kühnast C, Neuhäuser M (2008) A note on the use of the non-parametric Wilcoxon-Mann-Whitney test in the analysis of medical studies. GMS German Medical Science 6:Doc02 (in Chinese)

Leung KK, Choi CY, Clark NA, He T, Martinez J, Ren XT, Ziang L, Xue WJ, Green R (2022) A closed-population mark-resighting estimate of the number of Spoon-billed Sandpipers at Leizhou Peninsula, Guangdong Province, China during the boreal winter. Journal of Asian Ornithology 38:22–28. https://doi.org/10.17863/CAM.78585

Li H, Zhang L (2008) An experimental study on physical controls of an exotic plant *Spartina alterniflora* in Shanghai, China. Ecological Engineering 32:11–21. https://doi.org/10.1016/j.ecoleng.2007.08.005

Liu W, Maung-Douglass K, Strong DR, Pennings SC, Zhang Y (2016) Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. Journal of Ecology 104: 173–181. https://doi.org/10.1111/1365-2745.12487

Lu K, Han G, Wu H (2022) Effects of *Spartina alterniflora* invasion on the benthic invertebrate community in intertidal wetlands. Ecosphere 13:e3963. https://doi.org/10.1002/ecs2.3963

Lu Y, Tang C, Chen J, Chen J (2015) Groundwater recharge and hydrogeochemical evolution in Leizhou Peninsula, China. Journal of Chemistry 2015: 427579. https://doi.org/10.1155/2015/427579

Mao D, Liu M, Wang Z, Li L, Man W, Jia M, Zhang Y (2019) Rapid invasion of *Spartina alterniflora* in the coastal zone of mainland China: spatiotemporal patterns and human prevention. Sensors 19:2308. https://doi.org/10.3390/s19102308

Margalef R (1956) Información y diversidad específica en las comunidades de organismos. Investigación Pesquera 3:99–106

Martinez J, Allcock JA (2016) China's Spoon-billed Sandpiper highest winter count in Leizhou Peninsular, Guangdong Province. Spoon-billed Sandpiper Task Force News Bulletin No. 15:23–27

Meng W, Feagin RA, Innocenti RA, Hu B, He M, Li H (2020) Invasion and ecological effects of exotic smooth cordgrass *Spartina alterniflora* in China. Ecological Engineering 143:105670. https://doi.org/10.1016/j.ecoleng.2019.105670

Micael J, Navedo JG (2018) Macrobenthic communities at high southern latitudes: food supply for long-distance migratory shorebirds. Austral Ecology 43:955–964. https://doi.org/10.1111/aec.12645

Murray NJ, Phinn SR, Dewitt M, Ferrari R, Johnston R, Lyons MB, Fuller RA (2019) The global distribution and trajectory of tidal flats. Nature 565: 222–225. https://doi.org/10.1038/s41586-018-0805-8

Murray NJ, Phinn SP, Fuller RA, DeWitt M, Ferrari R, Johnston R, Clinton N, Lyons MB (2022) High-resolution global maps of tidal flat ecosystems from 1984 to 2019. Scientific Data 9:542. https://doi.org/10.1038/s41597-022-01635-5

National Marine Data and Information Service (2019) Tide tables 2020. Ocean Press, Beijing, China

Neira C, Grosholz ED, Levin LA, Blake R (2006) Mechanisms generating modification of benthos following tidal flat invasion by a spartina hybrid. Ecological Applications 16:1391–1404. https://doi.org/10.1890/1051-0761(2006)016[1391:MGMOBF]2.0.CO;2

Okoye OK, Li H, Gong Z (2020) Retraction of invasive *Spartina alterniflora* and its effect on the habitat loss of endangered migratory bird species and their decline in YNNR using remote sensing technology. Ecology and Evolution 10:13810–13824. https://doi.org/10.1002/ece3.6971

Patten K, O'Casey C (2007) Use of Willapa Bay, Washington, by shorebirds and waterfowl after Spartina control efforts. Journal of Field Ornithology 78: 395–400. https://doi.org/10.1111/j.1557-9263.2007.00128.x

Peng HB, Anderson G, Chang Q, Choi CY, Chowdhury S, Clark N, Zöckler C (2017) The intertidal wetlands of southern Jiangsu Province, China – globally important for Spoon-billed Sandpipers and other threatened waterbirds, but facing multiple serious threats. Bird Conservation International 27:305–322. https://doi.org/10.1017/S0959270917000223

Peng HB, Chan YC, Compton TJ, Cheng XF, Melville DS, Zhang SD, Zhang ZW, Lei GC, Ma ZJ, Piersma T (2021) Mollusc aquaculture homogenizes intertidal soft-sediment communities along the 18,400 km long coastline of China. Diversity and Distributions 27:1553–1567. https://doi.org/10.1111/ddi.13302

Piersma T (2012) What is habitat quality? Dissecting a research portfolio on shorebirds. Pages 383–407. In: Fuller RJ (ed) Birds and habitat: relationships in changing landscapes. Cambridge University Press, Cambridge, United Kingdom. https://doi.org/10.1017/CBO9781139021654.019

Piersma T, Goeij P, Tulp I (1993) An evaluation of intertidal feeding habitats from a shorebird perspective – towards relevant comparisons between temperate and tropical mudflats. Netherlands Journal of Sea Research 31: 503–512. https://doi.org/10.1016/0077-7579(93)90062-W

Piersma T, Van Gils J, Goeij P, Van Der Meer J (1995) Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. Journal of Animal Ecology 64: 493–504. https://doi.org/10.2307/5652

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Robichaud CD, Basso JV, Rooney RC (2022) Control of invasive *Phragmites australis* (European common reed) alters macroinvertebrate communities. Restoration Ecology 30:e13548. https://doi.org/10.1111/rec.13548

Rogers DI (2006) Hidden costs: challenges faced by migratory shorebirds living on intertidal flats. PhD Dissertation. Charles Sturt University, New South Wales

Sanzenbacher P, Haig S (2002) Residency and movement patterns of wintering Dunlin in the Willamette Valley of Oregon. Condor 104:271–280. https://doi.org/10.1093/condor/104.2.271

Shannon CE (1948) A mathematical theory of communication. The Bell System Technical Journal 27:379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Shen HK, Zhao BY, Chen MY, Huang RY, Yu KF, Liang W (2022) Changes of the area of *Spartina alterniflora* and mangroves in Guangxi Shankou Mangrove National Nature Reserve from 1995 to 2019. Chinese Journal of Applied Ecology 33:397–404. https://doi.org/10.13287/j.1001-9332.202202.015

Shepherd PCF, Lank DB (2004) Marine and agricultural habitat preferences of dunlin wintering in British Columbia. Journal of Wildlife Management 68:61–73. https://doi.org/10.2193/0022-541X(2004)068[0061:MAAHPO]2.0.CO;2

Song S, Wu Z, Wang Y, Cao Z, He Z, Su Y (2020) Mapping the rapid decline of the intertidal wetlands of China over the past half century based on remote sensing. Frontiers in Earth Science 8:16. https://doi.org/10.3389/feart.2020.00016

Strong DR, Ayres DR (2013) Ecological and evolutionary misadventures of spartina. Annual Review of Ecology, Evolution, and Systematics 44: 389–410. https://doi.org/10.1146/annurev-ecolsys-110512-135803

Studds CE, Kendall BE, Murray NJ, Wilson HB, Rogers DI, Clemens RS, Fuller RA (2017) Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nature Communications 8: 14895. https://doi.org/10.1038/ncomms14895

Tang L, Zhou QS, Guo W, Li P, Gao Y (2021) Importance of high severity in a physical removal treatment for controlling invasive *Spartina alterniflora*. Ecological Engineering 171:106375. https://doi.org/10.1016/j.ecoleng.2021.106375

Thaxter CB, Ross-Smith VH, Clark JA, Clark NA, Conway GJ, Marsh M, Burton NHK (2014) A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gulls and Great Skuas. Ringing & Migration 29:65–76. https://doi.org/10.1080/03078698.2014.995546

United-States-Geological-Survey. (2021) Copernicus sentinel data 2021. ESA, USGS EarthExplorer https://www.usgs.gov/ (accessed 27 Dec 2021)

Wang X, Kuang F, Tan K, Ma Z (2018) Population trends, threats, and conservation recommendations for waterbirds in China. Avian Research 9:14. https://doi.org/10.1186/s40657-018-0106-9

Wang X, Xiao X, Xu X, Zou Z, Chen B, Qin Y, Li B (2021) Rebound in China's coastal wetlands following conservation and restoration. Nature Sustainability 4:1076–1083. https://doi.org/10.1038/s41893-021-00793-5

Wetlands-International. (2017) The list of wetlands of international importance. Ramsar. https://rsis.ramsar.org/RISapp/files/RISrep/CN1157RIS.pdf (accessed 22 Sep 2023)

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York. https://doi.org/10.1007/978-3-319-24277-4

World Conservation Union. (2021) The IUCN red list of threatened species. https://www.iucnredlist.org/en (accessed 22 Sep 2023)

Xia S, Yu X, Millington S, Liu Y, Jia Y, Wang L, Jiang L (2017) Identifying priority sites and gaps for the conservation of migratory waterbirds in China's coastal wetlands. Biological Conservation 210:72–82. https://doi.org/10.1016/j.biocon.2016.07.025

Zhang W, Zou FS, Dai MY (2008) Present status of bird resources in Zhanjiang mangrove wetland and strategies for their conservation. Forest Inventory and Planning 33: 54–57 (in Chinese)

Zhao CY, Liu XY, Bai JD, Lv FC, Li JS (2014) Impact of *Spartina alterniflora* on benthic macro-invertebrates communities on mangrove wetland in Xicungang Estuary, Guangxi. Biodiversity Science 22:630–639. https://doi.org/10.3724/SP.J.1003.2014.00109

Zhao ZY, Xu Y, Yuan L, Li W, Zhu XJ, Zhang LQ (2020) Emergency control of *Spartina alterniflora* re-invasion with a chemical method in Chongming Dongtan, China. Water Science and Engineering 13:24–33. https://doi.org/10.1016/j.wse.2020.03.001

Zhou T, Liu S, Feng Z, Liu G, Gan Q, Peng S (2015) Use of exotic plants to control *Spartina alterniflora* invasion and promote mangrove restoration. Scientific Reports 5:12980. https://doi.org/10.1038/srep12980

Zou FS, Zhang HH, Dahmer T, Yang QF, Cai JX, Zhang W, Liang CY (2008) The effects of benthos and wetland area on shorebird abundance and species richness in coastal mangrove wetlands of Leizhou Peninsula, China. Forest Ecology and Management 255:3813–3818. https://doi.org/10.1016/j.foreco.2008.03.020

Zuo P, Zhao S, Liu CA, Wang C, Liang Y (2012) Distribution of *Spartina* spp. along China's coast. Ecological Engineering 40:160–166. https://doi.org/10.1016/j.ecoleng.2011.12.014

Supporting Information

The following information may be found in the online version of this article:

Table S1. The relationship between AFDM (A, g) and body size variable (L, mm) in different benthos groups.
Table S2. The habitat types of the study area and their sources.
Table S3. Statistical results for the comparison of different indices in different habitat types for birds.
Table S4. The list of benthic organisms recorded in this study.
Table S5. Statistical results for the comparison of different indices in different habitat types for benthic organisms.
Figure S1. The photo of excavating *Spartina alterniflora* in Fucheng.
Figure S2. Location fixes of all tracked birds pooled together in the southern section of our study area, in relation to the *Spartina alterniflora* eradicated areas in red polygons.
Figure S3. The time-lapse camera quadrats in 2019: C means bare tidal flat area and S means *Spartina alterniflora* present area (paired with same number).
Figure S4. The time-lapse camera quadrats in 2020: C and N mean bare tidal flat area, S means *Spartina alterniflora* present area and T means *S. alterniflora* eradication area (paired with same number).
Figure S5. Time-lapse camera placement diagram.
Figure S6. The benthic sampling quadrats for benthic organisms.
Figure S7. The occurrence frequency (the number of birds that appear in the quadrat per hour) of shorebirds, gulls, waterbirds, and all birds for *Spartina alterniflora* present areas (SPA) and bare tidal flats (CON).
Figure S8. The occurrence frequency (the number of birds that appear in the quadrat per hour) of shorebirds, gulls, waterbirds, and all birds for *Spartina alterniflora* eradicated areas (TRE) and bare tidal flats (CON).
Figure S9. Common Redshank with satellite trackers foraging on *Spartina alterniflora* eradicated areas and *S. alterniflora* in the foreground grew from seeding establishment.
Figure S10. The biomass (grams per square meter) and density (number per square meter) of different layers (top [0–5 cm], bottom [5–20 cm], and combined layer) for *Spartina alterniflora* eradicated areas (TRE) and bare tidal flats (CON) in the north sections which did not use shade cloth during eradication.
Figure S11. The biomass (grams per square meter) and density (number per square meter) of different layers (top [0–5 cm], bottom [5–20 cm], and combined layer) for *Spartina alterniflora* eradicated areas (TRE) and bare tidal flats (CON) in the middle and south sections which used shade cloth during eradication.

Guest Coordinating Editor: Pawel Waryszak

Received: 30 June, 2022; First decision: 17 November, 2022; Revised: 12 September, 2023; Accepted: 12 September, 2023