Key Points:

- A new eco-morphodynamic model is developed accounting for facilitation, competition and predation in mangrove-saltmarsh ecotones
- Ecotone dynamics at intertidal scale are determined by herbivory and the relative growth properties between mangroves and saltmarshes
- Tidal networks in saltmarsh-dominant ecotones are formed more rapidly and extensively with deeper channels

Mangrove-Saltmarsh Ecotones: Are Species Shifts Determining Eco-Morphodynamic Landform Configurations?

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Abstract Mangrove-saltmarsh ecotones are experiencing rapid alterations due to climate change and human activities, however, the ecological and morphological implications of these shifts remain largely unknown. This study systematically explores how interspecific interactions and herbivory influence the dominant wetland species, as well as the resultant morphological evolution and landscape configuration. To achieve this, we develop a new eco-morphodynamic model that integrates hydrodynamics, sediment transport, bed-level change, and vegetation dynamics. The novelty of the current model lies in newly incorporated modules to simulate biotic interactions between mangroves and saltmarshes, enabling exploration of eco-morphodynamic feedback in mangrove-saltmarsh ecotones in response to tidal flows and species interactions. Our results show that vertical growth rates of coexisting vegetation species are dominant factors in determining wetland dominance. When mangroves and saltmarshes exhibit comparable growth rates, mangroves typically become the dominant wetland species. Conversely, if mangroves grow more slowly than saltmarshes, they are unable to outcompete saltmarshes. Additionally, herbivory can fundamentally alter wetland dominance depending on herbivore food preferences. Our simulations further underline that saltmarsh-dominated wetlands develop channel networks more extensively and rapidly than mangrove-dominated systems. This pattern is also observed during species invasions, with invading saltmarshes extending channel networks, while invading mangroves inhibit ongoing network expansion. This study highlights the pivotal roles of relative growth properties and herbivory in driving ecotone development in respect to wetland dominance and channel network development at the intertidal scale.

Plain Language Summary In coastal areas where mangrove trees and saltmarsh grasses exist together, climate change and human activities significantly impact wetland development. This study uses a novel computer model to explore how different plants interact, how plant-eating animals influence plant distribution and how these factors affect the shape of coastal landscapes. Our findings reveal that mangrove trees with growth rates similar to saltmarsh grasses can outcompete saltmarshes and become the dominant wetland species. Additionally, animals that eat plants play a crucial role in determining which plants survive, with their effects highly dependent on their feeding preferences. Wetlands dominated by saltmarshes tend to develop deeper channels. This occurs because saltmarshes spread slowly and grow in patches, which changes water flow and promotes erosion in areas without vegetation. Conversely, wetlands where mangroves are taking over typically feature fewer and shallower channels. Overall, our study suggests that the growth rates of different plants and the presence of plant-eating animals are essential in shaping these coastal environments.

1. Introduction

Coastal wetlands are one of the most valuable ecosystems on the planet, providing critical benefits to coastal populations such as carbon sequestration, coastal protection, and biodiversity enrichment (Costanza et al., 2014). Among these wetlands, mangroves and saltmarshes are two common species, often found in similar geomorphic settings along low-lying coastlines (Barbier et al., 2011). Globally, mangrove trees and shrubs primarily dominate sheltered tropical shorelines, while grass-like saltmarshes prevail along temperate coastlines at higher latitudes

(Saintilan et al., 2019). However, both systems are facing increasing pressure from climate change and human activities, potentially reshaping their habitats across the globe. For example, decreases in extreme freeze frequencies have allowed mangrove species around the world to proliferate toward their poleward limits over the past half century, often at the expense of displaced saltmarshes (Cavanaugh et al., 2019; Saintilan & Rogers, 2015). In contrast, human introduction of non-native species, such as *Spartina alterniflora* saltmarshes, to limit coastal erosion has unexpectedly spread to mangrove ecosystems (Zhang et al., 2021; Zhu et al., 2019). The co-occurrence of these two vegetation types has created unique transitional zones known as mangrove-saltmarsh ecotones, which are facing unprecedented change. However, the dynamics of these ecotones and the possibility of species co-occurrence leading to shifts in dominant species with potential implications for wetland morphology remain largely unexplored. New eco-morphodynamic models accounting for more complex biotic interactions are needed to help understanding impacts of climate change and anthropogenically induced biological invasions, an important limitation of our current scientific understanding as outlined by the IPCC (IPCC, 2022).

Mangroves and saltmarshes share similar eco-morphodynamic feedback processes that shape the coastal landscape. They both have the ability to promote sediment deposition by attenuating tidal currents and dampening waves within vegetated areas (McKee et al., 2020; Möller et al., 2014), although the amount of sediment trapped per unit of time and surface, the so-called trapping efficiency, can vary with morphological configuration and vegetation species (Y. Chen et al., 2018; Morris et al., 2023; Rogers et al., 2006). Both vegetation species can deviate tidal currents and instigate erosion of adjacent unvegetated areas, thereby initiating channel formation (Schwarz et al., 2018; van Maanen et al., 2015).

Despite their similarities in ecoengineering effects, mangroves and saltmarshes display key differences in colonization strategies and growth patterns that fundamentally influence the characteristics of their ecoengineering effects. Mangroves typically colonize through a high amount of viviparous propagules, resulting in a relatively homogenous spatial distribution and faster colonization (Fromard et al., 2004; Schwarz et al., 2022). In contrast, temperate saltmarshes (e.g., dominated by the genus *Spartina* in their pioneer zone) tend to rely on asexual lateral expansion for habitat colonization, leading to an initial patchy cover and slower colonization (Cao et al., 2018; Taylor & Hastings, 2004). In terms of growth, mangroves at their latitudinal extremes undergo growth heavily influenced by temperature and photoperiod (Chapman et al., 2021; Krauss et al., 2008), typically featuring slow growth rates during winter months (Peng et al., 2018). In comparison, temperate saltmarshes demonstrate cyclical growth patterns in response to seasonal fluctuations, with peaking in biomass by late summer, and then experiencing die-off of aboveground stands in winter (S.-H. Li et al., 2018; Zheng et al., 2016). These differences in colonization strategies and growth patterns between mangroves and saltmarshes have been demonstrated to create distinct channel network properties, with fast/slow colonizing mangroves/saltmarshes creating sparser/denser channel networks (Schwarz et al., 2022). Nevertheless, it is unknown whether tidal channel formation is affected differently in systems colonized by single species of either mangroves or saltmarshes compared to systems where both mangroves and saltmarshes colonize simultaneously. Understanding the effects of multiple vegetation species and their potential shifts on wetland morphology are essential challenges for the effective management and conservation of coastal ecosystems.

Mangroves and saltmarshes, occupying overlapping ecological niches in coastal wetlands, undergo diverse biotic interactions, including facilitation, competition, and herbivory. For instance, saltmarshes can facilitate mangrove establishment by trapping mangrove propagules within their aboveground stands (Friess et al., 2012; McKee et al., 2007). However, the dynamics of mangrove-saltmarsh ecotones have shown to depend strongly on post-establishment competition (Howard et al., 2015), particularly regarding access to light and nutrients (Pickens et al., 2019; Simpson et al., 2013). Previous studies have revealed that saltmarsh replacement beneath mangrove forests typically results from limited light and resource availability when they compete with taller and larger mangrove stands (Krauss & Allen, 2003; Patterson et al., 1997; Raabe et al., 2012). Likewise, saltmarshes with tall stature and high density can outcompete short mangrove seedlings through similar processes. As observed in numerous mangrove-saltmarsh ecotones throughout China, *S. alterniflora*, an introduced saltmarsh species originating from the United States, has replaced native mangrove seedlings (e.g., *Kandelia obovata*) due to its rapid growth (Biswas et al., 2018; Lu et al., 2018). Yet, mangrove species like *Sonneratia apetala* also occurring along Chinese coasts, which demonstrate a similar vertical growth rate to *S. alterniflora* in early development, are able to effectively control *S. alterniflora* invasions by overshading them (Peng et al., 2018; Zhou et al., 2015). As various mangrove-saltmarsh competition outcomes occur, which are linked to varying vertical growth rates, relative growth properties between mangroves and saltmarshes could be an important determinant of mangrove-

saltmarsh dynamics. However, competition outcomes are intrinsically driven by both growth in response to inundation time, which results from eco-morphodynamic feedback, and growth in response to biotic interactions, underlying the necessity of new model development.

Herbivory, another important biotic interaction within coastal wetlands, was also shown to regulate vegetation dynamics (Van der Stocken et al., 2019; Xu et al., 2023). Herbivores, such as crabs, insects, and rodents, feed on seeds and young shoots, thereby affecting the survival of mangroves and saltmarshes (He & Silliman, 2016), as well as triggering eco-morphodynamic feedback (Hughes et al., 2024). However, the inclusion of herbivory within eco-morphodynamic models has so far been neglected and it thus remains uncertain how multiple biotic interactions are able to influence the dominance of a specific wetland species and wetland development.

Although several studies have monitored ecotone morphodynamics through field observations and experiments, there is a lack of systematic investigations into eco-morphodynamics over decadal scales, particularly concerning channel networks and sediment transport (Y. Chen et al., 2018; McKee et al., 2020). As such, numerical modeling presents a valuable approach in elucidating the interactions of the various processes affecting species dominance and wetland morphodynamics. While significant advancements have been achieved in coastal eco-morphodynamic modeling over the past decades, particularly in modeling vegetation dynamics and landscape evolution, many existing models oversimplify biotic interactions by using a preconfigured biomass productivity and competitive ability (Marani et al., 2013; Xie et al., 2020). Meanwhile, most modeling studies focus on a single vegetation species, neglecting the potential for vegetation shifts that characterize mangrove-saltmarsh ecotones, such as mangrove modeling (van Maanen et al., 2015; Xie et al., 2020) and saltmarsh modeling (Brückner et al., 2019; Schwarz et al., 2014). Importantly, mangrove-saltmarsh interactions are highly context-dependent (Guo et al., 2013; Reis et al., 2023) and the outcome of mangrove-saltmarsh interactions is not only a function of biotic interactions but also eco-morphodynamic feedback. Thus, it is essential to develop such a model for gaining a better understanding of how species interactions alter vegetation cover and landscape configuration.

In this study, we develop a new eco-morphodynamic model that incorporates mangrove-saltmarsh interactions, as well as the influence of herbivory. We use Zhangjiang Estuary as a reference site to set up our model since it (a) has experienced an ecosystem shift from a mangrove-dominated wetland to a mangrove-saltmarsh ecotone (Liu et al., 2017; Zhu et al., 2019), (b) hosts distinct herbivory effects across vegetation species (Peng et al., 2022; Zhang et al., 2018), and (c) provides ample field data for model setups and calibration. Our numerical experiments primarily focus on understanding vegetation-mediated sediment redistribution and corresponding morphological changes within the computational domain, rather than on understanding the system response to changes in external conditions (e.g., varying hydrodynamic, sedimentary, and ecological parameters). Regarding morphological changes and landscape evolution, we particularly focus on the development of tidal channel networks as these are key landscape features that control the movement of water, sediment and nutrients, and thus determine the longer-term resilience of wetland ecosystems (D'Alpaos et al., 2005; Van de Vijsel et al., 2023). Following model calibration, we carry out numerical experiments to answer: (a) What factors determine the dominant wetland species if both mangroves and saltmarshes are present during mudflat colonization? (b) Can newly colonizing saltmarshes or mangroves alter the dominant wetland species in established habitats? (c) How does a change in dominant wetland species affect morphology, particularly regarding sediment dynamics and channel networks?

2. Methods

Mangrove-saltmarsh ecotone dynamics are simulated by coupling a spatially explicit hydro-morphodynamic model (Delft3D) (Lesser et al., 2004) with well-calibrated vegetation dynamic models (Matlab), including mangroves (Xie et al., 2022), saltmarshes (Schwarz et al., 2014), and their competition (R. Chen & Twilley, 1998). Every ecological month, Delft3D provides hydro-morphodynamic information to Matlab for calculating vegetation dynamics, which are then fed back to Delft3D for subsequent hydrodynamic and morphodynamic calculations (Figure 1). Moreover, this eco-morphodynamic model contains a species-interaction module, which was specifically developed in this study to address biotic interactions between mangroves and saltmarshes, allowing us to investigate the factors determining the dominant wetland species when both mangroves and saltmarshes are present. To calibrate this new module, we compared the model results with field measurements from a marsh-organ experiment at the study site (Peng et al., 2018). Following calibration, different scenarios were designed to explore whether newly colonized saltmarshes or mangroves alter the
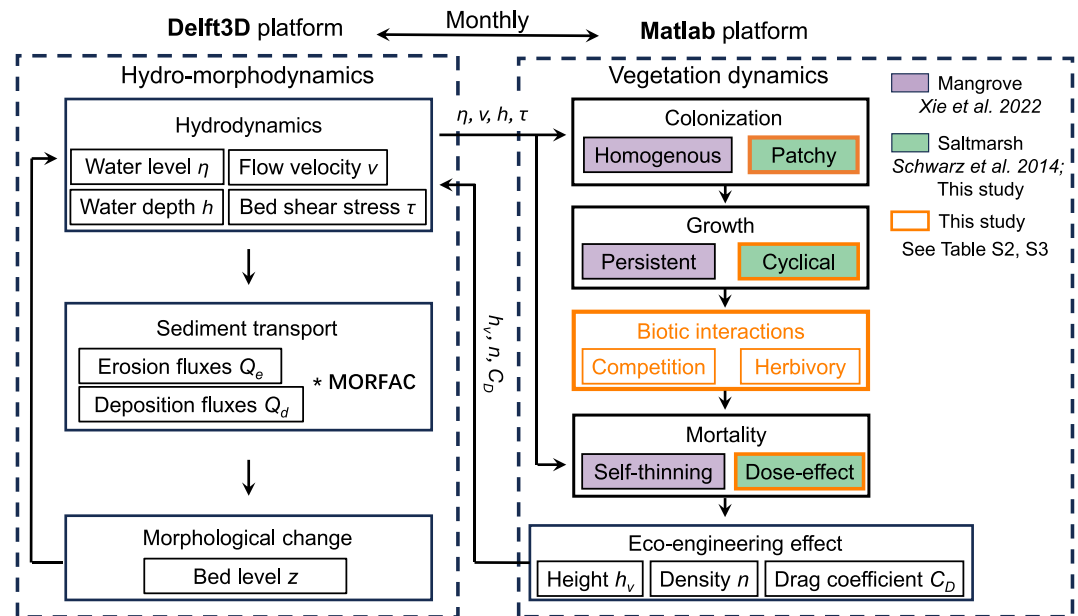
Figure 1. Schematic illustration of eco-morphodynamic interactions in mangrove-saltmarsh ecotones. The morphodynamics of the ecotone are controlled by both hydro-morphodynamics and vegetation-ecoengineering effects. The ecoengineering effects are determined by the biophysical properties of all vegetation species, such as aerial roots and stem height (h_v), density (n), and drag coefficient (C_D), which are strongly influenced by species-specific colonization strategies, growth patterns, and biotic interactions. The hydro-morphodynamic module interacts with the vegetation module every ecological month. The MORFAC represents the morphological acceleration factor.

dominant wetland species in established habitats and how changes in dominant wetland species affect morphology.

2.1. Study Site

Zhangjiang Estuary, located in southern China (117°25′E, 23°55′N), is situated within a back-barrier tidal basin, experiencing semidiurnal tides with an annual mean tidal range of 2.32 m and a maximum tidal range of 4.67 m (Wei et al., 2022; Zhang et al., 2006). Additionally, reservoir construction in upstream rivers has reduced the sediment supply to this area (Wu et al., 2024).

Vegetation within this wetland is dominated by the native mangrove species, *K. obovata*, which typically attains a mean height of 4.5 m in the upper intertidal zone, with a density of 30 trees/100 m^2 (Zhang et al., 2006). In recent decades, *S. alterniflora* has extensively colonized previously unvegetated lower intertidal zones (Liu et al., 2017; Zhu et al., 2019). The exotic mangrove species *S. apetala* was introduced to this site in 2006 and has since been growing amid native mangroves (Peng et al., 2018). *Rattus losea*, a common native rodent, inhabits this wetland and feeds on both mangrove and saltmarsh seedlings (Peng et al., 2022; Zhang et al., 2018). However, there are significant differences in their consumption preferences among species, resulting in distinct herbivory effects on plant colonization. For instance, rodent grazing rates, indicating the percentage of stems consumed during a given period, range from 70% to 100% for *K. obovata* and 40%–70% for *S. alterniflora*, whereas for *S. apetala*, it is only about 10% (Peng et al., 2022; Zhang et al., 2018).

K. obovata and *S. apetala* are two widely distributed mangrove species across Eastern Asia (Ren et al., 2009; Sheue et al., 2003). They exhibit distinct growth properties, experience varying impacts from herbivory, and demonstrate contrasting outcomes in competition with *S. alterniflora*. Therefore, our focus centers on these two mangrove species. *K. obovata*, hereafter referred to as slow-growing mangroves (Ms), grows notably slower than *S. alterniflora* in China (Peng et al., 2018). *S. apetala*, which has comparable growth rates to *S. alterniflora*, is referred to as fast-growing mangroves (Mf). The saltmarsh species *S. alterniflora* is simply termed S.

2.2. Eco-Morphodynamic Model Framework

Taking advantage of previously presented and well established eco-morphodynamic framework, coastal morphological evolution is simulated using a spatially explicit numerical model Delft3D. This model first derives hydrodynamic variables based on the shallow water equations and initial bathymetry, which are employed to compute sediment transport and associated morphological changes, forming a feedback loop between hydro-dynamics, sediment transport, and morphological changes (Figure 1). Utilizing the "Trachytope Module" in Delft3D, the model further integrates vegetation effects, with characteristics determined by vegetation bio-physical properties, such as stem height, density, and drag coefficient (Baptist et al., 2007). These vegetation variables dynamically change with growth and death, simulated by widely adopted mangrove and saltmarsh models in Matlab (Schwarz et al., 2014; Xie et al., 2022). To link the two vegetation models and incorporate interactions between mangroves and saltmarshes, a species-interaction module is introduced to this framework based on existing competition modeling approaches (R. Chen & Twilley, 1998). This enhancement allows for a more nuanced representation of ecotone dynamics and their effects on wetland morphology. Model parameters and their sources used to set up the model are summarized in Tables S1–S5 in Supporting Information S1.

2.2.1. Hydro-Morphodynamic Module

Delft3D is employed to compute the hydrodynamics and sediment dynamics governing the morphological changes of coastal mudflats (Lesser et al., 2004). The hydrodynamic module solves the depth-averaged shallow water equations to derive water levels and velocities along a rectilinear grid (Table S1 in Supporting Information S1). Using local flow velocities and eddy diffusivities, the sediment transport module solves the advection-diffusion equation for cohesive sediment, utilizing the well-known Partheniades-Krone formulation as a resuspension criterion (Partheniades, 1965). In this study, sediment composition is simplified as cohesive mud to streamline the effects of various sediment fractions and reduce model complexity. Changes in bed elevation resulting from erosion and deposition fluxes of sediment are incorporated into new bathymetry and used in the subsequent hydrodynamic calculations, forming a so-called hydro-morphodynamic cycle (Figure 1). Hydro-morphodynamic parameters are primarily based on previous studies (Xie et al., 2022; Zhou et al., 2022), which are summarized in Table S4 in Supporting Information S1.

2.2.2. Mangrove Module

Building on previous mangrove models (van Maanen et al., 2015; Xie et al., 2020), mangrove module captures the dynamic interplay of colonization, growth, and mortality in mangrove ecosystems. This module simulates the dispersal of mangrove propagules by assuming that mangroves can establish themselves on mudflats under favorable tidal conditions (Xie et al., 2022). These favorable conditions not only require suitable inundation but also a calm hydrodynamic environment that allows seedlings to settle and develop resilience against disturbances (Bouma et al., 2016; Hu et al., 2015). Inundation is estimated by the relative hydroperiod, which represents the proportion of time a grid cell remains submerged during each tidal cycle. Additionally, we compute the 90th percentile bed shear stress during each hydrodynamic time step, with a threshold value of 0.2 N/m^2 to identify favorable conditions for propagule settlement (Balke et al., 2011; Xie et al., 2022).

Once established, mangroves exhibit faster growth during the growing season and slower growth during the winter months (Figure S1 in Supporting Information S1). Their growth, including increases in stem diameter, tree height, and root number, is influenced by fitness effects and competition (Table S2 in Supporting Information S1) (Xie et al., 2022). Fitness is linked to the relative hydroperiod (Figure S2 in Supporting Information S1), with mangroves achieving maximum fitness at their optimal elevation and decreasing as inundation periods lengthen or shorten (Krauss et al., 2014). Competition for finite resources within the grid cell, such as space, further constrains their growth, as detailed in van Maanen et al. (2015). Interspecific competition with saltmarshes, described in the subsequent Section 2.2.4, can also impact mangrove growth.

Prolonged growth inhibition, either due to low fitness or intense competition, can lead to mangrove mortality (R. Chen & Twilley, 1998). We assess mangrove growth status using a metric determined by the product of fitness and competition, with a product below 0.5 indicating growth suppression (van Maanen et al., 2015). If this suppressed state persists for five consecutive years, tree density is reduced at the beginning of each new ecological year to simulate mangrove self-thinning (Osland et al., 2012). Detailed descriptions of the mangrove model can be

found in van Maanen et al. (2015) and Xie et al. (2022). The equations and parameters used in this mangrove module are listed in Tables S2 and S5 in Supporting Information S1.

2.2.3. Saltmarsh Module

In line with previous saltmarsh modeling studies, the development of saltmarshes is driven by processes such as establishment, growth, diffusion, and stress-induced mortality (Schwarz et al., 2014; Temmerman et al., 2007). When flooding conditions are suitable and water flow is below a critical threshold, saltmarsh seedlings are randomly allocated with a defined establishment probability to uncolonized grid cells, with initial stem density and plant height (Schwarz et al., 2014). Once established, saltmarsh growth follows logarithmic growth equations up to its maximum carrying capacity of density and height (Table S3 in Supporting Information S1) (Temmerman et al., 2007). Similar to mangroves, saltmarsh growth is also influenced by inundation-based fitness (Figure S2 in Supporting Information S1) and potential interspecific competition. Additionally, saltmarshes can expand laterally to neighboring cells, with a lateral expansion rate determined by the existing stands (Table S3 in Supporting Information S1).

Saltmarsh mortality is associated with high flow stress, quantified through a dose-effect relationship (van Oorschot et al., 2016). This relationship specifies minimum and maximum thresholds, indicating that saltmarshes remain unaffected when tidal forces are below the minimum threshold and are entirely removed when flow stress exceed the maximum threshold. Between these thresholds, the mortality fraction increases linearly with rising pressure (van Oorschot et al., 2017). Additionally, during non-growing seasons (Figure S1 in Supporting Information S1), saltmarshes enter a senescence phase, characterized by a gradual reduction in stand height and stem density. The equations and parameters used in this saltmarsh module can be found in Tables S3 and S5 in Supporting Information S1.

2.2.4. Species-Interaction Module

Mangroves and saltmarshes can potentially coexist within the same model grid cell, leading to interspecific competition for light and space. These interactions are modeled using the concept of the zone of influence (ZOI), a widely used approach in plant competition modeling (Berger & Hildenbrandt, 2000). Each plant accesses resources within a specific zone around its stem base, and when these zones overlap, competition ensues since only a limited number of plants can thrive in the shared area (Berger & Hildenbrandt, 2000). Light, a crucial and highly contested resource, plays a pivotal role in above-ground interspecific competition (Figure 2). Following the competition modeling of R. Chen and Twilley (1998), our model calculates the available light for shorter plants by considering the cumulative leaf area of their taller neighbors (Figure 2). For mangroves, leaf area (LA_m) is a function of diameter (D), while for saltmarshes, leaf area (LA_s) depends on height (H_s) and density (P):

$$LA_m = a_m \cdot D^{b_m} \tag{1}$$

$$LA_s = a_s \cdot H_s^{b_s} \cdot P \tag{2}$$

where a_m, b_m, a_s, and b_s are species-specific constants (Table S5 in Supporting Information S1). The available light (AL) after passing through taller plants is calculated as:

$$AL = e^{(-k \cdot LA \cdot (h_2 - h_1))} \tag{3}$$

where k is the attenuation constant (Table S5 in Supporting Information S1), and h_1 and h_2 are the heights of the shorter and taller vegetation, respectively. The reduction in available light, which inhibits photosynthesis and subsequently growth, is determined using the following relationships (Botkin et al., 1972; R. Chen & Twilley, 1998):

$$C_{\text{inter\_light}} = 0.5 \cdot (r_s + r_i) \tag{4}$$

$$r_s = 1 - e^{(-4.64 \cdot (AL - 0.05))} \tag{5}$$
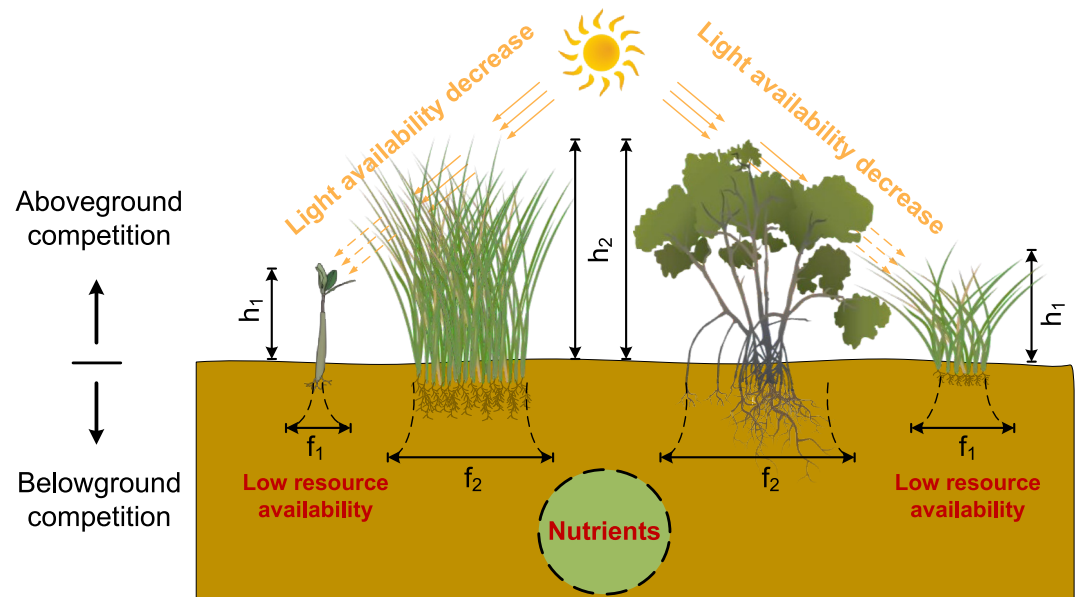
Figure 2. Conceptual sketch of aboveground and belowground competition between two neighboring plant species. Aboveground light competition is determined by the height differences between shorter plants (h_1) and taller plants (h_2). Belowground resource competition is estimated by the differences in fractions in each grid cell between lower-fraction plants (f_1) and larger-fraction plants (f_2).

$$r_i = 2.24 \cdot \left(1 - e^{(-1.136 \cdot (AL - 0.08))}\right) \tag{6}$$

where $C_{\text{inter\_light}}$ represents the shading effect on growth due to reduced photosynthesis, particularly impacting shade-intolerant plants. In this study, Ms, Mf, and S are all identified as shade-intolerant species (Peng et al., 2018; Zhang et al., 2012). r_s and r_i denote the reductions in photosynthesis rates for shade-tolerant and shade-intolerant species, respectively.

Nutrient inputs, another crucial factor in vegetative growth, can lead to belowground interspecific competition between coexisting vegetation species. Using the ZOI concept (Berger & Hildenbrandt, 2000), we simplify nutrient competition by assuming that mangroves and saltmarshes have similar nutrient uptake efficiencies. However, the species occupying a larger fraction of the grid cell can potentially gain more nutrients. Here, the fraction is defined as the ratio of the species' biomass in the grid to its maximum carrying capacity, representing its development level and area occupation in the grid. Nutrient competition is then evaluated by the relative fraction of two coexisting species (f_r), calculated as follows:

$$C_{\text{inter\_resource}} = \frac{1}{1 + e^{d_2(0.5 - f_r)}} \tag{7}$$

$$f_r = f_2 - f_1 \tag{8}$$

where d_2 is a constant controlling the shape of the competition curve, set to -12. f_1 and f_2 are the fractions of the species with the lower and greater fractions, respectively.

The ultimate outcome of interspecific competition hinges on whether light or nutrient competition has a greater impact, which means we choose the outcome with the greater impact to calculate the competition impact. When mangrove seedlings compete with saltmarshes, they can always survive the first 2 years of growth suppression by relying on the energy stored in their propagules, regardless of the intensity of saltmarsh competition. However, if the mangroves cannot overtop the saltmarshes by the end of these 2 years, they are presumed to die due to the inability to access essential external resources (Zhang et al., 2006). Additionally, when mangroves or saltmarshes

grow alone, we do not consider light or nutrient competition within their respective communities to reduce model complexity.

2.2.5. Herbivory Module

Herbivory predation, another critical biotic interaction, significantly influences the mortality of mangroves and saltmarshes (He & Silliman, 2016). Using data from the Zhangjiang Estuary (Peng et al., 2022; Zhang et al., 2018), we correlate potential predation rates on different species with tidal inundation regimes along the mudflat profile (Figure S3 in Supporting Information S1). To simplify our interpretation, we propose two hypotheses: (a) if predation occurs, all individuals of the targeted plant species within the grid are presumed dead; (b) if the plant is sufficiently robust (i.e., taller than 1 m), predation is insufficient to kill it (Z. Li et al., 2014; Zhang et al., 2018). Therefore, in this model, predation predominantly affects the survival of newly colonized seedlings. While mangroves and saltmarshes can also be consumed by other herbivores such as crabs and insects, this study focuses on the impact of a single herbivore (i.e., rodents) for simplicity. Peng et al. (2022) observed that herbivory predation in the Zhangjiang Estuary mainly occurs from December to January. Thus, our model initiates the predation process during the same period (Figure S1 in Supporting Information S1).

2.3. Model Setup and Output Analysis

2.3.1. Model Settings

A simplified two-dimensional tidal flat model is constructed to represent meso-tidal mangrove wetlands around the world (Friedrichs, 2011; Xie et al., 2022). This model features a gentle intertidal zone and a steeper subtidal zone influenced by an M2 tide with a 1.5-m amplitude (Figure S4a in Supporting Information S1), similar to field conditions (Zhang et al., 2006). The spatial resolution is set to 50 m in both the x and y dimensions (Xie et al., 2020). Since the study site is located in the interior of a semi-enclosed bay, wave effects are not taken into account to reduce model complexity. To mimic low sedimentary conditions resulting from the reduced sediment supply (Wu et al., 2024), external sediment input from the boundary is excluded. To expedite morphological changes and capture seasonal vegetation dynamics more effectively, a morphological acceleration factor (MORFAC) of 30 is adopted to update biophysical properties and ecoengineering effects every ecological month (van der Wegen et al., 2017; Xie et al., 2022). Furthermore, a 1-year hydrodynamic simulation period is designated, corresponding to morphological simulations and vegetation growth spanning 30 years (Figure S4 in Supporting Information S1), ensuring a complete development of vegetation and geomorphology. All hydro-morphodynamic parameters are summarized in Table S4 in Supporting Information S1.

2.3.2. Model Calibration

Utilizing data from a marsh-organ experiment conducted in Zhangjiang Estuary (Peng et al., 2018), we calibrated the vertical growth of the two mangrove species in our model, considering scenarios with and without saltmarsh competition (Figure 3). The data were measured monthly over 18 months in Zhangjiang Estuary by monitoring the initial growth of mangrove seedlings across different elevations and competitive settings (i.e., with and without saltmarsh presence). By synthesizing these field measurements, we generated time-series box plots to depict various growth characteristics. Based on species-specific fitness curves (Figure S2 in Supporting Information S1), and parameters from field observations (Table S5 in Supporting Information S1), our model initialized mangroves and saltmarshes from seedlings with heights similar to those observed in the field. We first calibrated vegetation growth for no-competition scenarios where the model grid cells were consistently inhabited by a single species. Then, keeping the parameters constant throughout subsequent simulations, we applied the competition module in scenarios where both mangroves and saltmarshes were present to account for competition-induced growth inhibition.

The comparison between field data and model outputs demonstrates the model's accuracy in capturing the initial growth stages of both mangroves and saltmarshes, as well as the influences of interspecific competition (Figure 3). Notably, the model reproduces the differing vertical growth of the two mangrove species throughout both growing and non-growing seasons, closely mirroring observations from field experiments (Figures 3a and 3c). Furthermore, saltmarsh competition significantly inhibits mangrove seedling growth (Figures 3b and 3d). However, due to the relatively short height and small biomass of mangrove seedlings in their early stages, their impact on saltmarsh growth remains insignificant. Consequently, saltmarsh height exhibits limited variation,
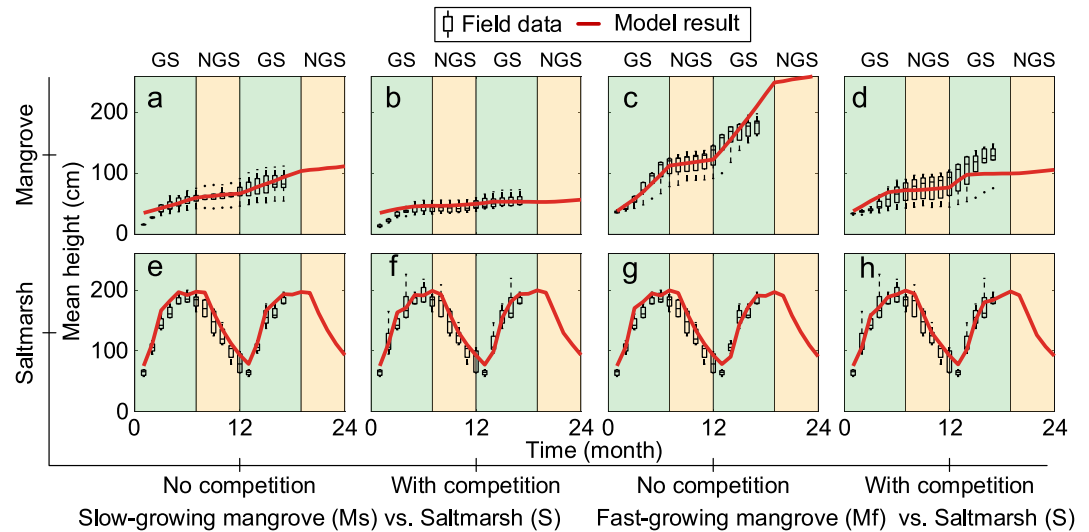
Figure 3. Comparison of initial growth evaluated over a 2-year period (red line) for mangroves (Ms and Mf) and saltmarsh (S) with and without competition against field experimental data (box plots). Panels (a, c, e, g) show scenarios without competition, while panels (b, d, f, h) illustrate scenarios with competition. Field data sourced from a marsh-organ experiment conducted at the study site by Peng et al. (2018). Green-shaded areas indicate growing seasons (GS), and yellow-shaded areas represent non-growing seasons (NGS). Time intervals are monthly.

regardless of the absence and presence of mangrove competition (Figures 3e–3h). While the field data covers only 18 months, we believe that our model produces realistic outcomes beyond this period by using field-based parameters.

2.3.3. Model Scenarios

To explore the impact of different species acting as eco-engineers and to understand the effects of various vegetation dynamics on landscape evolution, 18 model scenarios are designed with various combinations of species types and initial conditions (Table 1). We first investigate the eco-morphodynamic evolution of tidal flats under the influence of single species, namely slow-growing mangroves (Ms), fast-growing mangroves (Mf), and saltmarshes (S) either with or without herbivory (Single species/Mudflat colonization, Table 1). Subsequently, we conduct simulations to elucidate the effects of multi-species interactions on ecotone dynamics and mudflat evolution (Figure S4d in Supporting Information S1), including the competition between slow/fast-growing mangroves and saltmarshes (Multiple species/Mudflat colonization, Table 1). These scenarios address the first scientific question, elucidating factors that determine the dominant wetland species when both mangroves and saltmarshes are present during mudflat colonization.

Lastly, we simulate eight cases (No. 11–18, Table 1) to understand how newly colonizing saltmarshes or mangroves can alter the dominant wetland species in established habitats, and how changes in dominant wetland species affect morphology, particularly regarding sediment dynamics and channel networks (Figures S4e–S4f in Supporting Information S1). These aim to address the second and third scientific questions posed. In the context of these simulations, the results from the 30-year single-species simulations (No. 1–6, Table 1), capturing vegetation and morphological developments, serve as initial conditions to explore the effect of the invading species (Multiple species/Invasion, Table 1).

2.3.4. Output Analysis

To capture the evolving vegetation dynamics within intertidal zones, we compute the mean cover of each species by averaging their fraction across the entire intertidal area, thereby generating values ranging from 0 to 1. This result provides a holistic view of vegetation development in intertidal zones. Furthermore, to visualize vegetation colonization along the cross-shore profile over time, we calculate the alongshore-averaged cover by averaging the species fraction along each alongshore transect.

Table 1
Model Scenarios

No.	Vegetation species	Phase	Acronym	Species assemblage	Herbivory
1	Single	Colonization	Ms	*K. obovata*	-
2			Mf	*S. apetala*	-
3			S	*S. alterniflora*	-
4			MsH	*K. obovata*	R_{Ms}
5			MfH	*S. apetala*	R_{Mf}
6			SH	*S. alterniflora*	R_S
7	Multiple		MsS	*K. obovata + S. alterniflora*	-
8			MfS	*S. apetala + S. alterniflora*	-
9			MsHSH	*K. obovata + S. alterniflora*	$R_{Ms} + R_S$
10			MfHSH	*S. apetala + S. alterniflora*	$R_{Mf} + R_S$
11		Invasion	30MsS	30-year *K. obovata + S. alterniflora*	-
12			30MfS	30-year *S. apetala + S. alterniflora*	-
13			30MsHSH	30-year *K. obovata + S. alterniflora*	$R_{Ms} + R_S$
14			30MfHSH	30-year *S. apetala + S. alterniflora*	$R_{Mf} + R_S$
15			30SMs	30-year *S. alterniflora + K. obovata*	-
16			30SMf	30-year *S. alterniflora + S. apetala*	-
17			30SHMsH	30-year *S. alterniflora + K. obovata*	$R_{Ms} + R_S$
18			30SHMfH	30-year *S. alterniflora + S. apetala*	$R_{Mf} + R_S$

Note. R_{Ms}, R_{Mf}, and R_s indicate herbivory predation by rodents on Ms, Mf, and S, respectively.

Additionally, we assess the degree of channelization within the tidal system using two metrics: the mean unchanneled path length (mUpl) and the Hortonian drainage density (DD). The mUpl metric provides insights into the complexity of tidal channels by measuring the average distance a drop of water must traverse to reach the nearest channel, thereby characterizing channel intricacy (D'Alpaos et al., 2005). Also, the DD metric reveals the drainage efficiency of these channels, derived by dividing the total length of tidal channels by the watershed area (Marani et al., 2003).

To provide further details on morphological development, we also analyze bed-level changes separately within tidal channels and on platforms across various scenarios. Here, channels are defined as regions lying below mean sea level, while platforms refer to the areas between mean sea level and mean high water.

3. Results

In Section 3.1, we illustrate vegetation cover and eco-morphodynamic development for single-species scenarios (Figures 4 and 5). In Section 3.2, we delve into the ecological and morphological development for multiple-species scenarios during the mudflat colonization phase (Figures 6 and 7) and the invasion phase (Figures 8 and 9).

3.1. Single Species Dynamics

Due to differences in colonization strategies, mangroves and saltmarshes colonize mudflats in distinct patterns, creating different channel networks (Figure 4). Over time, mangroves exhibit a "fast-slow-fast" growth pattern, achieving maximum cover in about 15 years (Figures 4a and 4b). In contrast, saltmarshes grow at a relatively consistent pace, stabilizing after 20 years (Figure 4c). Moreover, saltmarshes reach their maximum height of 2 m within just 2 to 3 years after colonization, much quicker than mangroves (Figure 4c).

In terms of channel development, saltmarshes develop channel networks more extensively and rapidly than mangroves, as indicated by an overall smaller mean unchanneled path length (mUpl), greater drainage density (DD), and a faster decrease/increase in mUpl/DD with increasing vegetation cover (Figure 4f). Despite the
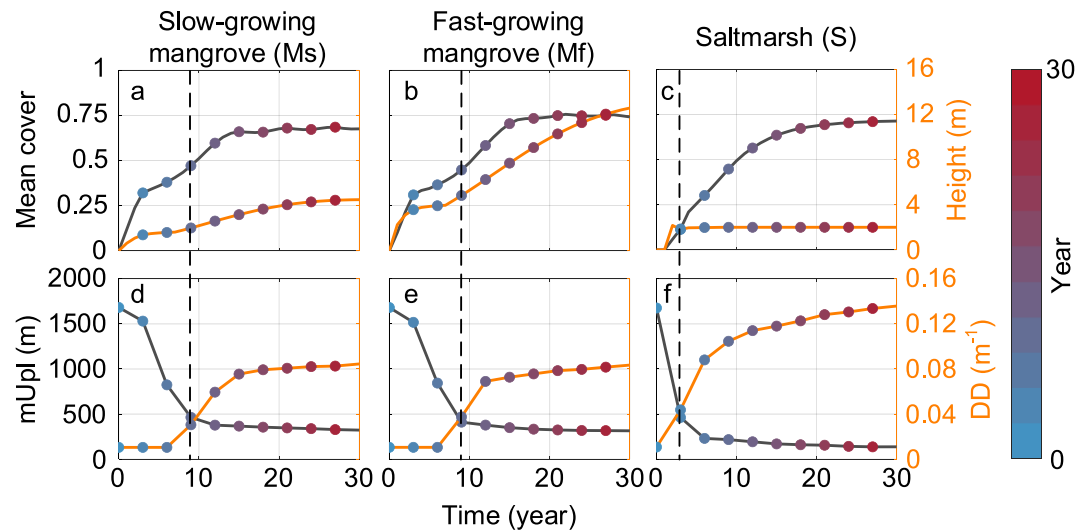
Figure 4. Development of vegetation and channels under the influence of single species over 30 years. Scenarios include: (a, d) slow-growing mangroves (Ms); (b, e) fast-growing mangrove species (Mf); (c, f) saltmarsh (S). Vegetation development is shown through the mean cover and the 90th percentile of plant height in panels (a–c). Channel development is depicted by the mean unchanneled path length (mUpl) and drainage density (DD) in panels (d–f). Vertical dashed lines indicate the time point of equivalent channel development.

varying growth rates of the two mangrove species, their shared colonization strategy creates comparable tidal channel systems (Figures 4d and 4e). Notably, it takes about 3 years for saltmarshes to develop equivalent channel networks with a mUpl of 500 m and a DD of 0.04 m^{-1} from bare mudflats, while it takes 9 years for mangroves.

Vegetation colonization in the seaward direction is significantly facilitated by eco-morphodynamic feedback (Figure 5). As vegetation develops and interacts with tidal flows, it leads to the formation of tidal channels and the redistribution of sediment within the tidal system. In the saltmarsh system, deeper tidal channels (Figure 5i) and higher platforms (Figure 5l) are observed compared to the mangrove system (Figures 5g and ;5h and 5j–5k). This platform accretion drives the progradation of tidal flats, which in turn supports vegetation seaward colonization (Figures 5a–5c).

3.2. Multiple Species Dynamics

3.2.1. Mudflat Colonization

Different mangrove species exhibit distinct responses to saltmarsh competition and herbivory (Figure 6). When Ms colonize mudflats together with S, Ms eventually occupy only 40% of the intertidal area (Figure 6a and Figure S5.3c in Supporting Information S1), whereas Mf can dominate up to 75% of the area (Figure 6b and Figure S5.3f in Supporting Information S1). Consequently, S have a larger cover in the MsS scenario compared to the MfS scenario (Figures 6a and 6b). When both competition and herbivory are present, few Ms survive on tidal flats due to high predation pressure, allowing extensive unoccupied mudflats to be dominated by S (Figure 6c and Figure S5.4c in Supporting Information S1). In contrast, Mf are less impacted by herbivory and can still dominate the tidal flats (Figure 6d and Figure S5.4f in Supporting Information S1).

To better reflect the interactions between mangroves and saltmarshes, we conducted a comparative analysis of mangrove/saltmarsh cover development relative to their single-species results. In the MsS scenario, both mangroves and saltmarshes exhibit lower cover compared to their growth alone, indicating negative interactions when they coexist (Figure 6e). Conversely, the presence of S seems to enhance the development of Mf during the first 15 years (Figure 6f), suggesting a facilitative role of S in Mf colonization. However, there is a simultaneous progressive reduction in S cover (Figure 6f), indicating significant growth suppression by coexisting Mf. When herbivory is factored in, Ms development is significantly inhibited, while S cover shows faster colonization during the first 12 years before reaching a similar level of development as in the reference case (Figure 6g).
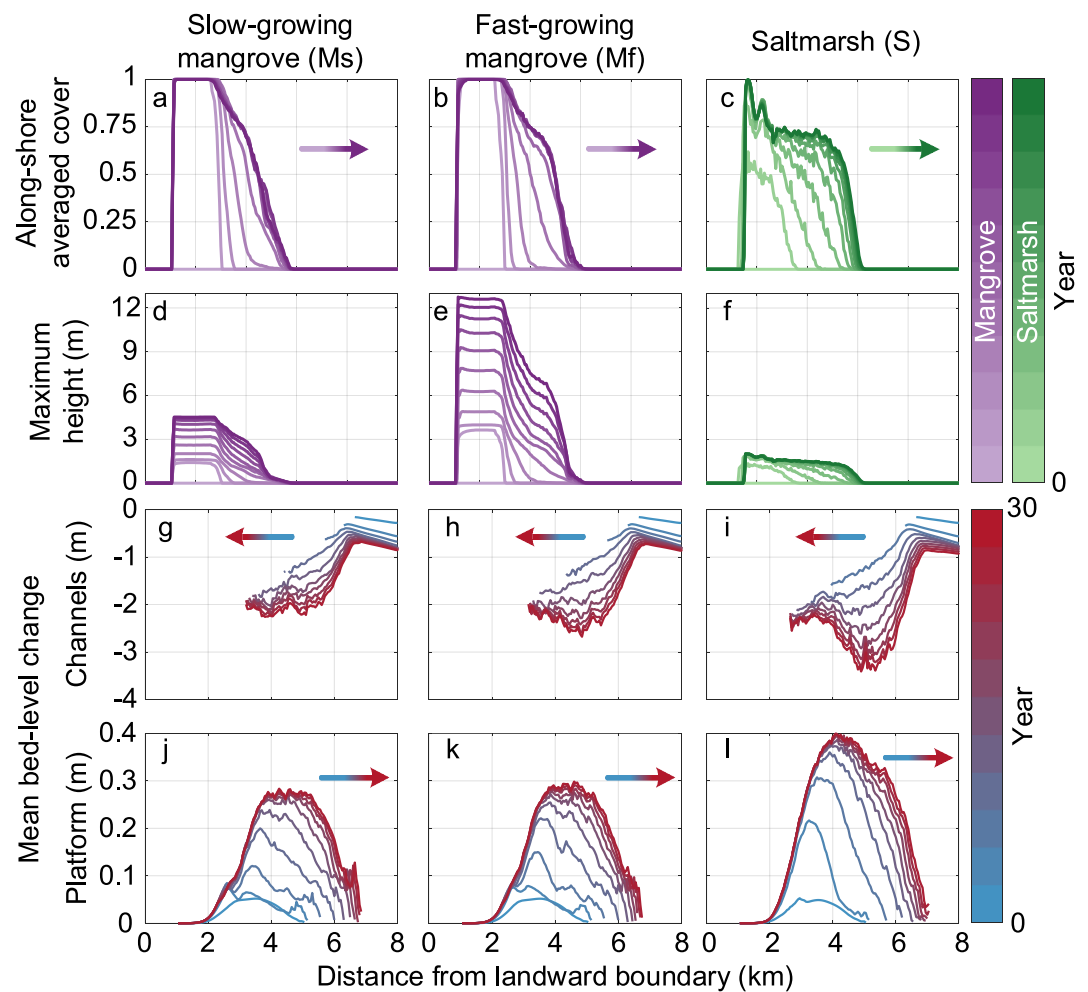
Figure 5. Spatial-temporal changes in vegetation and bed level along the cross-shore profile over 30 years. Scenarios include: (a, d, g, j) slow-growing mangroves (Ms); (b, e, h, k) fast-growing mangrove species (Mf); (c, f, i, l) saltmarsh (S). (a–c) Changes in alongshore-averaged vegetation cover on the cross-shore profile. (d–f) Stem height development, represented by the 90th percentile of the maximum height in each alongshore transect. (g–i) Alongshore-averaged bed-level change per 3 years compared to initial bathymetry in channels, and (j–l) on platforms.

Conversely, predation has limited impact on Mf and does not alter the interaction pattern between Mf and S (Figure 6h).

As single-species scenarios suggested that S creates more extensive channels, we used the S scenario as a reference to evaluate channel development in various multi-species scenarios. This comparison reveals a trend where reduced S cover correlates with fewer tidal channels. Concurrent colonization of mudflats by Ms and S results in decreased S cover (Figure 6e), leading to a higher mUpl and a smaller DD (Figures 6i and 6m). Similarly, in the MfS case, S coverage decreases further (Figure 6f), resulting in a much higher mUpl and a much smaller DD (Figures 6j and 6n). However, in the presence of herbivory and Ms, S dominate mudflats, yielding similar final mUpl and DD to the reference scenario (Figures 6k and 6o). Conversely, less tidal channels are once again observed in the mangrove-dominant system (Figures 6l and 6p).

After colonization, Ms and S establish a relatively stable distribution (Figure 7a). In contrast, Mf tend to outcompete S, compressing S habitats in the middle intertidal zone (Figure 7b). When competition and herbivory combine, Ms are confined to the upper intertidal zone near their optimum elevation, with S dominating most of the mudflats (Figure 7c). Conversely, predation does not significantly affect the interaction between Mf and S (Figure 7d).
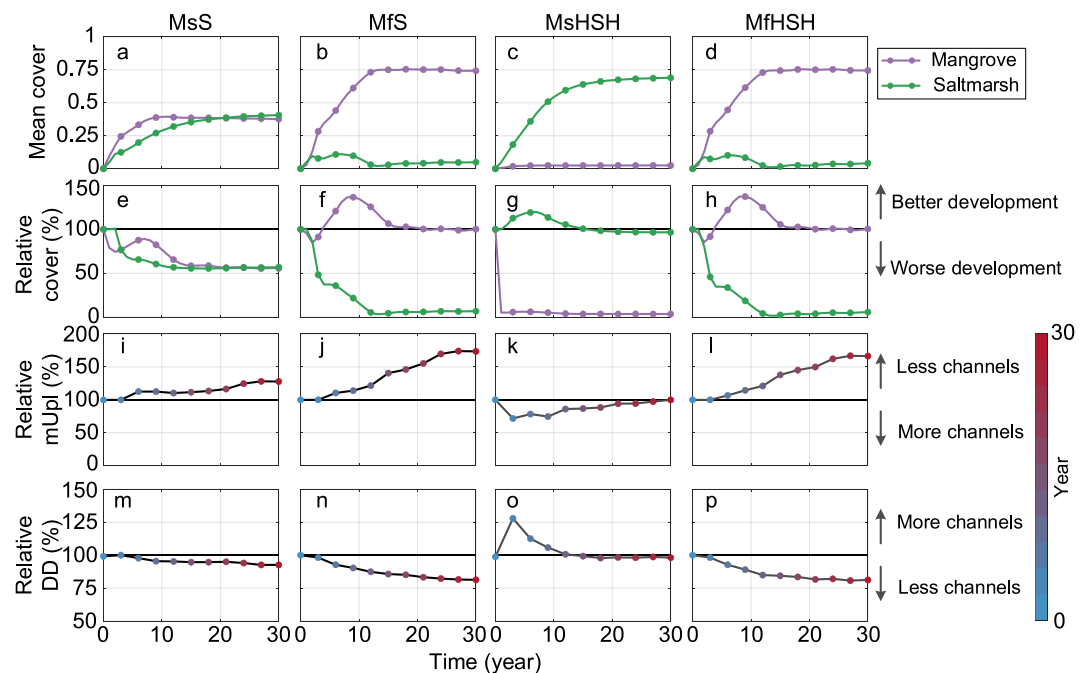
Figure 6. Vegetation and channelization development over 30 years, with results shown at 3-year intervals. Scenarios include: (a, e, i, m) slow-growing mangroves and saltmarshes (MsS); (b, f, j, n) fast-growing mangroves and saltmarshes (MfS); (c, g, k, o) slow-growing mangroves and saltmarshes with herbivory (MsHSH); (d, h, l, p) fast-growing mangroves and saltmarshes with herbivory (MfHSH). Panels (a–d) show changes in mean vegetation cover, (e–h) relative vegetation cover compared to their single-species scenario, and (i–p) relative mean unchanneled path length (mUpl) and drainage density (DD) compared to the saltmarsh scenario (S).

Regarding morphological changes, saltmarsh-dominated systems exhibit deeper tidal channels compared to mangrove-dominated systems, while the platform remains comparable. Over 30 years, bed-level changes show deeper channels forming in systems with higher S cover (Figure 7k). Conversely, systems with lower S cover and shorter S height develop shallower tidal channels (Figures 7j and 7l). However, platform accretion remains similar across different systems (Figures 7m–7p).

3.2.2. Species Invasion

When saltmarshes invade well-developed mangrove ecosystems, mangrove cover remains relatively unchanged, while the extent of saltmarsh colonization depends on the availability of bare mudflats. Notably, ecosystems dominated by Ms offer wider bare mudflats due to their lower inundation tolerance and higher susceptibility to predation (Figures 8a and 8c, Figures S5.5c, and S5.6c in Supporting Information S1). In contrast, Mf exhibit greater resistance to inundation and predation, allowing them to dominate wider mudflats and limiting space for saltmarsh colonization (Figures 8b and 8d, Figures S5.5f, and S5.6f in Supporting Information S1). All scenarios depict further development of tidal channels following saltmarsh invasion, with systems featuring higher salt-marsh cover post-invasion developing more extensive tidal channels (Figures 8e and 8g).

In scenarios where Ms invade existing saltmarsh ecosystems, they are unable to replace saltmarshes, and the dominant species remains the same, despite the presence or absence of herbivory (Figures 8i and 8k, Figures S5.7c, and S5.8c in Supporting Information S1). Conversely, Mf can replace saltmarshes, shifting a saltmarsh-dominant system to a mangrove-dominant system within 9 years (Figures 8j and 8l, Figures S5.7f, and S5.8f in Supporting Information S1). Subsequent to this displacement, the tidal channel is less developed compared to the reference case without mangrove invasion (Figures 8n and 8p).

Saltmarsh encroachment triggers a marginal landward retreat of Ms but has minimal influence on Mf, regardless of the presence of herbivory effects (Figures 9a–9d). Saltmarshes tend to colonize bare mudflats in front of mangrove stands and struggle to grow within well-established mangrove systems. Following saltmarsh invasion,
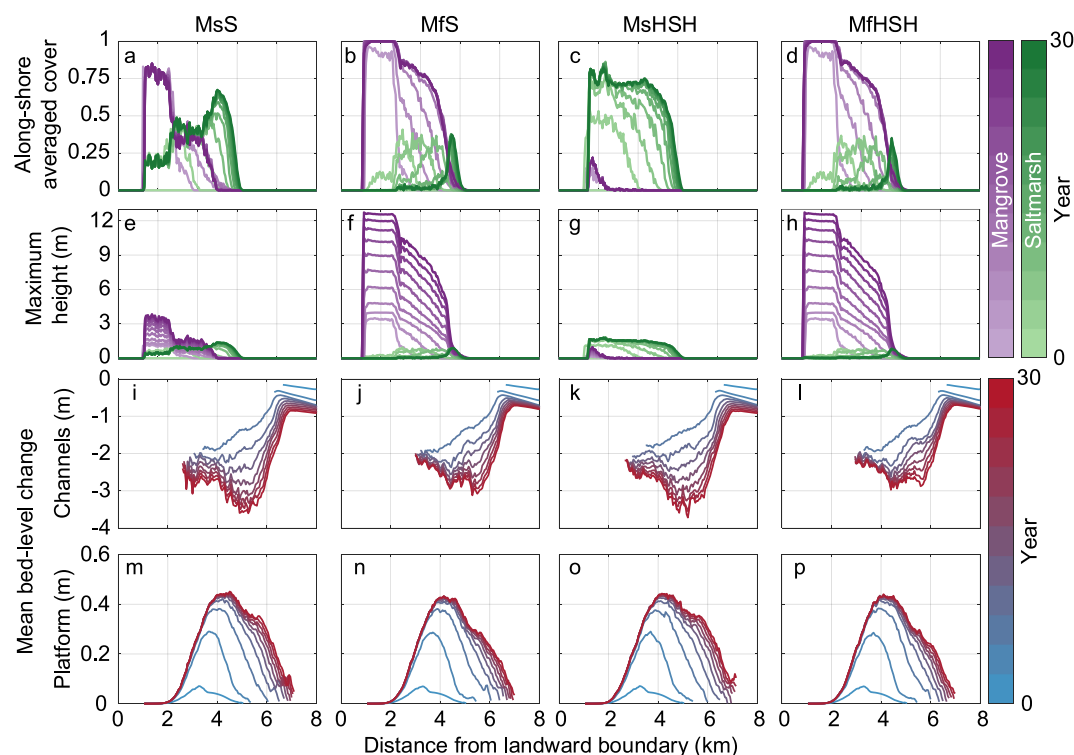
Figure 7. Spatial-temporal changes in vegetation and bed level along the cross-shore profile over 30 years. Scenarios include: (a, e, i, m) slow-growing mangroves and saltmarshes (MsS); (b, f, j, n) fast-growing mangroves and saltmarshes (MfS); (c, g, k, o) slow-growing mangroves and saltmarshes with herbivory (MsHSH); (d, h, l, p) fast-growing mangroves and saltmarshes with herbivory (MfHSH). Panels (a–d) show changes in alongshore-averaged vegetation cover along the cross-shore profile, (e–h) stem height development, estimated by the 90th percentile of the maximum height in each alongshore transect. (i–l) Alongshore averaged bed-level change per 3 years compared to initial bathymetry in channels, and (m–p) on platforms. Line colors refer to dots in Figure 6.

tidal channels deepen, with channel depth seemingly linked to saltmarsh cover (Figures 9e–9h). Channel erosion prompts sediment redistribution, where greater erosion correlates with higher platform deposition (Figures 9i–9l).

When Ms invade existing saltmarsh systems, saltmarsh cover remains largely unaffected in both the presence and absence of herbivore predation (Figures 9m and 9o). Conversely, Mf swiftly replace saltmarshes, transforming the ecosystem into a mangrove-dominated system, evidenced by a rise in mangrove cover and a corresponding decline in saltmarsh cover (Figures 9n and 9p). This shift toward a mangrove-dominated system results in reduced channel erosion and platform accretion compared to unaltered saltmarsh-dominated systems (Figures 9r–9x).

4. Discussion

The growth of mangroves and saltmarshes simulated with our novel eco-morphodynamic model aligns well with field experiments under both single-species and multiple-species conditions (Figure 3). Our numerical scenarios indicate that the rate of vertical vegetation growth is a key determinant of competition outcomes and dominance within ecotones, at least under current model parameterizations representing the Zhangjiang study site. What is more, biotic interactions such as facilitation, competition, and predation lead to distinct mangrove-saltmarsh dynamics across various developmental stages. Importantly, these ecotone dynamics result in different eco-morphodynamic feedback, leading to distinct changes in landform configuration. Consequently, in this section, we discuss the interactions between single-species development and morphological evolution (Section 4.1), how species interactions and growth properties influence ecotone dynamics and the corresponding eco-morphodynamic feedback during mudflat colonization (Section 4.2), species invasion (Section 4.3), and additional relevant factors influencing ecotone morphodynamics (Section 4.4).
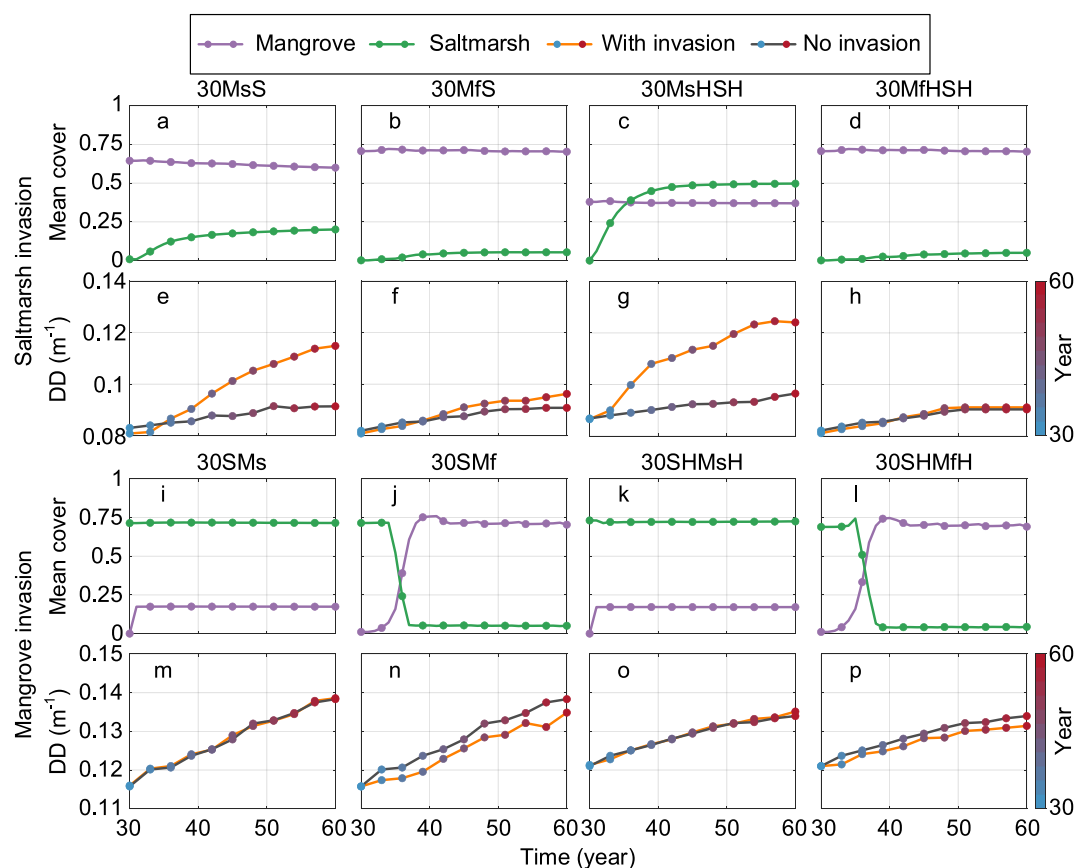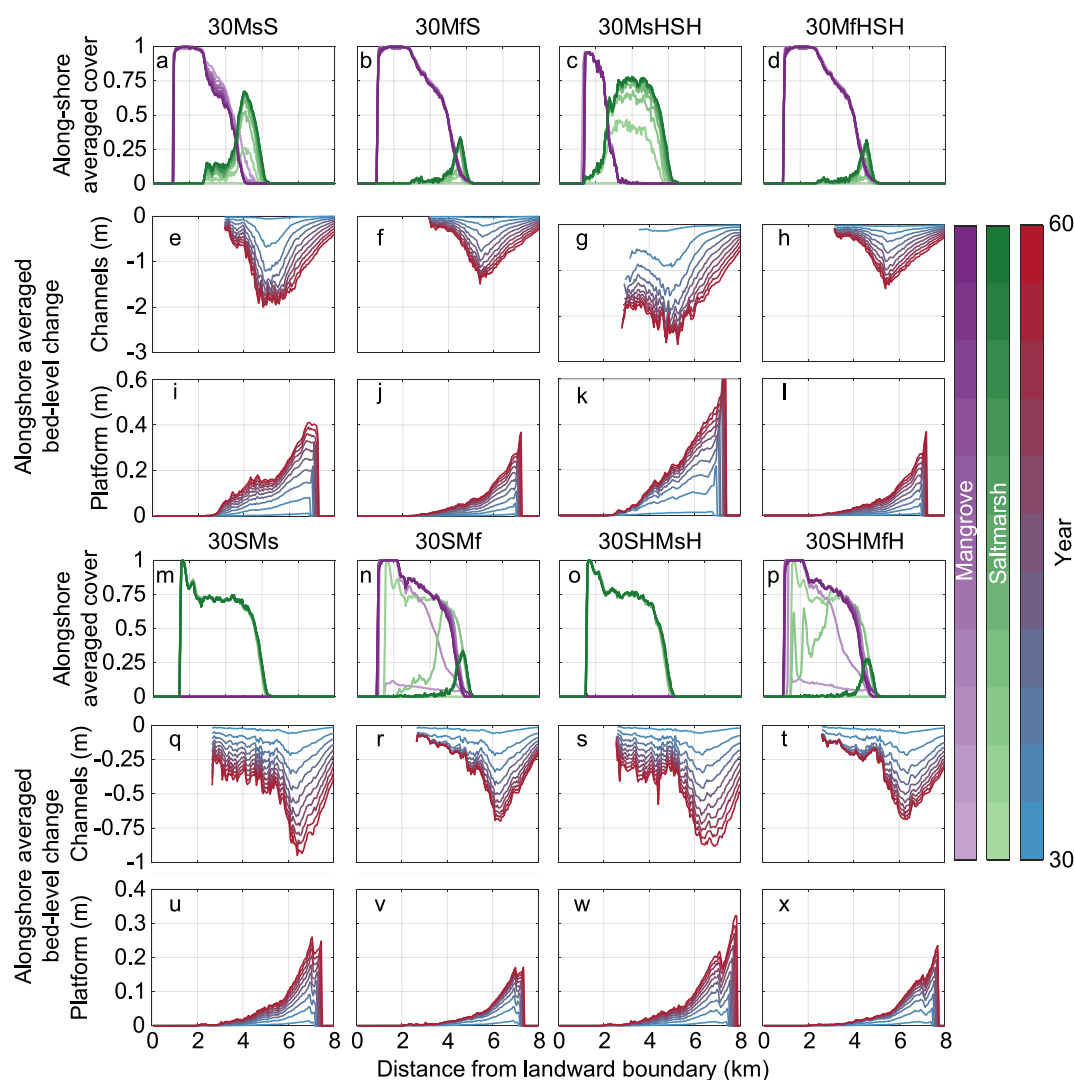
Figure 8. Vegetation and channel development following saltmarsh (a–h) or mangrove (i–p) colonization over 30 years. Scenarios include: (a, e) 30-year slow-growing mangroves and saltmarshes (30MsS); (b, f) 30-year fast-growing mangroves and saltmarshes (30MfS); (c, g) 30-year slow-growing mangroves and saltmarshes with herbivory (30MsHSH); (d, h) 30-year fast-growing mangroves and saltmarshes with herbivory (MfHSH). Panels (i–p) show the corresponding scenarios for mangrove colonization. (a–d) Changes in mean vegetation cover after saltmarsh colonization. (e–h) Comparison of drainage density (DD) development with and without saltmarsh colonization. (i–l) Changes in mean vegetation cover after mangrove colonization. (m–p) Comparison of DD development with and without mangrove colonization.

4.1. Eco-Morphodynamic Feedback From Mudflat Colonization by Single Species

This study aims to unravel how a change in dominant wetland species affects ecotone morphology, as such, understanding the landscape configuration resulting from eco-morphodynamic feedback of single mangrove/saltmarsh species becomes a prerequisite. Consistent with previous findings (Schwarz et al., 2022), our model predicts that saltmarshes, which colonize mudflats in a patchy manner and at a slower rate compared to mangroves, create more extensive channel networks (Figures 4d–4f). More specifically, the saltmarsh system exhibits a mean unchanneled path length (mUpl) of about 100 m (Figure 4f), whereas in mangrove systems, it can reach up to 300 m (Figures 4d and 4e). These channelization metrics align well with previous observations (Figure S6 in Supporting Information S1) (Schwarz et al., 2022).

Both mangroves and saltmarshes can attenuate tidal currents, allowing particles to settle in the vegetated zones and promoting platform progradation (Rodríguez et al., 2017; Temmerman et al., 2022). Additionally, peak sedimentation tends to occur at the seaward vegetation edge (Figures 5j–5l) (Adame et al., 2010; French & Spencer, 1993; Rogers et al., 2014). However, the different colonization strategies of mangroves and saltmarshes lead to distinct eco-morphodynamic feedback. Initially, fast-colonizing mangroves form a homogeneous cover limiting channel incision (Figures 5g and 5h, Figures S5.1a, and S5.1d in Supporting Information S1), potentially reducing sediment deposition in the upper intertidal zone (Figures 5j and 5k and Figure S7a in Supporting Information S1) (Swales et al., 2019; Xie et al., 2023). In contrast, saltmarshes establish in a patchy configuration that creates tidal channels earlier (Figure 4f) and facilitates sediment redistribution into the upper intertidal zone

Figure 9. Spatial-temporal changes in vegetation and bed level along the cross-shore profile following saltmarsh or mangrove colonization over 30 years. Scenarios include: (a, e, i) 30-year slow-growing mangroves and saltmarshes (30MsS); (b, f, j) 30-year fast-growing mangroves and saltmarshes (30MfS); (c, g, k) 30-year slow-growing mangroves and saltmarshes with herbivory (30MsHSH); (d, h, l) 30-year fast-growing mangroves and saltmarshes with herbivory (MfHSH). Panels (m–x) show the corresponding scenarios for mangrove colonization. (a–d) Changes in alongshore-averaged vegetation cover after saltmarsh colonization. (e–h) Alongshore averaged bed-level changes per 3 years compared to the bathymetry at year 30 in channels, and (i–l) on platforms. (m–p) Changes in alongshore-averaged vegetation cover after mangrove colonization. (q–t) Alongshore averaged bed-level change per 3 years compared to the bathymetry at year 30 in channels, and (u–x) on platforms.

(Figure 5l and Figure S7d in Supporting Information S1) (Allen, 2000; Boechat Albernaz et al., 2023; Temmerman et al., 2005). This implies that while mangroves and saltmarshes interact with tidal forcing in similar ways to promote sedimentation, their different colonization strategies exert distinct impacts on channel development and sediment dynamics.

4.2. Eco-Morphodynamic Feedback From Mudflat Colonization by Multiple Species

At the intertidal wetland scale, there is increasing recognition that biotic interactions play a crucial role in determining ecotone dynamics (Cui, DeAngelis, et al., 2024; Guo et al., 2013; McKee & Rooth, 2008; Stevens et al., 2006). Our findings suggest that these interactions evolve over time and vary among species. More specifically, facilitation may occur during early development stages, as indicated by a better development of mangroves or saltmarshes compared to single-species scenarios (Figures 6f–6h, years 3–10). This facilitation

arises from eco-morphodynamic feedback between coexisting vegetation and hydro-morphological changes. Pioneer saltmarshes, for example, attenuate tidal forces within vegetated areas, reducing bed shear stress on marsh platforms and promoting platform accretion and progradation (Figure S8.1 in Supporting Information S1). This creates favorable conditions for seaward mangrove colonization by enhancing their inundation-based fitness (Figure S8.2 in Supporting Information S1). Such facilitative interactions have been observed in field studies (Friess et al., 2012; Lewis, 2005; McKee et al., 2007) but, to the knowledge of the authors, are rarely incorporated into model predictions.

Despite initial facilitation, the dominant vegetation type is often determined by subsequent competition (Clarke & Myerscough, 1993; Howard et al., 2015), as predicted by our model. Our results show that competition outcomes are largely determined by the relative growth rates of mangroves and saltmarshes. Slow-growing mangroves (Ms) tend to share the mudflat with saltmarshes (S) (Figures 6a and 7a), while fast-growing mangroves (Mf) can dominate the vegetation cover within a decade (Figures 6b and 7b). This aligns with field observations in southeastern China, where native mangrove species (e.g., *K. obovata*) with slower growth rates (~0.35 m/yr) could not outcompete the rapidly growing *S. alterniflora* (Figure S9 in Supporting Information S1) (L. Chen et al., 2013; Peng et al., 2018; Zhang et al., 2012). In contrast, fast-growing species like *S. apetala*, with a vertical growth rate of about 1.1 m/yr, comparable to *S. alterniflora*, can outcompete and replace saltmarshes after introduction (H. Chen et al., 2014; Zhou et al., 2015). Similar outcomes have been observed in North American ecotones where mangrove species like *Avicennia germinans* frequently coexist with *S. alterniflora*, exhibiting similar vertical growth rates (~0.4 m/yr) (Yando et al., 2019). Over time, these mangroves grow taller and overshadow saltmarshes, leading to saltmarsh replacement—a phenomenon documented worldwide in recent decades (Cavanaugh et al., 2014; Osland et al., 2013; Saintilan et al., 2014). Thus, our simulations highlight that vertical growth rates are crucial in determining competition outcomes and species dominance within ecotones, aligning with existing ecological understanding (Biswas et al., 2018; Pyšek & Richardson, 2007).

Herbivory is another biotic interaction that can regulate the dominance between mangroves and saltmarshes. While mangrove-saltmarsh ecosystems globally hosts a variety of herbivores, the consumer pressure varies greatly between species and location (He & Silliman, 2016; Van der Stocken et al., 2019). In our model as well as field observations in the Zhangjiang Estuary, rodents (*R. losea*) significantly limit the colonization of *K. obovata* (Figure S5.2c in Supporting Information S1) but have less impact on *S. apetala* and *S. alterniflora* (Figures S5.2f and S5.2i in Supporting Information S1) (Peng et al., 2022; Zhang et al., 2018). As such, *S. alterniflora* can dominate in competition with *K. obovata* (Figure 7c), whereas *S. apetala* maintains its dominance despite predation (Figure 7d). This species-specific herbivory affects coastal geomorphology through eco-morphodynamic feedback. Herbivores cause plant mortality, potentially reducing platform accretion and increasing wetland edge retreat (Figure S5.2c in Supporting Information S1) (Hughes et al., 2024; Xu et al., 2023). As such, this top-down control by herbivores fundamentally shapes vegetation dominance within ecotones, adding complexity to ecotone dynamics and landform evolution.

Changes in vegetation distribution are known to control mudflat evolution through eco-morphodynamic feedback (Schwarz et al., 2018; Temmerman et al., 2007; van Maanen et al., 2015). Depending on biotic interactions, mangrove-saltmarsh ecotones tend to form either mangrove-dominant or saltmarsh-dominant systems. Our multi-species scenarios demonstrate that saltmarsh-dominant systems develop more channels than mangrove-dominant ones (Figure S6 in Supporting Information S1), as saltmarsh colonization in patches promotes earlier and deeper channel formation. These extensive channels enhance sediment redistribution, which may increase wetland resilience in sediment-poor environments by providing additional sediment for vegetation trapping (D'Alpaos & Marani, 2016; Van de Vijsel et al., 2023). Although platform accretion remains similar across different systems (Figures 7m–7p), saltmarsh-dominant systems exhibit a higher tendency to ebb-dominance, leading to greater sediment export (Figure S10 in Supporting Information S1) (Fagherazzi et al., 2013; Zhou et al., 2018). Thus, the dominant wetland species significantly impacts channel development, sediment dynamics, and potentially impacts long-term wetland resilience.

4.3. Eco-Morphodynamic Feedback From Species Invasion

While mangrove-saltmarsh dynamics are ubiquitously observed along transitional zones globally, with mangroves generally outcompeting tidal marshes (Kelleway et al., 2017; Osland et al., 2022). The reasons behind these changes are often site-specific, driven by factors such as rising temperatures, barriers to seed dispersal, and
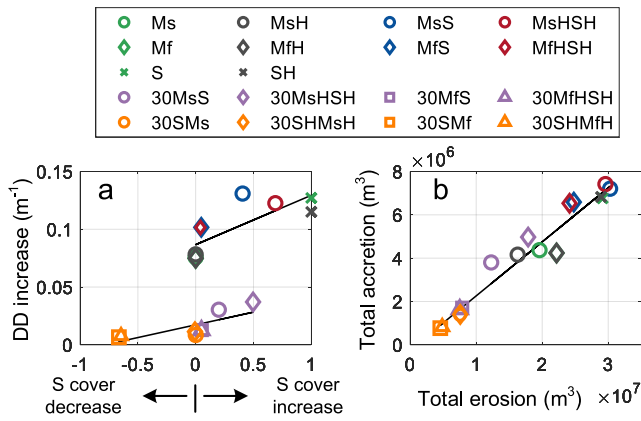
Figure 10. Changes in saltmarsh cover associated with increased drainage density (DD) compared to initial conditions (a). Comparison of total accretion and erosion volumes of different species colonizing or invading the tidal system within 30 years (b).

human activities (An et al., 2007; Osland et al., 2016; Rogers & Krauss, 2019; Van der Stocken et al., 2019). Field observations highlight that climatic conditions, such as temperature and water availability, play a crucial role in shaping mangrove-saltmarsh zonation and driving competition outcomes, often favoring mangroves over tidal marshes (Cavanaugh et al., 2019; Saintilan & Williams, 1999). However, our findings indicate that the outcomes and extent of these changes are also species-specific. When saltmarsh seedlings encroach upon mature mangrove ecosystems, they typically struggle to establish within dense mangrove forests. Instead, they often colonize seaward mudflats where mangrove development is limited (Figure 9a–9d, Figures S5.5, and S5.6 in Supporting Information S1). Consequently, the degree of saltmarsh invasion hinges on the availability of mudflats for colonization, which in turn depends on prior mangrove development shaped by factors such as flooding and herbivory. This pattern of saltmarsh invasion has been extensively observed in the ecotones along the southeastern coast of China, where saltmarshes commonly dominate the seaward low-intertidal zones (Liu et al., 2017; Zhang et al., 2021). In such cases, future climatic or anthropogenic disturbances (e.g., freezing, sea-level rise, and land-use changes) may exacerbate mangrove dieback, potentially leading to increased saltmarsh dominance (Cavanaugh et al., 2019; Navarro et al., 2021). By contrast, the outcome of mangrove invasion varies depending on the species involved: slow-growing mangroves typically fail to displace saltmarshes (Figures 8i and 9m), while fast-growing mangroves can lead to saltmarsh replacement (Figures 8j and 9n). These distinct outcomes have also been observed in China (Biswas et al., 2018; Zhang et al., 2022) and the United States (Kelleway et al., 2017; Osland et al., 2022), respectively. Thus, our model effectively captures diverse patterns of mangrove/saltmarsh invasion observed in the field.

Climate change and human activity are driving shifts in coastal ecotones worldwide (An et al., 2007; Osland et al., 2022), but the consequences of these transformations for ecosystem structure and services remain poorly understood (IPCC, 2022). Our findings suggest that mangrove invasion may inhibit the development of channel networks (Figures 8n and 8p), while saltmarsh invasion tends to promote their development (Figures 8e–8h), a trend observed in field studies where saltmarsh invasion has caused the lengthening of tidal channels (Cui, Ke, et al., 2024). However, this saltmarsh invasion does not significantly alter the overall configuration of channel networks; instead, it primarily inherits existing channels and causes minor erosion at channel heads (Figures S5.5 and S5.6 in Supporting Information S1), which may be difficult to discern in satellite images (Figure S9 in Supporting Information S1).

A clear correlation is identified in this study between changes in saltmarsh coverage and the degree of channelization (Figure 10a). Tidal wetlands with higher saltmarsh cover are expected to experience greater drainage density, potentially enhancing ecosystem resilience to disturbances as water, sediment, and nutrient fluxes are transported primarily through these channels (Kearney & Fagherazzi, 2016; Kirwan & Megonigal, 2013). Our model results suggest that higher saltmarsh cover leads to a more pronounced eco-morphodynamic feedback, resulting in increased channel erosion and platform deposition (Figure 10b). This greater sediment redistribution potentially enables more sediment to reach the upper vegetated areas, bolstering their resilience against projected increases in sea-level rise (Mariotti, 2018). Furthermore, our modeling results indicate that sediment deposition on platforms is considerably less than erosion in tidal channels (Figure 10b), suggesting that the strong eco-geomorphic feedback induced by saltmarshes may also lead to more sediment export (Figure S10b in Supporting Information S1). Understanding these distinct effects is crucial for predicting and managing the evolution of ecotones in response to environmental changes.

4.4. Model Limitations and Perspectives

This study presents a comprehensive eco-morphodynamic model to investigate how a change in dominant wetland species affects ecotone morphology. While the vegetation parameters and species interactions in our model are referenced to Zhangjiang Estuary, the model framework and conceptualization are developed from well-established and widely recognized modeling practices. This makes the model adaptable for application in other mangrove-saltmarsh ecotones by adjusting the vegetation parameters specific to the target study site (Text

S11 in Supporting Information S1). More importantly, the competitive outcomes modeled in our study align with field observations and established ecological principles derived not only from our specific study site but also from other terrestrial and freshwater wetland systems (Biswas et al., 2018; Pyšek & Richardson, 2007), making the insights gained likely to be widely applicable. In this study, the field data adopted only covers 18-month of vegetation dynamics within a mangrove-saltmarsh ecotone, and future field data collection should focus on longer-term observations across various sites. This will help to improve the reliability and accuracy of eco-morphodynamic model simulations, while at the same time providing deeper insights into the complex processes driving mangrove-saltmarsh ecotone shifts.

However, this study limits the consideration of more complex hydro-sedimentary conditions that may obscure certain eco-morphodynamic mechanisms. For instance, astronomic tides with varying tidal ranges and components cause water-level fluctuations, which can determine vegetation habitat range and growth properties (Balke et al., 2016; Kumbier et al., 2021), while also affecting sediment resuspension and transport in channels and on vegetated platforms (Mariotti & Zapp, 2022). Additionally, water availability can be a key factor limiting mangrove distribution in the intertidal zone (Osland et al., 2014). Climatic phenomena such as the El Niño Southern Oscillation significantly influence mangrove expansion or retreat. Increased rainfall may promote mangrove transgression by diluting salts in upper intertidal marsh soils, while droughts create hypersaline conditions that depress mangrove vigor and hinder their encroachment (Eslami-Andargoli et al., 2009; Saintilan & Williams, 1999). Moreover, wind waves have been documented to control plant settlement and colonization (Balke et al., 2011; Hu et al., 2015; Leonardi et al., 2016), thereby impacting associated eco-morphodynamic feedback (Xie et al., 2022). Additionally, ongoing sea-level rise and reduced sediment supply directly alter flooding conditions and local topography, consequently influencing accommodation space for plant colonization and growth (Kirwan & Megonigal, 2013; Krauss et al., 2011; Rogers et al., 2005). Incorporating some of these factors may enhance the accuracy of predicting mangrove-saltmarsh ecotones under natural conditions, but it is beyond the scope of our study and will also complicate the interpretation of complex bio-physical interactions.

While this study primarily focuses on channel development and sediment redistribution driven by ecotone dynamics in a low sedimentary environment, it is essential to recognize that organic matter and subsurface processes, which have not been considered, may also impact morphological changes (Cahoon et al., 2021; Rogers et al., 2014). The senescence of plant roots and leaf litter, combined with allochthonous organic matter imported by tidal currents, can be important contributors to accretion in both mangrove and saltmarsh wetlands (McKee, 2011; Morris et al., 2016; Xie et al., 2023). However, high vertical accretion does not mean a net increase in the surface elevation, as sub-surface processes such as compaction and subsidence can offset elevation accretion (Cahoon et al., 2021; Rogers et al., 2005). Therefore, future studies should integrate some of these complex processes to better understand the effects of ecotone dynamics on landscape evolution (Xie et al., 2022). This is also needed to advance our understanding of the vulnerability of these sensitive ecosystems to both natural and anthropogenic pressures, with the ultimate goal to develop sustainable management strategies (Osland et al., 2022).

5. Conclusions

Our study focuses on the role of biotic interactions in shaping mangrove-saltmarsh ecotone development, while also examining eco-morphodynamic feedback influencing landscape evolution. Specifically, we focus on how species dynamics influence channel development and sediment dynamics during both mudflat colonization and invasion phases, using a well-calibrated numerical model that integrates vegetation-induced ecoengineering effects on hydrodynamics.

A key finding is that the competitive outcomes between mangroves and saltmarshes, which determine the dominant wetland species, are significantly influenced by relative growth rates and herbivory predation. Mangrove species with vertical growth rates comparable to coexisting saltmarshes can outcompete them. Conversely, their colonization is significantly impeded by saltmarshes if their growth rates lag behind. Additionally, herbivory predation emerges as a crucial factor in seedling survival, with the potential to reverse species dominance and exert varying effects among different species.

Ecotone dynamics, shaped by diverse biotic interactions, play a pivotal role in channel development and sediment dynamics through eco-morphodynamic feedback. During mudflat colonization, tidal wetlands dominated by saltmarshes tend to develop channel networks more extensively and rapidly than those dominated by mangroves,

a consequence attributed to their initial patchy cover and slower colonization. Saltmarsh-dominant systems also foster deeper channels and facilitate more extensive sediment redistribution, resulting in higher platform development compared to mangrove systems. During invasion stages, saltmarshes struggle to compete with well-established mangrove forests and instead tend to colonize pioneer bare mudflats. Herbivores can facilitate salt-marsh colonization by restricting mangrove distribution. Wetlands with greater saltmarsh cover post-invasion facilitate channel development, while mangrove invasion can potentially displace existing saltmarshes, leading to a less developed channel network.

Overall, this study highlights that competition and herbivory are fundamental drivers of ecotone dynamics at the intertidal scale. The resulting mangrove- and saltmarsh-dominant systems exhibit distinct eco-morphodynamic feedback on mudflat evolution. Therefore, research on ecotone dynamics and associated morphodynamics should adequately consider the relative growth properties of mangroves and saltmarshes, as well as the significance of biotic interactions.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Delft3D is an open-source code available online from Deltares (2020). The mangrove model code with a representative setting can be accessed in Xie (2023). The mangrove-saltmarsh ecotone model code with a representative setting is available in https://github.com/yizhangw/Mangrove-Saltmarsh-Ecotone.git and archived at Wei (2024).

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