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ECOLOGY

An invasive species erodes the performance of coastal wetland protected areas

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The world has increasingly relied on protected areas (PAs) to rescue highly valued ecosystems from human activities, but whether PAs will fare well with bioinvasions remains unknown. By analyzing three decades of seven of the largest coastal PAs in China, including World Natural Heritage and/or Wetlands of International Importance sites, we show that, although PAs are achieving success in rescuing iconic wetlands and critical shorebird habitats from once widespread reclamation, this success is counteracted by escalating plant invasions. Plant invasions were not only more extensive in PAs than non-PA controls but also undermined PA performance by, without human intervention, irreversibly replacing expansive native wetlands (primarily mudflats) and precluding successional formation of new native marshes. Exotic species are invading PAs globally. This study across large spatiotemporal scales highlights that the consequences of bioinvasions for humanity's major conservation tool may be more profound, far reaching, and critical for management than currently recognized.

INTRODUCTION

To remediate the sixth global mass extinction and maintain ecosystem services needed for human well-being in the Anthropocene, protected areas (PAs) have been called for and relied on (including the Aichi Biodiversity Targets and the Half-Earth Project) (1–3). To answer this call to arms, PAs have more than tripled in number and size, giving rise to a rapidly expanding global network over the past 40 years (1). Mounting evidence has revealed that PAs can effectively conserve habitats and biodiversity against losses driven by human activities such as overfishing, hunting, timber harvesting, and land reclamation (4, 5). This expanding global network of PAs, however, has been increasingly challenged by exotic species invasions, an issue recognized by a growing number of international conservation conventions, agreements, and organizations (6).

Although exotic species have been reported in PAs globally (6, 7) and been increasingly found to perform equally well or better in PAs than in non-PAs (6, 8, 9), their impacts on the performance of PAs

in saving native species and ecosystems remain poorly understood. Existing assessments have focused on the abundance and richness of exotic species and their direct impacts, often at small spatiotemporal scales (e.g., competitive replacement at plot scales over 1 or a few years) (6, 8, 9). These assessments, however, might offer limited insights into conservation actions that take place at large spatiotemporal scales, as the impacts of exotic species invasions can vary over spatial and temporal scales (10, 11). For example, the competitive impact of exotic species invasions on native species can be strong at small spatiotemporal scales and weaken at large spatial scales (11) or over time (12). The impacts of exotic species invasions may also be driven by different processes at different spatiotemporal scales. Many of the world's worst invasive species are not only superior competitors that replace native species in invaded areas but also powerful ecosystem engineers that create novel biogenic structures and modify geomorphology, thereby causing indirect, long-lasting impacts on native species and ecosystems across invaded and adjacent, uninvaded areas [i.e., landscape metamorphosis (13, 14)]. To our knowledge, nonetheless, assessments of the impacts of exotic species invasions on the performance of PAs at large spatiotemporal scales are still unavailable.

Here, we assess the large-scale, long-term impact of plant invasions on the performance of China's major PAs across the Yellow Sea in conserving internationally renowned coastal wetlands, including four World Natural Heritage and/or Wetlands of International Importance sites (Fig. 1A). Over the past few decades, >65% of natural coastal wetlands in the Yellow Sea have been lost, primarily because of land reclamation (i.e., human conversion of coastal wetlands by land filling and diking activities; Fig. 1B) (15). Among these coastal wetland ecosystems are expansive tidal flats—critical stopover habitats for millions of migratory shorebirds of the East Asian-Australasian Flyway (16) and iconic “Red Beach” marshes dominated by the red native succulent *Suaeda salsa*—one of the world's most visually stunning ecosystems (17). The loss of these coastal wetlands not only threatens important shorebird habitats (16) but will also likely lead to substantial decreases in economic and tourism potential (17).

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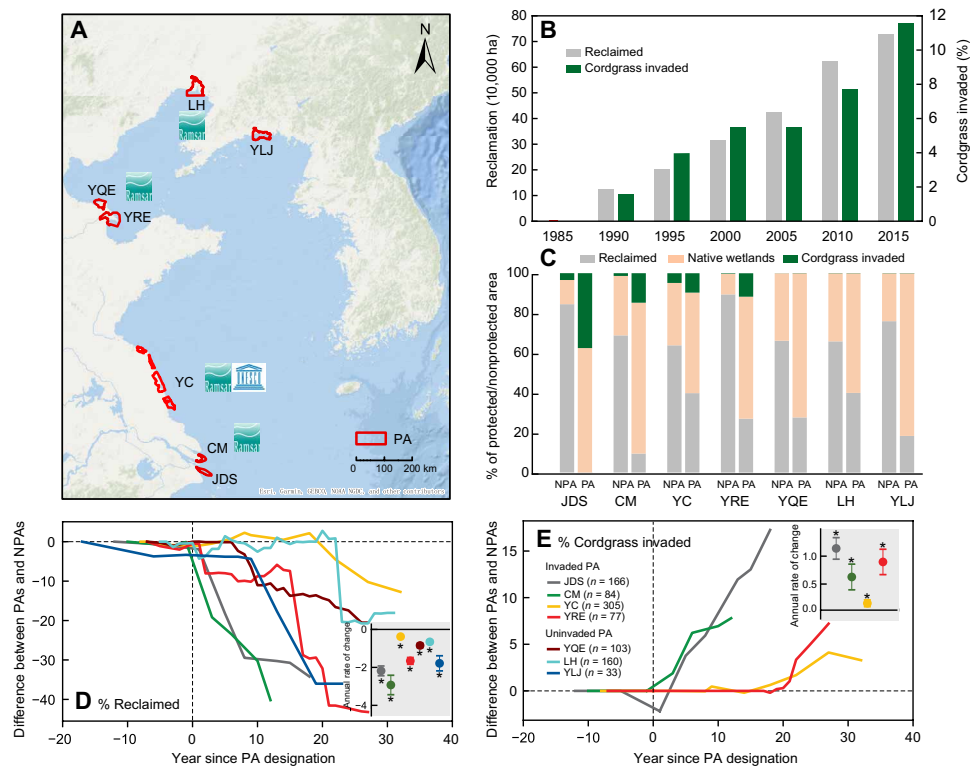


Fig. 1. China's largest coastal PAs have reduced wetland reclamation but are increasingly invaded by exotic plants. NPA, non-PA controls selected with statistical matching. **(A)** Locations of seven of the largest wetland PAs along the Yellow Sea coastline (JDS, Jiuduansha; CM, Chongming; YC, Yancheng; YRE, the Yellow River estuary; YQE, Yiqian'er; LH, the Liaohe Estuary; and YLJ, Yalu Jiang; see table S1 for full PA names and other details). PAs designated as World Natural Heritage and/or Wetlands of International Importance are indicated with respective icons. GEBCO, General Bathymetric Chart of the Oceans; NOAA NGDC, National Oceanic and Atmospheric Administration National Geophysical Data Center. **(B)** Increases in wetland reclamation and cordgrass invasion across China's Yellow Sea coastline. Reclamation was set as zero in 1985. Data for reclamations and cordgrass invasions were extracted from (19, 60), respectively. **(C)** Proportions of reclaimed, cordgrass-invaded, and remaining native wetlands in PAs and non-PA controls (all data are for 2018, except the CM and YC PAs where data in 2011 and 2015 before eradicating cordgrass in part of the PAs were used, respectively). **(D and E)** Mean differences in reclamation (D) and cordgrass invasion (E) between PAs and non-PA controls before and after PA designation. The legend given in (E) also applies to (D). Reclamation and cordgrass invasion were measured as percentage of a 1-km² grid (with sample size shown; see Methods), and negative and positive values indicate lower and higher reclamation/cordgrass invasion in PAs than non-PA controls, respectively. Insets are annual average rates of change since PA designation (or since invasion initiation in PAs for invasions that initiated after PA designation), error bars are 95% confidence intervals, and significant rates of change ($P < 0.05$) are indicated with an *.

Although many large PAs have been established between the 1980s and 2000s to prevent further loss of coastal wetlands to reclamation, their effectiveness in conserving highly valued native wetlands is uncertain, given ongoing plant invasions and climate change. The exotic cordgrass *Spartina alterniflora*, a global coastal invader and powerful ecosystem engineer (18), has aggressively invaded the Yellow Sea coastline (Fig. 1B) (19). Many studies have documented these invasions and their replacements of native marshes and open tidal mudflats (i.e., replacement effects), leading to the loss of native biota and habitats, including key shorebird habitats (18, 20–22) [although exotic cordgrass may provide compatible habitats for certain songbirds and marshbirds; reviewed in (18)]. Compared with many native marsh plants, exotic cordgrass is not only a superior competitor but is also more tolerant to flooding and wave stresses and more capable of trapping sediments (18, 20, 21). Besides directly replacing mudflats and native marshes (through competitive exclusion), cordgrass invasion can also indirectly impair native wetlands by precluding formation of new native marshes on accreting mudflats by preemptively monopolizing unvegetated mudflats (priority effects) (23). These direct and indirect mechanisms of impacts led

us to predict that cordgrass invasion may weaken or nullify the successes of PAs in conserving native wetlands over large spatio-temporal scales.

To test this prediction, we constructed a long-term dataset of mudflats, native marshes, exotic cordgrass marshes, and reclaimed lands in seven of the largest coastal PAs (see table S1 for a summary of basic information) and matched non-PA controls in China, using Landsat images and a rigorously validated classification algorithm implemented on Google Earth Engine (GEE) (see Methods). We then used this long-term data to quantify cordgrass invasion and wetland reclamation in PAs and non-PA controls. While PA designation is expected to nullify wetland reclamation, due to enforcement issues, whether this expectation has been fulfilled often needs assessment (1, 24). Furthermore, we examined the replacement effects of cordgrass invasion on native wetlands and key shorebird habitats using spatial change detection techniques (see Methods). Lastly, priority effects of cordgrass invasion on new native marsh formation were examined by comparing plant colonization of mudflats that accreted before and after the initiation of cordgrass invasion (see Methods).

RESULTS

Underperformance of coastal wetland PAs facing plant invasions

The success of China’s major coastal PAs in conserving native wetlands is being hampered by cordgrass invasion. Over the past three decades, both wetland reclamation and cordgrass invasion escalated along China’s Yellow Sea coastline (Fig. 1B). Establishing PAs slowed reclamation but did not reduce cordgrass invasion (Fig. 1, D and E). After PA designation, wetland reclamation decreased in PA sites more than in statistically matched non-PA control sites (Fig. 1D). Over time, reclamation became significantly lower in PA than non-PA control sites for all seven PAs (Fig. 1, C and D, and table S2). These results were observed in all seven PAs, although the magnitude of decrease differed and was small but still significant for Yancheng (YC) (Fig. 1, C and D). In contrast, cordgrass invasion increased more in PA than non-PA control sites (Fig. 1E and fig. S1). Over time, the extent of exotic cordgrass marshes became significantly greater in PA than non-PA control sites (Fig. 1C and table S2). Despite variation in cordgrass invasion history (table S1), these results were observed for all the four PAs currently invaded by cordgrass. In general, compared to non-PA control sites, PA sites still had significantly more native wetlands and key shorebird habitats [referred to as mudflats

and native sedge/succulent marshes, excluding native grass marshes dominated by *Phragmites australis* that are often avoided by shorebirds (25); also see Methods] (fig. S2 and table S3). Nonetheless, in the periods with cordgrass invasion, although natural unreclaimed wetlands in PA sites continued to increase relative to non-PA control sites, native wetlands and key shorebird habitats increased at lower rates or even decreased (fig. S2). The above findings generally held when only the strictly protected core zones of PAs were analyzed (figs. S3 and S4 and tables S2 and S3).

Widespread and irreversible replacement of native wetlands

Exotic cordgrass invaded and often, without human intervention, irreversibly replaced critical shorebird habitats including mudflats, native sedge marshes, and native succulent-dominated Red Beach marshes. Spatial analysis of all possible wetland transformations [see Fig. 2A for the Yellow River estuary (YRE) PA for example] revealed that, regardless of wetland type, cordgrass replacement was comparable or higher in PAs than in non-PA controls (Fig. 2B). Replacement of native wetlands occurred primarily to mudflats (Fig. 2B), while there were limited replacements of native grass and succulent marshes [but replacement of native sedge marshes was considerable at Jiuduansha (JDS) and Chongming (CM) PAs] (Fig. 2B).

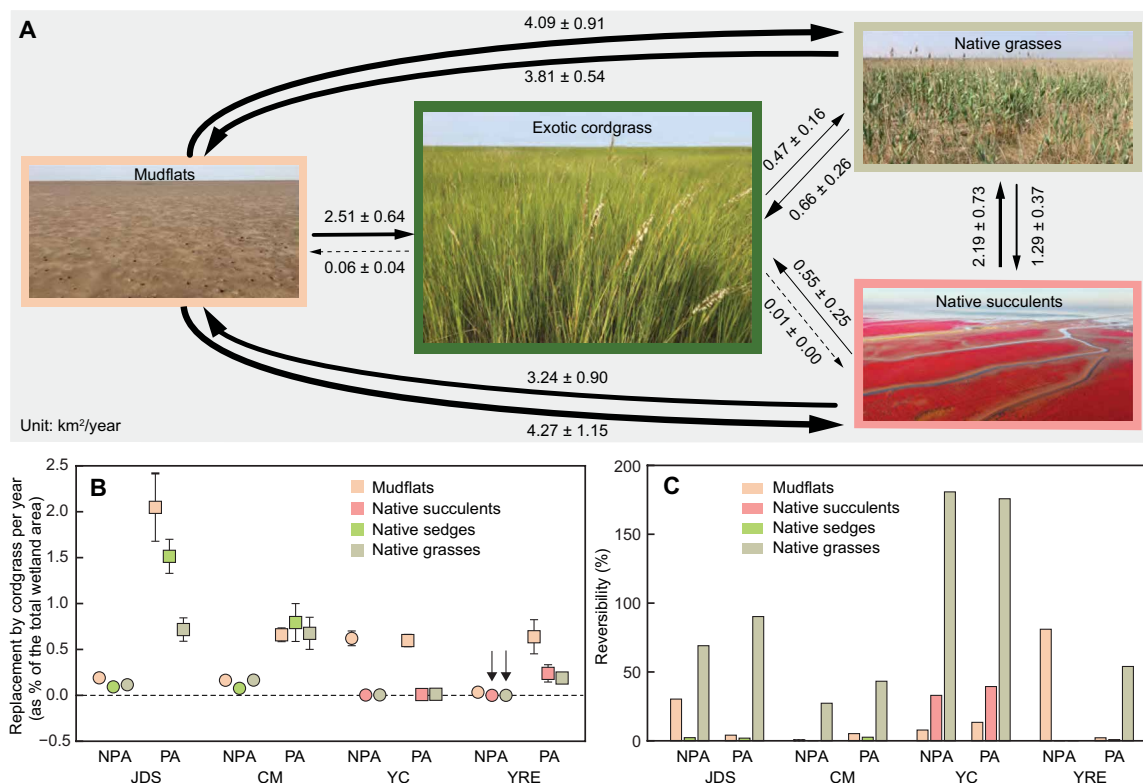


Fig. 2. Plant invasions replace native wetlands more extensively in PAs than non-PA controls. (A) Pathways of wetland transformation in unreclaimed areas in the YRE PA after cordgrass invasion initiated in 2009. Arrows indicate all possible pathways of transformation among wetland types, and line thickness is proportional to average rates of annual transformation, which are shown as means ± SEs. Mudflats and seagrasses/algae (small in extent) were combined. Photo credit: Qiang He, Fudan University (mudflats, exotic cordgrass, and native grasses) and Hong’an Ding, the Yellow River Estuary Association of Photographers (native succulents). (B) Annual replacement rates of native wetlands (mudflats, native succulent marshes, native sedge marshes, and native grass marshes) by exotic cordgrass. Data are means ± SEs. (C) Reversibility of exotic cordgrass marshes to different types of native wetlands. Reversibility is calculated as the percentage of total wetland area changing back from exotic cordgrass to a native wetland across all years with invasion after PA establishment. Reversibility is >100% when native plants replace more exotic cordgrass than the reverse. Reversibility is not given if the replacement rate of a native wetland by cordgrass does not significantly differ from zero [indicated with an arrow in (B), $P > 0.05$].

Regardless of protection status [main effect: $F_{1,16} = 0.15$, $P = 0.70$ and interaction effect: $F_{2,16} = 0.18$, $P = 0.84$; two-way analysis of variance (ANOVA)], cordgrass replacement of mudflats, native sedges, and native succulents, but not of native grasses, appeared to be irreversible (main effect: $F_{2,16} = 7.75$, $P = 0.0044$). We found minimal reversions of these replacements (Fig. 2A), and reversibility (i.e., the percentage of total wetland areas changing back from exotic cordgrass to mudflats, native sedges, and native succulents) was generally <15% (except for native succulents in YC PA and non-PA and mudflats in JDS and YRE non-PAs with limited cordgrass replacements; Fig. 2C). Reversibility for these native wetlands was even smaller when analyzed at the entire PA/non-PA scale (fig. S5). In contrast, there were considerable reversions from cordgrass-replaced native grasses (Fig. 2A and fig. S5), with much higher reversibility (often >50%; Fig. 2C).

Preclusion of new native marsh formation via primary succession

Cordgrass' irreversible replacement of accreting mudflats blocked, via priority effects, the formation of new native marshes via natural colonization. Mudflats were often expansive in PAs, while non-PA mudflats were usually lost to reclamation (fig. S6). The invasion priority effects were particularly conspicuous in JDS and YRE PAs characterized by rapid mudflat accretion of comparable rates before and after cordgrass invasion (fig. S7) and for Red Beach and sedge marshes dominated by competitively inferior native plants that showed little reversion once invaded by cordgrass. In JDS, for example, native sedges were pioneer colonizers of mudflats that accreted preceding cordgrass invasion. Native sedge cover increased to a maximum of 20 to 50% in 5 to 15 years (Fig. 3A) but declined quickly

when cordgrass invaded and reached a cover threshold of 20 to 30% (Fig. 3B). For mudflats that accreted after the initiation of cordgrass invasion, the cover of pioneer native sedges changed only slightly with time and remained generally <10% even in the longest time series (Fig. 3A). On these mudflats, exotic cordgrass was approaching the 20 to 30% cover threshold when it was expected to severely suppress native sedges through competition (Fig. 3B). Similarly, in YRE, native succulents were pioneer colonizers of accreting mudflats before cordgrass invaded, reaching 10 to 20% cover within 10 years. For mudflats that accreted after the initiation of cordgrass invasion, however, native succulents remained largely absent even in the longest time series (Fig. 3C), although cordgrass quickly took over a large proportion of the space available and exceeded the cover threshold (~20%) where it was expected to severely suppress native succulents through competition (Fig. 3D). Thus, once cordgrass began invading accreting mudflats, successional formation of native Red Beach and sedge marshes was largely precluded.

DISCUSSION

With increasing global reliance on PAs, conservation has been doubling its emphasis on and resources for restricting human activities to enhance the success of PAs (4, 5). Here, we document that these increased investments can be undermined by exotic species invasions due to direct and indirect invasion impacts operating at large spatiotemporal scales. Our multidecadal analysis of seven of the largest coastal wetland PAs in China shows that, although PAs have been achieving success in slowing reclamation-driven loss of iconic wetlands and critical shorebird habitats, this success is being counteracted by escalating exotic plant invasions. The PAs that we studied

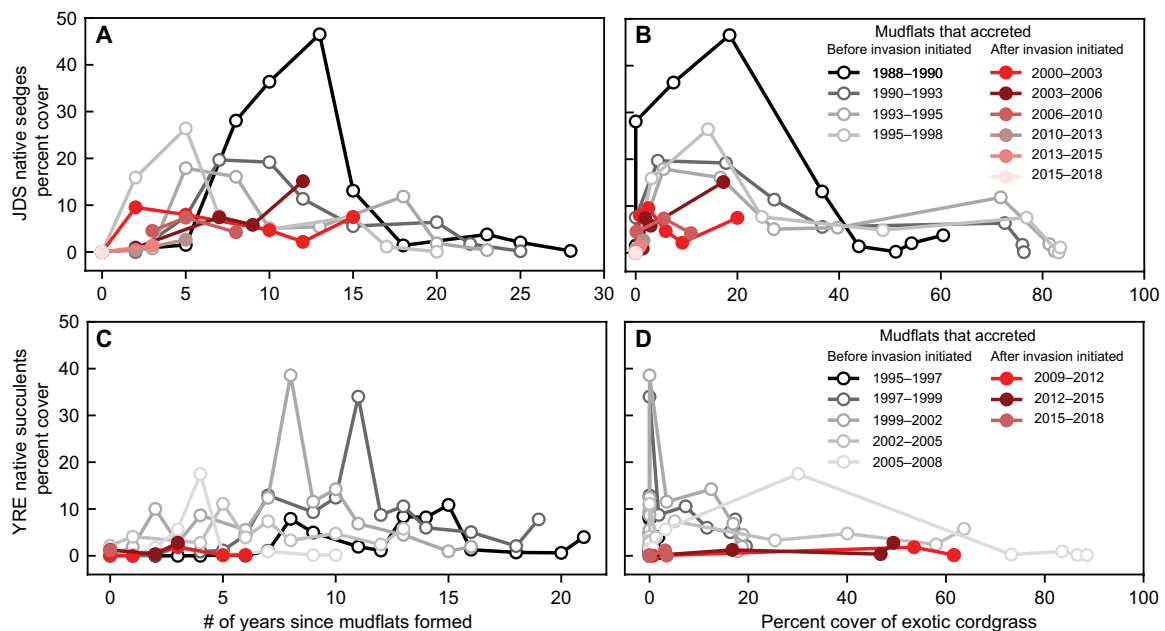


Fig. 3. Plant invasions preclude new native marsh formation via primary succession in PAs with rapid mudflat accretion. Data are percentage of the total area of intertidal mudflats that accreted in different periods before versus after cordgrass invasion initiated. Mudflats that accreted in different periods were given every 2 to 4 years, depending on the availability of Landsat images. The two PAs (JDS and YRE) with rapid wetland accretion were considered in this analysis. Note that mudflats that accreted before the initiation of cordgrass invasion might have become invaded at a later time point. (A and C) Changes in the percent cover of native sedges [JDS (A)] and succulents [YRE (C)] over time. (B and D) Percent cover of native sedges [JDS (B)] and succulents [YRE (D)] as a function of that of exotic cordgrass.

were vulnerable to invasion not only because protection from reclamation left more native habitats (primarily mudflats) open to direct replacement by cordgrass but also because cordgrass invasions generated indirect, long-lasting impacts by precluding formation of new native marshes on mudflats via primary succession. These findings at large spatiotemporal scales highlight that the impacts of exotic species invasions on coastal wetland PAs can be more profound and far reaching than currently recognized and emphasize the need of controlling exotic species invasions to avoid large-scale, long-term dysfunction of PAs. Through the lens of China's largest coastal wetland PAs in the Yellow Sea, our findings can inform understanding and managing the impacts of exotic species invasions on PAs in coastal wetlands in many other regions as well as those in other ecosystems.

Cordgrass invasion impacts on coastal wetland PAs at large spatiotemporal scales

To our knowledge, this study is the first assessment of the large-scale, long-term impacts of exotic species invasions on the performance of PAs. In our case with the smooth cordgrass, a notorious coastal plant invader, although cordgrass planting by humans had either a shorter history in PAs (JDS, CM, and YC) compared to non-PAs or was absent (YRE) (see table S1), our results reveal that cordgrass invasions were more extensive in PAs and produced particularly destructive impacts on PAs. Although direct competitive replacements have been often emphasized in studies at small spatiotemporal scales (26–28), our study shows that the impacts of exotic cordgrass invasion on PAs can be more profound and far reaching because of multiple direct and indirect mechanisms operating at large spatiotemporal scales. Besides competitive replacement of native marshes, cordgrass invasions also (i) preemptively and irreversibly replaced expansive mudflats at lower elevations and (ii), through priority effects, precluded the successional formation of new native marshes in PAs with rapidly accreting mudflats.

First, our assessment at large spatial scales found that direct competitive replacements of native marshes at upper elevations were generally limited, especially for those dominated by native succulents and native grasses. This finding is in contrast to previous small-scale studies that often emphasize strong competitive replacements by exotic cordgrass as found in zones where exotic and native plants overlap or in artificially assembled plots (27, 28). Limited competitive replacement of native succulents by cordgrass at large spatial scales is likely due to a trade-off between competitive ability and salt tolerance. Compared with marsh succulents, cordgrass, even in its native range (29), is typically competitively superior but less tolerant of hypersaline stress at upper tidal elevations where native succulents prevail (30). Replacement by cordgrass was also limited for native grasses dominated by *P. australis*, which has been shown to be competitively dominant over exotic cordgrass in certain conditions, especially in low-salinity conditions (31). This also explains why reversibility of cordgrass's replacement was high for native marsh grasses and could even exceed 100%, such as in YC. This is supported by other studies that have found areas where exotic cordgrass was replaced by native grasses (32).

In contrast to limited competitive replacement of native marshes at upper elevations, we found that preemptive replacements of mudflats at lower elevations were often substantial in PAs. Intertidal mudflats at lower elevations were a vacant habitat (33, 34) for exotic cordgrass and were expansive inside PAs but largely reclaimed outside

(fig. S6). Reclamation often begins at upper elevations and gradually extends to lower elevations. Outside PAs, reclamation is often more extensive, and both upper and lower elevation wetlands are reclaimed, while inside PAs, relatively low levels of reclamation still concentrate on upper elevations, setting aside large areas of low-elevation mudflats. The broad tolerance of cordgrass to flooding and wave stresses (18) allows preemptive colonization of mudflats, converting these expansive shorebird habitats in PAs into dense tallgrass meadows that are typically avoided by shorebirds (18). Besides protecting mudflats from reclamation, PAs are also vital areas for natural sediment accretion and new intertidal mudflat formation. By comparison, in non-PAs, mudflat accretion is often reduced or prevented by reclamation that limits sediment input and exacerbates wave action (35). Note that variation in development policies can affect reclamation in some regions or in some periods. Nonetheless, our finding that PAs slowed reclamation is consistently observed in all seven PAs and supported by our analyses showing that (i) there was a significant trend of decreasing reclamation in PA sites compared to non-PA control sites (Fig. 1D) and (ii) reclamation became significantly lower in PA than non-PA control sites in the most recent year of investigation (table S2). These indicate its robustness to potential policy variation.

Furthermore, our analysis at large spatiotemporal scales importantly reveals that preemptive, irreversible replacements of mudflats by exotic cordgrass precluded the natural succession from mudflats to native marshes, generating indirect and long-lasting consequences for the performance of PAs in saving native wetlands. Although PAs are vital areas for mudflat accretion and, subsequently, formation of new native marshes, our results suggest that cordgrass's preemptive and irreversible replacement of mudflats creates a new invaded stable state, where colonization of native plants and new native marsh formation are precluded. The priority effect documented here is analogous to invasive “backseat driver” processes, whereby invasive species colonize open, unoccupied habitats generated by disturbances and subsequently exclude native competitors (34). As mudflats are rapidly accreting in many protected coastal wetlands (36) and plant colonization of mudflats lays the foundation for primary succession, invasion-driven priority effects may have unexpected long-lasting consequences (23, 37). These chronic impacts of exotic species invasions cannot be adequately understood using short-term studies that span a few years, and our study highlights the value of long-term assessments for such understanding (10). Besides priority effects, cordgrass invasions can also affect PAs via other indirect mechanisms. For example, cordgrass invasions can impair the performance of PAs indirectly by altering wetlands in proximity to invaded areas by acting as “biological dams,” modifying local geomorphology, and weakening tidal access to adjacent, upper marshes [adjacency effects, *sensu* (38); reviewed in (39)]. These adjacency effects are part of a suite of long-distance interactions that link ecosystems and have been documented in other invaded ecosystems (32, 38).

Guarding the future of PAs from exotic species invasions

Our findings have important implications for understanding and managing the impacts of exotic species invasions on PAs in coastal wetlands in many other regions as well as those in other ecosystems. Besides the Yellow Sea, coastal wetland PAs in many other regions have also experienced a shift in the dominant anthropogenic impact from reclamation or other types of direct human disturbance to exotic plant invasions. Examples include the common cordgrass

Spartina anglica in the European Wadden Sea (40), the exotic mangroves *Sonneratia apetala* in southern China (41) and *Rhizophora mangle* in Hawai'i, USA (42), and exotic seaweeds (e.g., *Gracilaria vermiculophylla*) in Europe and North America (43). Compared to their native counterparts, those exotic species are also often competitively superior, more tolerant of abiotic stresses, and more capable of creating novel biogenic structures on mudflats and driving major geomorphic changes (14, 18, 42). Although empirical studies have yet to be conducted, these invasions are also likely to impair the performance of PAs in saving native wetlands similarly by preemptively monopolizing expansive mudflats and precluding successional formation of native marshes, mangroves, and seaweed/seagrass beds on mudflats.

Beyond coastal wetlands, exotic species invasions have also been found to be extensive in PAs in other ecosystems, although their impacts on the performance of PAs and the underlying ecological processes have yet to be investigated. In forest ecosystems in Mauritius, for example, although PAs reduced habitat destruction, they experienced rapid invasions of exotic plants, a putative driver of the decline of endemic island plant species (44). On subtidal reefs in northwestern Washington state (the United States) (9), western Iberian Peninsula in Spain (45), and San José Gulf in Argentina (46), despite restriction of human disturbance and access, PAs became highly invaded by exotic seaweeds. Exotic species invasions are indeed becoming increasingly common in terrestrial and marine PAs globally (6, 47), necessitating assessment and management of their impacts on PAs worldwide, especially for those with strict biodiversity conservation objectives (International Union for Conservation of Nature PA categories Ia and Ib) (6, 7).

Our findings suggest that, to safeguard PAs as effective refugia for highly valued native ecosystems and biodiversity and sustain their function into a changing future, a two-pronged approach that combines traditional protection and active control of exotic species invasions is needed. Some efforts have successfully eradicated exotic species in PAs [including a recent project in CM in China (48)], but whether these efforts lead to recovery of native communities and improve the performance of PAs over large spatiotemporal scales remains uncertain (48, 49). Our study also suggests that active control of exotic species in PAs should be habitat and species specific. Compared to PAs, non-PAs with stronger human disturbances and more open habitats are typically expected to be more vulnerable to exotic species invasions (6, 50). Our findings highlight that PAs can be more vulnerable to exotic species invasions than non-PAs when protection from human activities (e.g., reclamation) sets aside more habitats (e.g., open mudflats) that are vulnerable to invasions. Active control of exotic species invasions in PAs targeted to conserve such habitats may be particularly critical. As specific native species may be more affected than others (e.g., native succulents and sedges in our study), active control of exotic species invasions, along with restoration of native species, may also need to be prioritized toward species most at risk.

METHODS

The studied PAs

The seven coastal wetland PAs studied—JDS, CM, YC, YRE, YQE (Yiqian'er), LH (Liaohu), and YLJ (Yalu Jiang)—are all national nature reserves of China, initially established as local nature reserves between 1983 and 2000 (so all PAs have been established for at least

20 years). PAs focusing on conserving sandy beaches, rocky shores, and nearshore waters were not considered. A summary of these PAs' basic information including year of designation, cordgrass invasion history, and current extent of exotic cordgrass is provided in table S1. YRE and YQR are two spatially separated regions of the Yellow River Delta National Nature Reserve and were considered separately because of their different histories of cordgrass invasion. Cordgrass has so far invaded JDS, CM, YC, and YRE PAs but not YQR, LH, and YLJ PAs. Cordgrass was intentionally planted inside and outside JDS, CM, and YC PAs for shoreline stabilization. There was no cordgrass planted inside YRE and YQE PAs, although cordgrass was planted at a non-PA site ~20 km north of the YRE PA and has since naturally dispersed into the PA likely via waterborne seeds and rhizomes. No cordgrass has been planted inside or in proximity to LH and YLJ PAs. The climates of the seven PAs span from subtropical (JDS, CM, and YC) to temperate (YRE, YQE, LH, and YLJ). In our analysis, all areas [including core zones strictly protected from human disturbances, experimental zones that allow sustainable use such as ecotourism, and buffer zones in between (51)] within the boundaries of the seven PAs were included. For PAs (YC and YLJ) whose boundaries were adjusted, which was done often to meet the need to reclaim part of the PA for local socioeconomic developments (51), we analyzed areas protected throughout.

Non-PA controls for each PA were selected on the basis of two approaches: common-centroid matching and statistical matching. For common-centroid matching, non-PA controls were delimited by creating buffers around the centroid of the PA with 5-km increments and selecting the buffer within which the size of the natural wetlands unprotected throughout was closest to that of the corresponding PA when it was established (for YLJ PA located near the China–North Korea boundary, only non-PA areas on the China side were included). This approach assumed that a PA and its surrounding area had comparable environmental conditions and has been widely adopted to assess the performance of PAs [e.g., (52)]. Considering that PA placement may be biased toward areas with certain environmental conditions [e.g., low suitability for human use (53)], we further reinforced this matching approach with statistical matching to account for potential confounding effects of social, biological, and physical factors other than the PA treatment. To do so, each PA and its non-PA control area delimited with common-centroid matching were split into 1 km by 1 km grids (i.e., sites). For each of these sites (excluding permanent water surfaces), we extracted values of the following social, geographical, and biological factors from various datasets (see table S4): human population density, road density, distance to shoreline, distance to river, percent land cover, and NDVI (the normalized difference vegetation index, a widely used vegetation index). Then, we used propensity score matching (nearest neighbor and glm distance) to identify a non-PA control site for each PA site and attempted to reduce the standardized mean differences between PA and non-PA sites to below 5% (53). Lastly, 166, 84, 305, 77, 103, 160, and 33 matched PA and non-PA sites were selected for JDS, CM, YC, YRE, YQE, LH, and YLJ, respectively.

Constructing the wetland dataset

To construct a long-term dataset of mudflats, native marshes, exotic cordgrass marshes, and reclaimed lands in PAs and matched non-PA controls in periods before and after PA designation, we developed a rigorously validated classification procedure for classifying Landsat images on GEE. This procedure consists of three main steps: (i)

delineating wetland boundaries, (ii) classifying wetland types, and (iii) validation (detailed in text S1). We used standard Landsat Thematic Mapper (TM), Enhanced Thematic Mapper Plus (ETM⁺), and Operational Land Imager (OLI) surface reflectance products (T1_SR; six tiles) archived on the GEE platform in all analyses, except that, for PAs established in the 1980s and early 1990s, Landsat Multispectral Scanner (MSS) images were used when necessary, to extend the analyzed periods before PA designation to cover at least 5 years. A single Landsat scene covering the whole of a PA (for all but YC) or its large majority (~80% for YC) was used. Cloud-free, low-tide Landsat images were selected where available (lists of all selected Landsat images are given in tables S5 to S7).

First, to map the wetland extent (defined as the area between the seaward boundary of reclaimed land and the low-tide waterline) in each of the seven PAs, we developed a delineating algorithm (fig. S8). The seaward boundary of reclaimed land in a given year was determined by digitizing roads, dams, and dikes visible on the Landsat image (or high-resolution Google Earth images when available). The seaward boundary of reclaimed land the first year of the analysis period was set to be the permanent landward boundary of the region analyzed in our study for each of the seven studied PAs. The low-tide waterline was determined by classifying land and water surfaces using selected Landsat images with a tidal height within the lower 20% of the tidal range between mean high water springs and mean low water springs (see text S1 for tidal height estimation methods; information on the offshore stations used for tidal predictions for different PAs is given in table S8). Land and water surfaces were then classified using a threshold of the normalized difference water index, a water index widely used for delineating open water features from terrestrial environments (54), assisted with a support vector machine (SVM) classifier correcting sediment-loaded water near the river mouth and coastline (present in some of the Landsat images). We also used the SVM classifier to classify land and water for Landsat MSS images. We selected the SVM method because it is a potent supervised classification method whose accuracy has been repeatedly demonstrated (54). The wetland extent in a given year was then demarcated as the area enclosed by the landward boundary and the low-tide waterline in that year.

Second, to classify different wetland types, we devised a hierarchical classification algorithm (fig. S9). First, reclaimed and unreclaimed areas were delineated by digitizing roads, dams, and dikes as their boundaries. Second, we calculated NDVI and distinguished bare mudflats from vegetation by setting the bare land/vegetation threshold NDVI as 0.15 or 0.2 on the basis of selected mudflat and vegetation samples in different PAs (image pixels with NDVI < 0.10 to 0.20 are typically identified as bare, nonvegetated soils; fig. S10) (30). Third, Otsu's threshold selection method (55) was used to separate exotic cordgrass from native wetlands if natural wetlands were invaded by cordgrass. Exotic cordgrass and native grasses/sedges were spectrally indistinguishable from single Landsat scenes (fig. S11), although they have different phenologies where vegetative growth and senescence of native grasses/sedges dominated by *P. australis* and *Scirpus mariqueter* begin approximately 1 month earlier than in exotic cordgrass (56). To use this difference in phenology, the threshold selection method was applied on the NDVI difference between an early-season (April to June) and late-season (October to November) scene of the Landsat imagery. Note that in YC, another noninvasive cordgrass—*Spartina patens*—was present in the 1980s and early 1990s, which was identified but excluded from our analysis

[see text S1 and (57)]. Fourth, an SVM classifier (hereafter, the native SVM classifier) was used to separate native succulents/sedges, native grasses, and seagrasses/algae (where present) in all PAs except YLJ (with only native grasses). The native SVM classifier incorporated six spectral bands [blue, green, red, near infrared, shortwave infrared-1 (SWIR-1), and SWIR-2] and two composite spectral indices. Native succulents, native grasses, and seagrasses/algae could not be distinguished using only the visible to SWIR-2 bands (fig. S11). We found, however, that the relative reflectance of band red versus band green was higher in native succulents—a unique reddish-colored vegetation (Fig. 2A)—than green vegetation such as native grasses and seagrasses/algae. Furthermore, the relative reflectance of band red versus band SWIR-1 (often used for discriminating vegetation moisture content) was much higher in seagrasses/algae (often found in constantly water-saturated low tidal zones) than in salt marshes in upper tidal zones. The two composite spectral indices—the green/red vegetation index (GRVI) and the normalized difference senescent vegetation index (NDSVI)—were therefore included to improve the classifier. GRVI and NDSVI are calculated as

$$\text{GRVI} = \frac{\rho_{\text{green}} - \rho_{\text{red}}}{\rho_{\text{green}} + \rho_{\text{red}}} \quad (1)$$

$$\text{NDSVI} = \frac{\rho_{\text{SWIR-1}} - \rho_{\text{red}}}{\rho_{\text{SWIR-1}} + \rho_{\text{red}}} \quad (2)$$

where ρ_{green} , ρ_{red} , and $\rho_{\text{SWIR-1}}$ are green, red, and SWIR-1 bands of a Landsat TM/ETM+/OLI image. The native SVM classifier for each PA was trained using samples selected on the basis of drone images (~3 cm in resolution) taken in October 2018 (YRE and LH) and high-resolution Google Earth images in August 2015 (CM and JDS) and July 2015 (YC), and the trained classifier was then applied to the adjusted Landsat images of other years. Before training the native SVM classifier, an empirical line method for relative correction (fig. S12) was used to achieve consistency through time and across all Landsat sensors (the atmospheric correction and cross-sensor correction of Landsat T1_SR products achieved on GEE were not always satisfactory) (58).

Lastly, the classified outputs were rigorously validated in three different exercises, and the validation procedure was independent of the classification procedure. First, we assessed the performance of the hierarchical classification flow using validation samples (for each wetland type in each PA) independently selected on the basis of (i) field surveys, (ii) high-resolution true color drone images, (iii) high-resolution satellite (WorldView-2, QuickBird, and SPOT-7) images, and (iv) high-resolution Google Earth images. Second, we verified the performance of our classifiers for classifying relatively corrected Landsat images of a different year using validation samples selected on the basis of corresponding high-resolution satellite images of the same year and season. Third, we assessed the accuracy of classified outputs based on Landsat images against those based on high-resolution satellite images of the same season and year (where available), which were classified with the same algorithms and training samples. Assessed using the confusion matrix, the overall accuracies of the classified wetland types across the seven PAs were all above 88% in all cases, and user's and producer's accuracies of individual wetland types were consistently high, ranging from 72 to 100% (detailed in tables S9 to S11). The Kappa coefficients were all above 0.84 (tables S9 to S11). The classified outputs using Landsat images also showed a close correlation with those using high-resolution satellite

images [for CM + JDS, slope = 0.941, coefficient of determination (R^2) = 0.99 and for YRE, slope = 0.996, R^2 = 1.00]. These confirmed that the algorithms that we developed for using Landsat images to classify coastal wetland types were satisfactory.

Overall trends and replacement of native wetlands

Using the classified maps of wetland types, the areal extents of total land, reclaimed areas, exotic cordgrass marshes, native grass marshes, native sedge marshes, native succulent marshes, and key shorebird habitats were quantified to examine their trends in each of the seven PAs and their non-PA controls. Key shorebird habitats included mudflats (including small areas of seagrass/algal beds) and native sedge/succulent marshes, which are widely known to host abundant shorebirds (25). Native grass marshes dominated by *P. australis* that are tall and dense are primarily habitats for passerines, not shorebirds (25). Nonetheless, inclusion of native grass marshes as key shorebird habitats did not alter our main findings, especially in YC and YRE where native grasses can be stunted in salty areas of the expansive wetlands (figs. S2 and S4). Native grasses are generally tall and dense in JDS and CM on the banks of the Yangtze estuary with high freshwater input.

For each of the seven PAs, we estimated the extents of cordgrass invasion and reclamation as percentage of the total wetland area of a statistically matched PA or non-PA site in the year of PA designation, calculated their difference between each matched PA and non-PA site in each year, and tested whether their difference increased or decreased significantly over time since PA designation using linear mixed-effects models (LMMs; with year as the fixed effect and site as the random effect). Similarly, we estimated the extents of remaining natural unreclaimed wetlands, native wetlands, and key shorebird habitats; calculated their difference between each matched PA and non-PA site in each year; and tested whether their difference increased or decreased significantly over the period of cordgrass invasion after PA designation. In the above analyses, we focused on testing temporal trends in the difference between PA and non-PA control sites. This analysis approach to assessing the performance of PAs has been recommended, as it can show whether PAs have been taking effect over time and deal with extraneous sources of spatial and temporal variability that may confound PA versus non-PA comparisons of single time points (59). In addition, to test whether the extents of cordgrass invasion and reclamation differed significantly between PA and non-PA control sites, we constructed LMMs with year, protection status (PA or non-PA), and their interaction as the fixed effects and site as the random effect. Post hoc pairwise comparisons were used to test whether differences between PA and non-PA control sites were significant in the PA designation year and the most recent year of investigation, respectively. We similarly tested whether the extents of remaining natural unreclaimed wetlands, native wetlands, and key shorebird habitats differed significantly between PA and non-PA control sites in the year before cordgrass invasion and the most recent year of investigation using LMMs followed by post hoc multiple comparisons. The above analyses were conducted separately for each PA and included all core, buffer, and experimental zones of a PA. We repeated these analyses for only the strictly protected core zones to test whether our results were robust to PA management zoning. LMMs and post hoc pairwise comparisons were conducted using the R lmerTest and lsmeans packages, respectively.

For each of the four invaded PAs and their non-PA controls, we further quantified replacements of all and each type of native

wetland (native succulents, native grasses, native sedges, and mudflats) by exotic cordgrass and annual average replacement rates using change detection analysis in ArcGIS 10.4. We examined whether replacement rates significantly differed from zero using two-sided *t* test or nonparametric Wilcoxon test. Similarly, we quantified reversions from exotic cordgrass marshes to mudflats and native marshes and annual average transformations between other types of wetlands. To estimate the degree of reversion from exotic cordgrass marshes to mudflats and native marshes, we calculated the reversibility index as $A_R/A_T \times 100$, where A_T is the total area of a certain type of native wetlands replaced by cordgrass over the analysis period and A_R is the total area of cordgrass marshes changing back to that type of native wetlands over the same analyzed period. A two-way ANOVA was used to test the effects of protection, native wetland type (mudflat, native sedge/succulent, and native grass), and their interaction on the reversibility index across the four invaded PAs (model fits were checked using residual plots and Q-Q normal plots). All classified maps were used in the above replacement and reversibility analyses, with temporal intervals ranging from 1.3 years for YRE to ~3.5 years for the other three invaded PAs. To address the potential influence of this difference in temporal interval among classified maps (changes between wetland types could be hidden with greater temporal intervals), we further analyzed replacements of native wetlands by cordgrass and their reversibility for YRE using four selected classified maps with ~3-year interval and found limited changes in our results (fig. S13).

Preclusion of new native marsh formation via primary succession

To determine the priority effects of cordgrass invasion on formation of new native marshes, we analyzed trends in marsh vegetation change in newly accreted mudflats in periods before and after the initiation of cordgrass invasion, respectively, in two PAs—YRE and JDS. In these PAs, mudflat accreted at comparable rates in the periods that we analyzed before and after cordgrass invasions (see fig. S7), so our analysis of marsh succession was not confounded by variation in accretion rate. Mudflat accretion was minimal in YC over the period that we analyzed and accretion rate in CM strongly differed between pre- and postinvasion periods (see fig. S7), so those two PAs were excluded from this analysis.

For YRE, we first delineated newly accreted intertidal areas every 2 to 4 years before and after the initiation of cordgrass invasions, respectively. Coastal wetlands in this PA have formed after the mouth of the Yellow River was rerouted in 1976. The river mouth was rerouted slightly (from southeast to northeast) again in 1996 and has since remained unchanged, apart from minor natural movements. Our analysis was focused on the current estuary where coastal wetlands were steadily accreting because of heavy sediment deposition (in the other regions of the PA, accretion of coastal wetlands did not consistently occur over the study period; fig. S14A). Delineation of newly accreted intertidal areas was carried out by over layering classified wetland maps of different years between 1995 and 2018 and extracting the difference between those maps. Then, we calculated the percent cover of native succulents and exotic cordgrass in each year with available classified images for each newly accreted intertidal area since it formed. For JDS, we used similar workflow to delineate newly accreted intertidal areas across the entire PA every few years between 1988 and 2018 (fig. S14B) and estimated the percent cover of native sedges and exotic cordgrass in each year with available classified images for each newly accreted intertidal area since it formed.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <https://science.org/doi/10.1126/sciadv.abi8943>

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An invasive species erodes the performance of coastal wetland protected areas

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