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Reciprocal facilitation between annual plants and burrowing crabs: Implications for the restoration of degraded saltmarshes

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Abstract

1. Increasing evidence shows that facilitative interactions between species play an essential role in coastal wetland ecosystems. However, there is a lack of understanding of how such interactions can be used for restoration purposes in saltmarsh ecosystems. We therefore studied the mechanisms of reciprocal facilitative interactions between native annual plants, *Suaeda salsa*, and burrowing crabs, *Helice tientsinensis*, in a middle-elevation saltmarsh (with generally high plant density and moderate tides) in the Yellow River Delta of China.
2. We investigated the relationship between the densities of the plants and crab burrows in different seasons. Then, we tested whether and how saltmarsh plants and crabs indeed facilitate each other in a series of field and laboratory experiments. Finally, we applied the results by creating a field-scale artificial approach for microtopographic modification to restore a degraded saltmarsh.
3. We found that the density of plant seedlings in spring was positively correlated with the density of crab burrows in the previous autumn; moreover, the density of crab burrows was correlated with the density of plants in summer. The concave–convex surface microtopography created by crabs promoted seed retention and seedling establishment of saltmarsh plants in winter and spring. These plants in turn facilitated crabs by inhibiting predators, providing food and reducing physical stresses for crabs in summer and autumn. The experimental removal of saltmarsh plants decreased crab burrow density, while both transplanting and simulating plants in bare patches promoted crabs. The microtopographic modification, inspired by our new understanding of the interactions between saltmarsh plants and crabs, showed that these degraded saltmarsh ecosystems can be restored by a single ploughing intervention.
4. *Synthesis*. Our results suggest a reciprocal facilitation between annual plants and burrowing crabs in a middle-elevation saltmarsh ecosystem. This knowledge yielded new restoration options for degraded coastal saltmarshes through the one-time ploughing initiation of microtopographic variation, which could promote the re-establishment of ecosystem engineers and lead to the efficient recovery of pioneer coastal vegetation and associated fauna.

KEYWORDS
ecosystem engineers, facilitative interaction, geomorphic perturbation, *Helice tientsinensis*, restoration, saltmarsh, *Suaeda salsa*

1 | INTRODUCTION

The high rates of degradation and regional die-off in coastal ecosystems all over the world due to combinations of coastal land reclamation and engineering, extreme climate change and pressure from herbivores are of increasing concern (Bulleri & Chapman, 2010; He et al., 2017; Silliman et al., 2005; Yu et al., 2017). These areas provide vital ecosystem services, such as flood protection (Leonardi et al., 2018), providing high primary productivity (Trilla et al., 2010) and regulating carbon cycling (Kirwan & Mudd, 2012). Ecological restoration has become one of the important strategies to halt the degradation and restore the health of coastal ecosystems through human intervention, and some efforts have been made all over the world (Wang et al., 2018; Wolters et al., 2005). However, some restoration efforts have had low efficiency (high cost relative to results) or have not resulted in effective recovery (Li et al., 2015; Williams & Faber, 2001). Thus, understanding the essential ecosystem processes that maintain the functionality and stability of ecosystems, such as the different interactions between species, is really significant and necessary to promote the coastal restoration success.

Different interactions, such as facilitative, neutral and antagonistic, are possible between coastal wetland biota, all of which are important for the structure, process and functioning of ecosystems (Traveset & Richardson, 2014). Compared with other interaction types, such as competition and predation (Estes et al., 1998; Schnedler-Meyer et al., 2016), facilitation has received relatively less attention from ecologists (Traveset & Richardson, 2014), especially in coastal ecosystems. Reciprocal facilitations are interactions in which both organisms enhance each other's fitness, often involving a reciprocal benefit: each partner uses a ‘service’ from and produces a ‘reward’ for the other partner (Bronstein, 1994). When species involved in this type of interaction also have a role as ecosystem engineers or foundation species (Angelini & Silliman, 2014; Jones et al., 1994), these reciprocal facilitations have wider importance for the structure and functioning of the whole ecosystem.

Various reciprocal facilitative interactions have been identified in coastal ecosystems. Shallow-water coral reefs, where colonies of calcium carbonate-excreting coral polyps live in symbiosis with Zooxanthellae (single-celled photosynthetic dinoflagellates), are the most famous example. Many soft-bottom coastal systems are also frequently structured by reciprocal facilitative interactions, such as between cordgrass *Spartina alterniflora* and mussels *Geukensia demissa* in saltmarshes (Derksen-Hooijberg et al., 2017), between mangrove trees *Rhizophora mangle* and sponges *Tedania ignis* in mangroves (Ellison et al., 1996), and between seagrass *Zostera noltii* and a lucinid bivalve *Loripes lacteus* in seagrass ecosystems (van der Heide et al., 2012). An increasing number of studies have suggested that such positive interactions play an important role in structuring communities and promoting the functionality and stability of ecosystems (Derksen-Hooijberg et al., 2017; Nomann & Pennings, 1998). This is because positive interactions can ameliorate physical stress and consumer pressure and increase resource availability (Bertness & Callaway, 1994; Stachowicz, 2001). However, although coastal ecosystems are known to be sustained by multiple reciprocal facilitative interactions, how such interactions can be restored once lost has so far rarely been addressed.

Coastal systems are often characterized by a combination of strong hydrodynamic forces from waves and tides with high physico-chemical stress, for example, from anoxic sediments, with high sulphide concentrations. However, such stress factors can be ameliorated by plants that—once established—reduce hydrodynamic forces and aerate sediments. Such biogeomorphic feedbacks, however, generally only work beyond a certain plant density threshold, thus requiring a Window of Opportunity (WoO) of hydrodynamic quiet conditions to establish (Figure 1A,C, Balke et al., 2014). The WoO concept has been put forward in a range of systems, including saltmarshes, mangroves and seagrass beds (Corenblit et al., 2015; Hu et al., 2015).

When reciprocal facilitations between plants and animals are additionally important, this causes similar ‘chicken-and-egg’ issues; each species can establish only if the other species on which it depends is already abundant to some extent. In Figure 1B,D, we propose an extension to the WoO framework for situations in which biogeomorphic impacts (i.e. on the physical structure of the habitat) by animals facilitate plants (and the plants, in turn, facilitate the animals). Once lost, such systems can benefit from a restoration intervention that helps one species cross the establishment threshold (even for a short WoO), after which both species can persist unsupported (Figure 1B,D). For example, coral reefs are formed by reciprocal facilitations between corals and microalgae, and once strongly degraded, it can be difficult for this interaction to recover naturally. In such cases, establishment on artificial hard structures, such as wire frames, can help the coral polyps and their Zooxanthella microalgae cross a density threshold, after which calcium carbonate excretion supports the further spontaneous development of the reef (Rinkevich, 2005). Similar mechanisms may also operate in soft-bottom ecosystems, in which the bioturbation caused by burrowing crabs is important for facilitating saltmarsh plants, and these plants, in turn, facilitate the crabs. Additionally, in this case, a single intervention mimicking the structures created by animals could provide calmer hydrodynamic conditions and restore the reciprocal facilitation between plants and animals within a short (and therefore common) WoO.

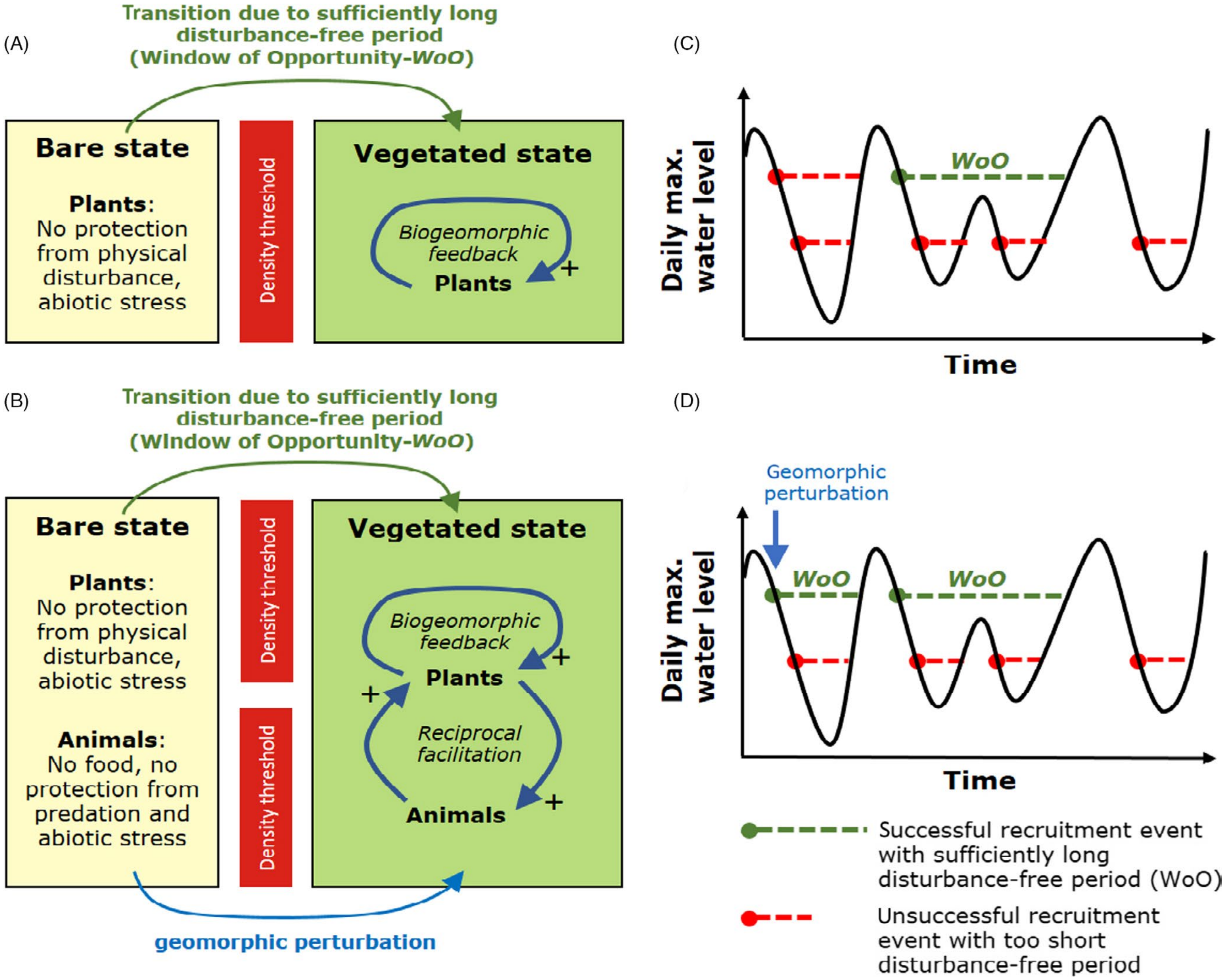

FIGURE 1 The (A, C) previous 'Windows of Opportunity' (WoO) framework proposed by Balke et al. (2014) extended with (B, D) reciprocal facilitation between plants and animals. The original framework suggests that biogeomorphic systems need to surpass a minimum biomass density to shift from a bare to a vegetated state, for example, during a sufficiently long period of hydrodynamically calm conditions. Once over this threshold, when the disturbance-free WoO is long enough (C), the vegetation creates positive feedbacks to support its own density, for example, by reducing erosion and trapping sediment. Below this threshold, vegetation establishment is limited by physical disturbance due to sediment transport and fluid motion. (B, D) Our proposed extension of this conceptual framework includes reciprocal facilitation between plants and bioturbating animals. In this case, a one-time geomorphic perturbation mimicking the impact of the bioturbating animals could facilitate the establishment of the reciprocal facilitation between the plants and animals, potentially with a much shorter disturbance-free WoO period (D). These mechanisms may apply not only to biogeomorphic systems with reciprocal facilitations, such as in the pioneer saltmarshes studied here, but also to coral reefs, in which artificial hard structures can initially be used over an establishment threshold to support the self-building properties of the system

The Yellow River Delta is a typical soft-bottom coastal wetland on the Pacific coast of Northeast China, hosting large areas of intertidal saltmarshes dominated by the native annual plant *Suaeda salsa* and the burrowing crab *Helice tientsinensis*. Additionally, saltmarshes are important habitats for different species of macrobenthos (Yan et al., 2020) and sea birds (Li et al., 2011). However, mainly due to extreme climatic events (He et al., 2017) and some human activities, salinity and drought stress increase to levels that exceed the tolerance limits of crabs and plants, or the drought stress in combination with pressure from crab grazers generate enough stress to trigger die-off of plants, large bare areas of degraded saltmarsh are increasingly found. In these habitats, both plants and crabs are lost, with a negative impact on the ecosystem health and biodiversity of the whole Yellow River delta (He et al., 2017; Wang et al., 2018). Thus, efficient, evidence-based restoration measures are necessary and urgently needed for the restoration of these degraded saltmarsh areas. Previous study found that the grazing effect of crabs *H. tientsinensis* on *S. salsa* plants was really strong in many areas with relatively not high plant density and in areas with frequent tides, while the grazing effect was relatively weak in areas with high plant density (He, 2012). While these crabs negatively grazed *S. salsa* plants, we also observed that the concave–convex microtopography generated by crabs trapped many plant seeds, facilitating seedlings to establish in winter and spring in the middle-elevation saltmarshes with generally high plant density and moderate tides, where the effects of ecosystem engineering by crabs are more likely to exceed the effects of grazing. Additionally, we also observed that most crabs seem to prefer to burrow and settle down under the plants in summer and autumn in these areas, and here the food provision by *S. salsa* for crabs is also a performance of the facilitation of crabs by plants. Thus there are several different mechanisms of how such reciprocal facilitation between *S. salsa* and *H. tientsinensis* could work in the middle-elevation saltmarshes, which need investigation. Additionally, restoration practices for degraded saltmarshes need to be tested using insight into such mechanisms.

In this study, field investigations and manipulative experiments were conducted to examine the reciprocal facilitation between annual pioneer plants and crabs in a middle-elevation saltmarsh (with generally high plant density and moderate tides) in the Yellow River Delta. Specifically, we investigated whether (a) the experimental alteration in microtopography by crabs facilitates seed retention and seedling establishment of saltmarsh plants in winter and spring, (b) these annual plants facilitate burrowing crabs by providing protection from predators, supplying food and reducing physical stresses in summer and autumn and (3) the experimental one-time ploughing creation of microtopography in flat degraded bare patches re-establishes the interaction between plants and crabs (Figure 1B,D), thus yielding restoration opportunities applicable at the landscape scale.

2 | MATERIALS AND METHODS

2.1 | Study site and species

Fieldwork was carried out in a middle-elevation saltmarsh ecosystem with a generally high density of plants (37°49′N, 119°05′E; Figure 2A–C) located in a moderately wave-exposed area in a temperate estuary of the Yellow River Delta, Northeast China. The tides in this saltmarsh ecosystem are irregular and semidiurnal (Hu & Cao, 2003), which has important effects on the composition, distribution and behaviour of intertidal organisms.

Suaeda salsa is a key plant species of coastal saltmarshes in northern China and is particularly widespread in the middle-elevation intertidal saltmarshes of the Yellow River Delta. It is an annual plant, reproducing by small and light seeds, which are easily dispersed by tides in winter (Wang et al., 2018). Seeds are generally formed and dispersed between November and January, followed by a period of seedling establishment generally from February to April.

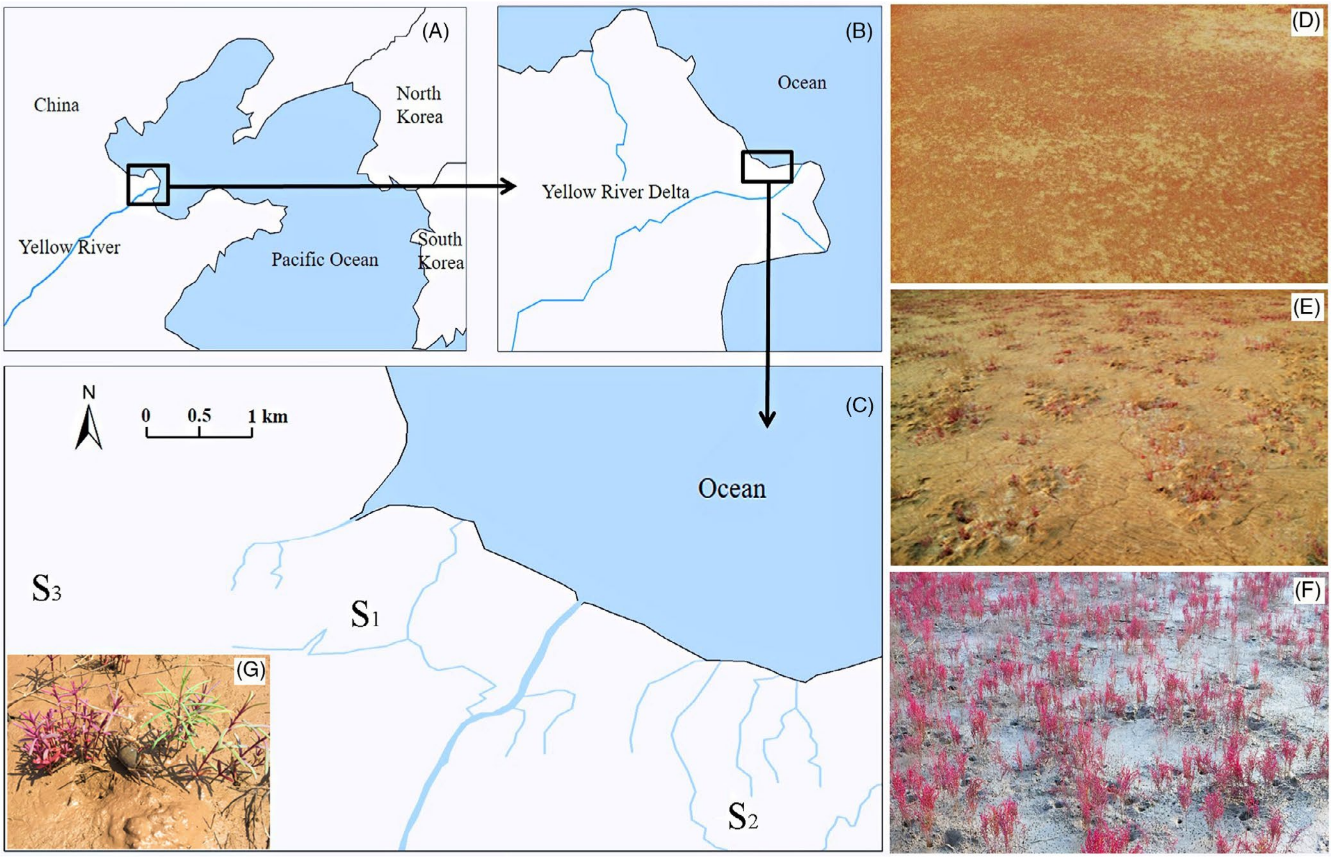

FIGURE 2 (A–C) Map showing the study sites in the Yellow River Delta, Northeast China. (D) Drone photograph of the patchy landscape. (E) The concave–convex microtopography generated by crabs facilitates the establishment of *Suaeda salsa* seedlings in winter and spring. (F) Crabs prefer to burrow under the *S. salsa* plants in summer and autumn. (G) Interaction between crabs and *S. salsa*

Helice tientsinensis is the main burrowing crab species in the middle-elevation saltmarshes of the Yellow River Delta dominated by the annual plant *S. salsa*. These crabs live in burrows in the sediment, generating a concave–convex surface microtopography of alternating small hollows and small mounds. Field observations suggest a positive relationship between crabs and *S. salsa* in the middle-elevation saltmarshes, even resulting in a patchy landscape in healthy saltmarsh ecosystems (Figure 2D). Some small bare patches with few plants and few crabs and flat microtopography occurred in this landscape. In spring, many seedlings of *S. salsa* were established in areas with a concave–convex microtopography generated by crabs before hibernation (Figure 2E). After the establishment of *S. salsa* seedlings, the crabs finish their hibernation and become active. In summer, most crabs seem to prefer to burrow and settle down under *S. salsa* plants (Figure 2F–G). To reveal the mechanisms of a potentially reciprocal facilitation between *S. salsa* and *H. tientsinensis*, two representative field study sites (S_1 and S_2) of the middle-elevation intertidal saltmarsh were chosen to conduct field investigations and experiments, and a laboratory experiment on predation risk was conducted at a field station at study site S_3 (Figure 2a–c).

2.2 | Field investigations

In late autumn 2018, before crabs started hibernation, 150 sampling plots (50 cm × 50 cm) in the middle-elevation saltmarsh were randomly selected and fixed, and the density of crab burrows was counted. In spring 2019, the density of established seedlings was recorded in each sampling plot. Then a laser scanner (GScan, ZG Technology Ltd.) was used to quantify the surface microtopography map and the actual curved surface area in these plots. The microtopography roughness was calculated by the ratio of the actual curved surface area to the projected area. Additionally, photographs from the field investigations are provided to illustrate how the concave–convex microtopography generated by burrowing crabs facilitated the seed retention and seedling establishment of *S. salsa* (Figure S1).

In summer 2017, when the *S. salsa* plants were mature and lush, 600 sampling plots (100 cm × 100 cm) in the middle-elevation saltmarsh were randomly selected to record the density of *S. salsa* plants and crab burrows (Figure S2).

2.3 | Field manipulation experiment involving microtopography and crab exclosure

To verify whether the concave–convex microtopography generated and maintained by crabs could facilitate the seed retention and seedling establishment of *S. salsa* in winter and spring, we conducted a field manipulative experiment involving microtopography and crab exclosure (Figure S3) at study site S_1. In November 2017, two treatments with four replicates (size 100 cm × 100 cm) were established in small naturally bare patches with flat microtopography (with few or no naturally present crabs and plants); the treatments included 'artificially concave–convex microtopography treatment' and 'control plot with naturally flat microtopography'. The soil in the artificially concave–convex microtopography treatments was manually ploughed with a small shovel to about 10 cm deep, after which the microtopography of the soil got the tidal influence and gradually became similar to that created by crabs. The control plots with naturally flat microtopography were marked with corner poles and established near the artificially concave–convex microtopography treatments.

Additionally, two treatments with four replicates (size 100 cm × 100 cm) were established in the vegetated regions (also with many crabs); the treatments included 'artificially flat microtopography treatment' and 'control plots with naturally crab-generated concave–convex microtopography'. In the artificially flat microtopography treatments, plants, crabs and crab burrows initially present were all removed, the microtopography was flattened to an extent, and cages were used to exclude crabs. The cages were covered by a 0.5 cm × 0.5 cm metal mesh, which was inserted into the sediment to a depth of 30 cm and reached a height of 50 cm, after which the microtopography soon became flat due to the tidal water and lack of crabs. The control plots with naturally crab-generated concave–convex microtopography (the plants were removed) were marked with corner poles (to allow free entry of crabs) and established near the treatments with artificially flat microtopography.

The soil samples were taken from a depth of 5 cm in all four treatments using a soil auger with a diameter of 5 cm in February 2018. The soil seed bank in each plot was analysed by observing seedling emergence in a climatic chamber (following the procedures described by ter Heerdt et al., 1996). The densities of the established seedlings of *S. salsa* and crab burrows in each plot type were recorded separately in April and June 2018; and the soil penetration resistance, moisture content, salinity and organic matter in each plot type were recorded in June 2018.

The soil penetration resistance was measured by a soil penetrometer (model SHM-22, Takemura) in the field. After this, the fresh soil samples were taken to the laboratory for determination of gravimetric soil moisture, salinity and organic matter. The fresh soil samples were weighed, placed in a drying oven at 60°C for more than 72 hr and weighed again to determine their dry weight. The soil moisture content was calculated by dividing the difference between the fresh and dry soil weights by the dry soil weight. The dried soil samples were then ground and sieved, after which a subsample of 8 g was mixed with 40 ml of deionized water in a centrifuge tube. This tube was placed on a shaker for 30 min to ensure intensive soil and water mixing and then left to stand for 2 hr. A conductivity-based soil salinity metre (model Jenco 3010M) was used to measure the salinity of the supernatant. An acidification treatment with 1 M dilute hydrochloric acid solution was used to remove all the soil inorganic carbon of 0.5 g soil subsample, after which the treated soil was dried, weighed and ground again, and then the content of the soil organic carbon was measured and calculated using an elemental analyser (Vario El). The content of soil organic matter was then calculated by multiplying the soil organic carbon content by 1.724.

2.4 | *Suaeda salsa* removal experiment

To test whether crabs indeed prefer to burrow under *S. salsa*, a plant removal experiment was performed at study site S_1 (Figure S4). On 28 July 2017, six replicate 100 cm × 100 cm sampling plots were randomly chosen from vegetated areas, and all the plants were removed. Then, six replicate 100 cm × 100 cm sampling plots in vegetated regions with many plants and six replicate 100 cm × 100 cm plots in bare patches with no plants were chosen and marked. The densities of the crabs in each treatment (*S. salsa* plots, *S. salsa* removal plots and bare patch plots) were recorded on the first day (July 28th), after about 10 days (August 8th), after 20 days (August 18th), after 50 days (September 18th) and after 80 days (October 18th).

2.5 | Field manipulation experiment of *S. salsa* and predation risk field laboratory experiment

Our observations showed that some predators (sea birds) regularly prey on crabs in the small bare patches rather than in the *S. salsa*-covered areas (Figure S5c,d). To investigate whether the *S. salsa* plants facilitate crabs by providing safety from predators, by providing food or by reducing physical stresses for crabs, field manipulation experiment of *S. salsa* and predation risk field laboratory experiment were performed.

On 18 June 2017, at the field study site S_1, four replicate 200 cm × 200 cm quadrats in small bare patches with few or no plants and crabs were randomly chosen as experimental quadrats, and then each quadrat was divided into four 100 cm × 100 cm plots. Whole real *S. salsa* plants, plastic mimics of *S. salsa*, pieces of real *S. salsa* and no *S. salsa* were transplanted or placed in each 100 cm × 100 cm plot (Figure S5a,b). The coverage of the plots with real and plastic *S. salsa* was kept similar. The fresh pieces of *S. salsa* were replaced every several days to maintain them throughout the experiment. Then, the densities of crabs in each type of plot were recorded on the first day (June 18th), after about 30 days (July 18th), after 60 days (August 18th), after 90 days (September 18th) and after 120 days (October 18th). Additionally, in July and September 2017, the soil penetration resistance, soil moisture content, soil salinity, soil organic matter, photosynthetically active radiation and soil temperature in each plot were measured. The soil temperature was measured 5 cm below the soil surface with a soil thermometer (model 6310, Spectrum Technologies) and the photosynthetically active radiation was quantified 10 cm above the soil surface with a quantum light metre (model 3415, Spectrum Technologies); these two factors were quantified between 11:00 and 12:00 on sunny days. Other factors were measured using the same methods as described before.

On 28 July 2017, in an abandoned field station at study site S_3 surrounded by water, vegetation and many birds (Figure S6a), a predation risk field laboratory experiment was performed, including bird interference treatments (with and without birds present) and *S. salsa* treatments (real *S. salsa*, plastic *S. salsa*, pieces of *S. salsa* and no *S. salsa*). Eight plastic basins (160 cm long × 120 cm wide × 50 cm deep) were filled with 30 cm deep sediment from the saltmarsh. Each basin was divided into four 80 cm × 60 cm plots. Real *S. salsa*, plastic *S. salsa*, pieces of *S. salsa* and no *S. salsa* were transplanted or placed in each 80 cm × 60 cm plot (Figures S6 and S7). The coverages of the real and plastic *S. salsa* plants were similar. The fresh pieces of *S. salsa* were replaced every several days to maintain them throughout the experiment. Then, 50 healthy crabs caught in the saltmarsh were put into each plastic basin, and some seawater was added to keep the soil moist, similar to the intertidal saltmarsh. Then, four replicate plastic basins were put in the kind of room with birds: the door to the room was opened to allow birds to enter and rice was put on the floor to attract them. Daily direct observations combined with observations of bird droppings, plumage and crab body part remains in the basins showed that different birds were coming in almost every day, some of which fed on crabs in basins (Figure S6b,d). The other four replicate plastic basins were placed in the other kind of room without birds: the door was closed to keep birds out, and the windows were opened a little to let outside air in; this maintained the environmental factors similar to that in the room with birds while keeping birds out. Then, the densities of crab burrows in each kind of plot in the different laboratory rooms with and without birds present were continuously recorded after about 5 days (August 2nd), after 10 days (August 7th), after 30 days (August 28th) and after 60 days (September 28th).

2.6 | Large-scale ploughing restoration practice

Several large sites with flat microtopography and without crabs and *S. salsa* plants were present in the study area. In these bare sites, we conducted a large-scale microtopography restoration practice as a case study (Figure S8), testing whether the saltmarsh plants and crabs could be re-established by microtopographic modification. In late November 2017, we restored the microtopographic conditions in a large degraded bare patch at study site S_2 through a ploughing treatment carried out with a tractor, ploughing to a depth of around 10–15 cm over a total area of 180 m × 120 m. As we also conducted a similar small-scale microtopographic modification experiment in several small bare areas (with true replicates) in the field manipulation experiment involving microtopography and crab exclosure, here we established only one large-scale restoration plot to examine the effects of this approach at appropriately large scales. Before the microtopographic restoration in November 2017, we recorded the densities of *S. salsa* and crab burrows in six replicate 100 cm × 100 cm plots in forthcoming restored areas, degraded bare plots and naturally vegetated plots. In April and October 2018 and April 2019 (after the microtopographic restoration), the densities of *S. salsa* and crab burrows and soil penetration resistance, moisture content and salinity in six replicate 100 cm × 100 cm restored treatments, adjacent degraded bare plots and naturally vegetated plots were recorded or measured using the same methods as described before.

2.7 | Statistical analyses

A log10 ($x + 1$) transformation was applied to some of the variables to improve their normality and homogeneity of variances. In the field manipulation experiment involving microtopography and crab exclosure, for the normalized data (including the data normalized by typically used transformations), we used randomized–blocked ANOVA followed by Tukey's HSD multiple comparisons tests to compare the densities of *S. salsa* seeds and seedlings, densities of crab burrows and environmental indices among the different treatments at each sampling time; the data that did not meet the assumptions of ANOVA even after typically used transformations were applied were analysed by nonparametric Kruskal–Wallis tests. In the *S. salsa* removal experiment and *S. salsa* field manipulation experiment, repeated-measures ANOVA followed by Bonferroni post hoc tests were used to examine the effects of different plant treatments on the density of crab burrows at each sampling time. Randomized–blocked ANOVA followed by Tukey's HSD multiple comparisons tests were used to compare the environmental indices among the different treatments in the *S. salsa* field manipulation experiment. To overcome the lack of true replications in the bird treatments in the predation risk field laboratory experiment, we just used repeated-measures ANOVA followed by Bonferroni post hoc tests to examine the effects of different plant treatments (which have true replicates) on the density of crab burrows at each sampling time in the treatments with and without birds respectively; we did not perform direct statistical analysis between the treatments with and without birds. In the large-scale ploughing restoration practice, we used one-way ANOVA followed by Tukey's HSD multiple comparisons tests to compare the biotic and abiotic indices among the different treatments at each sampling time (nonparametric Kruskal–Wallis tests were used to analyse the data that did not meet the assumptions of ANOVA even after typically used transformations were applied). The relation among the density of crab burrows in the previous autumn, the density of *S. salsa* seedlings in spring and the microtopographic roughness in spring, and the relation among the density of *S. salsa* plants and crab burrows in summer were tested using second-order polynomial regressions when relation among these variables in the field investigations suggested an optimum. The statistics were conducted using SPSS version 22 (IBM).

3 | RESULTS

3.1 | Facilitation of *S. salsa* plants by crabs

3.1.1 | Field investigation

During our field investigations, we found that the crabs generated clear concave–convex microtopography on the surface of the saltmarsh. When the crabs hibernated underground in winter, the concave–convex microtopography still persisted to an extent in the middle-elevation mashes with moderate tides, which seemed to facilitate *S. salsa* seed retention and seedling establishment during winter and spring (Figure S1). As Figure S9 shows, in spring more seedlings occurred in the areas of concave microtopography created by crabs, as the elevation difference and microtopographic roughness were relatively high (Figure S9a–c). However, there were fewer seedlings in some areas of flat microtopography without crabs (Figure S9d–f). Compared over all the plots, the microtopographic roughness in spring increased with the density of crab burrows in the previous autumn (Figure 3A). Additionally, the density of *S. salsa* seedlings increased with microtopographic roughness in spring (Figure 3B) and with the density of crab burrows in the previous autumn (Figure 3C).

3.1.2 | Field manipulation experiment involving microtopography and crab exclosure

The number of seeds in the plots with naturally and artificially concave–convex microtopography was significantly higher than that in the plots with naturally and artificially flat microtopography (Figure S10a). In both April and June, the densities of the seedlings in the plots with naturally and artificially concave–convex microtopography were significantly higher than those in the plots with naturally and

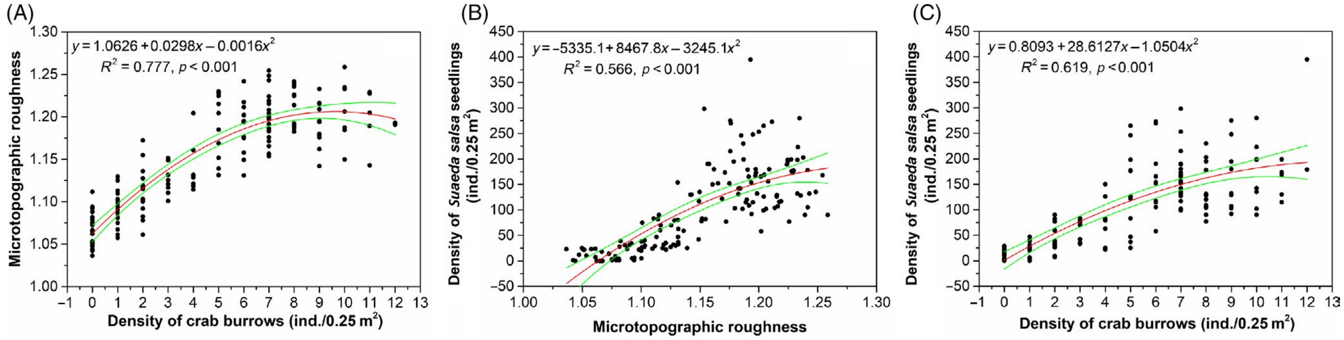

FIGURE 3 (A) Relationship between the microtopographic roughness in spring and the density of crab burrows in the previous autumn; (B) relationship between the density of plant seedlings and the microtopographic roughness in spring; (C) relationship between the density of plant seedlings in spring and the density of crab burrows in the previous autumn, with the red line showing the regression line and the green lines showing the 95% confidence intervals

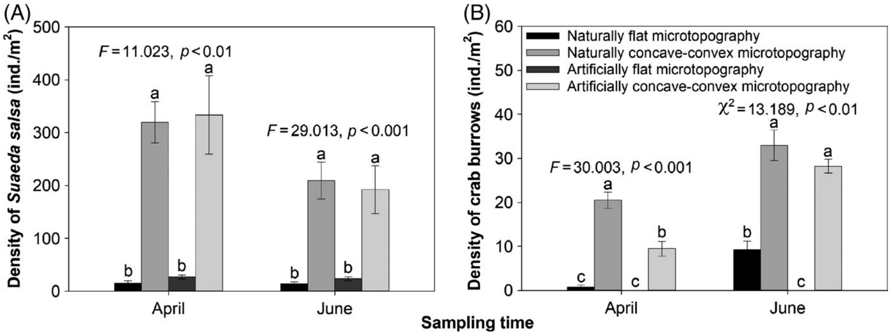

FIGURE 4 Comparisons of the (A) densities of plant seedlings, and (B) densities of crab burrows among the different treatments in the field manipulation experiment involving microtopography and crab exclosure in April and June 2018. The data are shown as the means ± *SE* ($n = 4$). The results from the randomized–blocked ANOVAs are reported by the *F* and *p* values, while the results from the Kruskal–Wallis tests are reported by the χ^2 and *p* values. In each month, the means with the same letter are not significantly different from one another ($p > 0.05$; post hoc multiple comparisons)

artificially flat microtopography. The seedling densities between the plots with naturally and artificially concave–convex microtopography were not different, nor were the seedling densities between the plots with naturally and artificially flat microtopography (Figure 4A). In both April and June, the densities of crab burrows in the plots with naturally and artificially concave–convex microtopography were significantly higher than those in the plots with naturally and artificially flat microtopography. In April, the density of crab burrows in the plots with naturally concave–convex microtopography was significantly higher than that in the plots with artificially concave–convex microtopography; however, in June, this difference disappeared (Figure 4B). The soil penetration resistance and salinity in the plots with naturally and artificially concave–convex microtopography were both significantly lower than those in the plots with naturally and artificially flat microtopography (Figure S10b,d). The soil moisture content and organic matter in the plots with naturally and artificially concave–convex microtopography were significantly higher than those in the plots with naturally and artificially flat microtopography (Figure S10c,e).

3.2 | Facilitation of crabs by *S. salsa* plants

3.2.1 | Field investigation

The density of crab burrows initially increased with the density of *S. salsa* plants in summer. However, when the density of *S. salsa* plants was more than 350 ind./m^2 and had nearly reached its maximum value in summer, the density of crab burrows did not increase further (Figure 5). The quadratic term of the regression model was significant ($p < 0.001$), indicating that this model with an optimum was statistically better than a linear model (continuous increase).

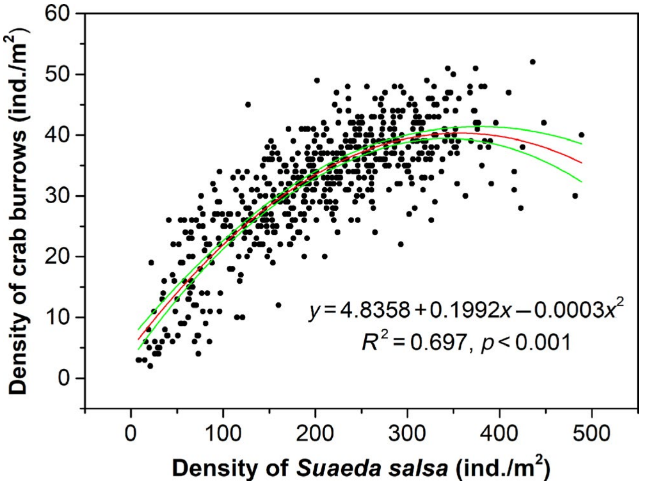

FIGURE 5 Relationship between the density of crab burrows and the density of *Suaeda salsa* plants in summer, with the red line showing the regression line and the green lines showing the 95% confidence intervals

3.2.2 | *S. salsa* removal experiment

The interaction between sampling time and plant treatment had significant effects on the density of crab burrows (Table S1). At the beginning of the *S. salsa* removal experiment, there was no significant difference in the densities of crab burrows between the *S. salsa* plots and the *S. salsa* removal plots, both of which had significantly higher crab densities than the bare patch plots (Figure 6A; Table S2). During the experiment, we found that an increasing number of abandoned crab burrows were blocked by tidal sediment deposition in the *S. salsa* removal plots (Figure S4c–e). Throughout the experiment, the crab burrow density in the *S. salsa* removal plots gradually decreased (Figure 6A; Table S2), and the differences in the densities of crab burrows between the *S. salsa* plots and the *S. salsa* removal plots became significant 20 days after removing the *S. salsa* plants (August 18th).

3.2.3 | Field manipulation experiment of *S. salsa*

The interaction between sampling time and plant treatment had significant effects on the density of crab burrows (Table S3). During the

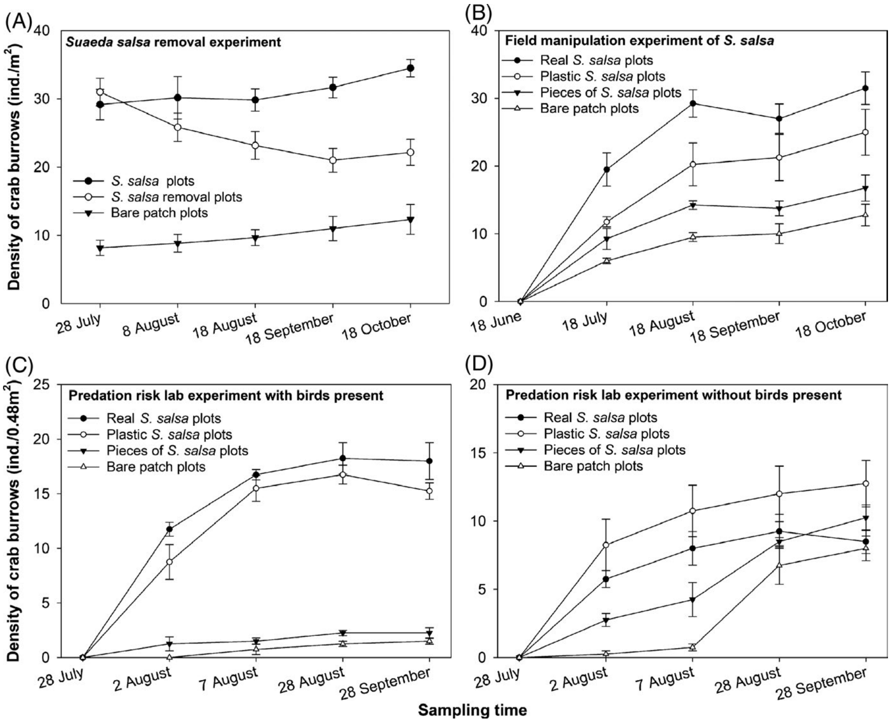

FIGURE 6 Comparisons of and changes in the densities of crab burrows of the different treatment plots, in the (A) *Suaeda salsa* removal experiment (*n* = 6), (B) field manipulation experiment of *S. salsa* (*n* = 4), (C) predation risk field laboratory experiment with birds present (*n* = 4) and (D) predation risk field laboratory experiment without birds present (*n* = 4). The data are shown as the means ± *SE*

field experiment, in general, the density of crab burrows in the real *S. salsa* plots was always highest, followed by the plots with plastic *S. salsa* and then the plots with the pieces of *S. salsa* (Figure 6B; Table S4; Figure S5b). In both July and September, the soil penetration resistance, soil salinity, photosynthetically active radiation and soil temperature in the plots with real *S. salsa* and plastic *S. salsa* were almost all lower than in the plots with pieces of *S. salsa* and in bare patch plots. The soil moisture content and organic matter content in the plots with real *S. salsa* and plastic *S. salsa* were generally higher than those in the bare patch plots (Figure S11).

3.2.4 | Predation risk field laboratory experiment

The interaction between sampling time and plant treatment had significant effects on the density of crab burrows in the treatments both with and without birds (Table S5). In the treatments with birds, the densities of crab burrows in the plots with real *S. salsa* and plastic *S. salsa* were both always significantly higher than those in the plots with pieces of *S. salsa* and in the bare patch plots. The densities of crab burrows were not different between the real and plastic *S. salsa* plots or between the plots with pieces of *S. salsa* and the bare patch plots (Figure 6C; Table S6; Figure S6e). In the treatments from which birds were excluded, at the beginning, most crabs preferred to burrow in the plots with real or plastic *S. salsa* plants. However, after 30 days (August 28th) and after 60 days (September 28th), the density of crab burrows became similar between all the treatments (Figure 6D; Table S6; Figure S6f). Additionally, on August 7th (10 days after the beginning of the experiment), the total number of crab burrows in all the treatments became stable and almost reached a maximum in the treatment with birds, while it continued increasing and changing in the treatment without birds (Figure 6C,D).

3.3 | Large-scale ploughing restoration practice

The large-scale microtopographic ploughing restoration practice showed that we were able to successfully revert the degraded bare patches to saltmarsh vegetation ecosystems (Figure 7; Figure S8; Table S7). Before the microtopographic restoration (November 2017), there was no difference in the densities of plants and crabs (few of both were present) between the degraded bare plots and the forthcoming restored treatment plots, all of which were significantly lower than the densities in the naturally vegetated plots (Figure 7). However, after microtopographic restoration, throughout 2018 and early 2019, the plant densities in the naturally vegetated plots and the restored treatments were both significantly higher than that in the degraded bare plots, while the difference in plant densities between the naturally vegetated plots and the restored treatments was not significant (Figure 7A). The densities of crab burrows in the naturally vegetated plots and the restored treatments were both significantly higher than that in the degraded bare plots. The density of crab burrows in the restored treatments continued to increase during 2018 but remained significantly lower than that in the naturally vegetated plots in April. However, in October 2018, the crab densities were no longer significantly different between the naturally vegetated plots and the restored treatments (Figure 7B).

Throughout 2018 and early 2019, the soil penetration resistance and salinity in the naturally vegetated plots and the restored treatments were not different, and both treatments had significantly lower values than those in the degraded bare plots

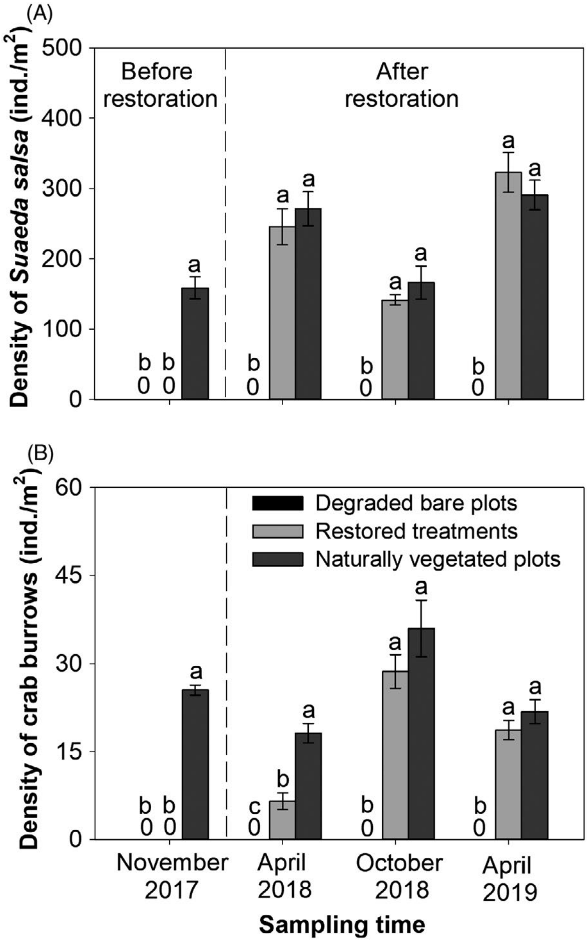

FIGURE 7 Comparisons of the (A) densities of *Suaeda salsa* and (B) densities of crab burrows in the three treatments of the large-scale ploughing restoration practice in November 2017 (before restoration), April and October 2018, and April 2019 (after restoration). The data are shown as the means ± *SE* ($n = 6$). The means with the same letter are not significantly different from one another ($p > 0.05$; post hoc multiple comparisons)

(Figure S12a,c). The soil moisture content in the naturally vegetated plots and the restored treatments were both significantly higher than that in the degraded bare plots, and not different from each other (Figure S12b).

4 | DISCUSSION

This study on the middle-elevation saltmarshes of the Yellow River Delta revealed multiple lines of evidence for a reciprocal facilitative interaction between annual saltmarsh plants and burrowing crabs. The burrowing crabs facilitated seed retention and seedling establishment of the annual saltmarsh plants in winter and spring by modifying the microtopographic environment of the sediment, and the plants facilitated the crabs by providing protection from predators, providing food and reducing physical stresses in summer and autumn. This reciprocal facilitation inspired an efficient restoration method for saltmarsh vegetation that entailed one-time ploughing of bare patches. A field-scale test of this method led to the successful recovery of degraded saltmarsh patches.

4.1 | Facilitation of plants by crabs

Many studies have emphasized that the high intensity of crab herbivory can negatively affect plants in some coastal ecosystems (Altieri et al., 2013; Holdredge et al., 2009), while other studies have shown that some crabs can also facilitate important plant species in some coastal ecosystems (Bertness, 1985; Gittman & Keller, 2013). In the saltmarshes of the Yellow River Delta, previous studies found that the crab *H. tientsinensis* negatively affected the native plant *S. salsa* through herbivory, especially in large areas with no high density of plants and areas with relatively frequent and strong tides (He, 2012). During the extreme drought climate, drought stress in combination with pressure from crab grazers could even generate enough stress to trigger die-off of plants (He et al., 2017). However, here we also found that the burrows made by the crabs studied have important positive effects on *S. salsa* plants in the middle-elevation saltmarshes (with generally high plant density and moderate tides) of the Yellow River Delta, where the effects of ecosystem engineering by crabs are more likely to exceed the effects of grazing. This study clearly showed that in these areas the concave–convex microtopography modified and generated by crabs promotes *S. salsa* seed retention and seedling establishment in winter and spring through different investigations and experiments, which are critical phases in plant life cycles that can determine vegetation community structure (Balke et al., 2013) and vegetation restoration efficacy (Wang et al., 2018).

The positive correlation among the density of crab burrows in autumn, the microtopographic roughness and the density of *S. salsa* seedlings in spring the next year indicated that the concave–convex microtopography generated by crabs persists to some degree during the winter when the crabs hibernate and that this persistent microtopographic variation facilitates *S. salsa* seed retention in winter and seedling establishment in spring. While some studies have reported that crab activities could benefit seed dispersal and viability and seedling establishment of mangroves (Lindquist et al., 2009; Minchinton, 2001), to the best of our knowledge, there are really few studies showing that this microtopographic modification by crabs in fact facilitates seed retention and seedling establishment of saltmarsh plants, thus leading to a reciprocal benefit. In the small-scale manipulations of microtopography, the seed bank investigations showed that significantly more seeds are trapped in areas with both naturally (crab-generated) and artificially (ploughing) concave-convex microtopography than in areas with flat microtopography. Tidal export and the resulting sediment dynamics can be a dominant factor limiting seed dispersal to and retention in suitable sites in coastal ecosystems (Zhu et al., 2014). This causes the final distribution of seeds before germination to result from the interactions among waves, tidal currents and trapping agents (Chang et al., 2008). The densities of established seedlings were higher in the plots with naturally and artificially concave–convex microtopography than in the flat plots. Indeed, our experiment also found that both the naturally and artificially concave–convex microtopography increased soil moisture content and organic matter and decreased soil penetration resistance and salinity, thus providing a more favourable and suitable environment for seed germination and seedling establishment. This confirms results from other studies showing that microtopographic structures can promote seed germination and seedling establishment (Olff et al., 1994; Wang et al., 2018).

4.2 | Facilitation of crabs by plants

Previous studies have shown that plant cover can facilitate macrobenthic communities by reducing physical stresses and by providing a greater availability of detritus which served as a food source, suitable attachment sites and refuges from predation (He & Cui, 2015; Lana & Guiss, 1992). However, the mechanisms driving these facilitative effects are often less addressed. Our results suggest that the *S. salsa* plants facilitated *H. tientsinensis* crabs through a combination of mechanisms: by providing food, by yielding more safety from predators and by decreasing abiotic stresses.

Predation has a special role in this two-way interaction. Vegetation could facilitate crabs by providing safe sites and cover against avian predators (He & Cui, 2015; Nomann & Pennings, 1998). In the intertidal saltmarsh of the Yellow River Delta, different species of seabirds commonly feed on crabs. Behavioural observations on seabirds show that they prefer to feed in unvegetated habitats (Figure S5c–d), likely because the lack of plants makes it easier for the birds to walk, catch prey and spot their own predators. This likely partly explains why the existence of *S. salsa* also reduces crabs' risk of predation, as obstruction during foraging provides better escape options.

Crabs can also benefit from plants in other ways. Previous studies (He, 2012; He et al., 2015) and our observation in the field showed that *S. salsa* plants are eaten by the crabs, and our observation also found that these plants can intercept some other potential food for crabs (Figure S13). Additionally, we found that *S. salsa* also affected some environmental factors, such as increased soil moisture content and soil organic matter, and decreased soil penetration resistance, soil salinity, photosynthetically active radiation and soil temperature which are all important determinants of crab distribution (He & Cui, 2015; Li et al., 2018).

The densities of crab burrows generally increased with *S. salsa* plant densities in summer in the middle-elevation saltmarshes, achieving the generally highest burrow density when the plant density nearly reached its maximum value. This was shown to be a causal relation, because the removal of the plants decreased the crab burrow density. Some abandoned burrows then became blocked by tidal sediment deposition. In the field, transplanting real plants and placing plastic plants and pieces of plants in bare patches all increased the number of crab burrows. Thus, plants can possibly facilitate crabs by providing food, shelter and a more benign environment. Structure is really important, as the plots with the plastic plants attracted really many crabs, which did not provide food but did offer shelter structure for the crabs.

The predation risk laboratory experiment showed that the crabs burrowed more quickly in the treatments with birds than in the treatments without birds, which indicated that quick burrowing is a response to increased perceived predation risk. The higher densities of crab burrows in both the real and plastic *S. salsa* plots with predators indicated that plants provide an environment that is perceived as safer by the crabs. The lack of difference in crab burrow densities between the plots with pieces of *S. salsa* and the bare patch plots indicated that crabs seemed to be more concerned with predation risk than with food in the presence of predators. In the treatments without predators, when the crabs eventually learned that there was no predation risk, they started to burrow anywhere and were not associated with the plants.

4.3 | Reciprocal facilitation and its implications

Many studies have shown that promoting facilitative interactions between important species can increase the success of the ecosystem restoration (Derksen-Hooijberg et al., 2017; Gagnon et al., 2020). Our results suggested a reciprocal facilitation between annual saltmarsh plants and burrowing crabs in the middle-elevation saltmarshes of the Yellow River Delta, that the crabs facilitated plant seed retention and seedling establishment in winter and spring by modifying the sediment microtopography and the plants facilitated the crabs by providing protection from predators, providing food and reducing physical stresses in summer and autumn. Based on this important reciprocal facilitation, our study also yielded important restoration implications for degraded coastal saltmarshes.

In addition to the ecological importance, the famous ‘red carpet’ of *S. salsa* saltmarshes is an important natural Chinese landscape with high potential for tourism. However, mainly due to some extreme climatic events (He et al., 2017), the salinity and drought stress in these marshes increased to levels that exceeded the tolerance limits of crabs and plants, or the drought stress in combination with pressure from crab grazers generated enough stress to trigger die-off of plants, resulting in large degraded bare patches with flat microtopography, no crabs and no plants; it is unlikely that these areas would be able to recover independently. Additionally, some coastal engineering projects, such as the construction of dams, roads and oil fields (Wang, 2018; Yu et al., 2017), have also influenced some neighbouring habitats, mainly by changing elevation and hydrology, which has resulted in abiotic stresses for crabs and plants. It is relatively difficult for seeds to become established in bare areas with flat microtopography and tidal disturbances within saltmarshes (Clark et al., 2007); in these areas, there is a lack of trapping agents (Nilsson et al., 2010), and seeds are not easily retained on smooth surfaces (Johnson & Fryer, 1992). Additionally, increasing physical stresses (such as moisture and salinity) also limit the survival and growth of *S. salsa*. Thus, it is difficult for *S. salsa* plants to establish and grow in degraded bare areas with flat microtopography. With the increasing physical stresses and danger from predators, *H. tientsinensis* clearly did not burrow or settle down in these exposed areas. Without the burrowing activity of crabs, the microtopography of the sediment in these marshes would always remain flat, restricting the rehabilitation of natural marshes. Understanding these interactions, however, provides a perspective on the opportunity for the restoration of degraded saltmarshes through the one-time ploughing of degraded patches (Figure S14). This process provides calmer hydrodynamic conditions that helps crabs and annual plants reach an establishment threshold and develop their reciprocal facilitation in a shorter disturbance-free WoO, an intervention that we showed was effective in the field.

This restoration approach was tested at a large scale in this study, and we achieved significant restoration success, which supported our hypotheses on the functioning of this system. After our ploughing treatment, the artificial concave–convex microtopography successfully became constructed and maintained, associated with a high density of plants and crabs. Our results therefore make a strong case that a single ploughing intervention can help saltmarsh systems reach a recovery threshold and provide numerous hydrologic, edaphic, vegetative and even ecosystem recovery benefits, which also make a clear identification of the underlying feedback mechanisms and demonstration of practical feasibility. Additionally, we suggest that this kind of intervention method, which could facilitate the critical recruitment of vegetation and its interplay with fauna, could be applicable and useful for the management or restoration of hydrodynamically forced vegetated coastal or river ecosystems world-wide. For example, perhaps it could enhance restoration in coastal mangrove swamps (Minchinton, 2001) and in other types of saltmarshes (Chang et al., 2008), and also be used in the restoration of river bank ecosystems influenced by riverine floods (O'Hare et al., 2012).

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AUTHORS' CONTRIBUTIONS

D.Q., B.C., H.O., X.M. and J.Y. conceived the ideas and designed the methodology; D.Q., X.M., F.W., F.G. and H.S. collected the data; D.Q. analysed the data; J.v.d.K., Y.C., T.X. and J.B. provided some important guidance on methods and writing; D.Q., H.O. and B.C. led the writing of the manuscript. All the authors contributed critically to the drafts.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.cz8w9gj2k (Qiu et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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