



Pattern formation in marsh ecosystems modeled through the interaction of marsh vegetation, mussels and sediment

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ABSTRACT

Spatial self-organization, a common feature of multi-species communities, can provide important insights into ecosystem structure and resilience. As environmental conditions gradually worsen (e.g., resource depletion, erosion intensified by storms, drought), some ecological systems collapse to an irreversible state once a tipping point is reached. Spatial patterning may be one way for them to cope with such changes. We use a mathematical model to describe self-organization of an eroding marsh shoreline based on three-way interactions between sediment volume and two ecosystem engineers – smooth cordgrass *Spartina alterniflora* and ribbed mussels *Geukensia demissa*. Our model indicates that scale-dependent interactions between multiple ecosystem engineers drive the self-organization of eroding marsh edges and regulate the spatial scale of shoreline morphology. Spatial self-organization of the marsh edge increases the system's productivity, allows it to withstand erosion, and delays degradation that otherwise would occur in the absence of strong species interactions. Further, changes in wavelength and variance of the spatial patterns give insight into marsh recession. Finally, we find that the presence of mussels in the system modulates the spatial scale of the patterns, generates patterns with shorter wavelengths, and allows the system to tolerate a greater level of erosion. Although previous studies suggest that self-organization can emerge from local interactions and can result in increased ecosystem persistence and stability in various ecosystems, our findings extend these concepts to coastal salt marshes, emphasizing the importance of the ecosystem engineers, smooth cordgrass and ribbed mussels, and demonstrating the potential value of self-organization for ecosystem management and restoration.

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1. Introduction

Tidal marshes support a diversity of wildlife, protect coastal regions from the impact of storms and erosion, improve water quality and provide many other ecosystem services (Barbier et al., 2011). Despite efforts to protect and restore marsh ecosystems (Broome et al., 1988; Van Hulzen et al., 2007; Silliman et al., 2012), marshes around the world remain vulnerable to erosion, sea level rise, and direct human impacts (Allen, 2000; Fagherazzi et al., 2013; Kirwan and Megonigal, 2013; Crosby et al., 2016; Törnqvist et al., 2021). In general, marshes are more stable along the vertical direction (the height of the marsh relative to sea level) than the horizontal direction (erosion perpendicular to the shoreline) (Kirwan et al., 2016; Ganju et al., 2017; Ladd et al., 2019). Horizontal evolution of the marsh is a dynamic process that

involves various counteracting forces such as wave erosion, vegetation growth, sediment deposition and seaward marsh expansion (Allen, 2000; Mariotti and Fagherazzi, 2010; Marani et al., 2011; Fagherazzi et al., 2013; Fagherazzi, 2013; Leonardi and Fagherazzi, 2014; Crotty et al., 2017; Crotty et al., 2020; Ladd et al., 2019). Therefore, insight into the balance between these forces is crucial for understanding and modeling the fate of marshes.

Spatial self-organization refers to a nonuniform spatial arrangement of individuals that results from interactions between individuals, and that does not depend strictly on underlying environmental heterogeneity. Positive and negative species interactions occurring at different spatial scales are deemed scale-dependent feedbacks and are essential for self-organization (Gierer and Meinhardt, 1972; Green and Sharpe, 2015; Hiscock and Megason, 2015). Pattern formation driven by such scale-dependent feedbacks has been observed in terrestrial, aquatic and marine ecosystems such as arid grasslands (Lefever and

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Lejeune, 1997; Yokozawa et al., 1999; Couteron and Lejeune, 2001; Borgogno et al., 2009; van der Heide et al., 2012; Dibner et al., 2015; Pringle and Tarnita, 2017), intertidal mussel beds (van de Koppel et al., 2005a; Liu et al., 2012; Liu et al., 2014; Sherratt, 2016) and other multi-species communities (Rietkerk and van de Koppel, 2008). Spatial self-organization is a common feature of many ecological systems and can provide insight into their resilience and adaptation to environmental change (Rietkerk et al., 2004; Dakos et al., 2011; Dakos et al., 2015; Scheffer et al., 2015) and help anticipate their proximity to a critical transition (e.g., shift to a degraded state) (Chen et al., 2015). In the case where environmental conditions gradually worsen (e.g., resource depletion, erosion intensified by storms, drought), some ecological systems may collapse to an irreversible state once a “tipping point” is reached. Spatial patterning may be one way for such systems to optimize resource distribution and cope with these disturbances (Siteur et al., 2014; de Paoli et al., 2017).

Anticipating and predicting a system's proximity to a tipping point has become of great interest in recent years. Various general indicators to anticipate critical transitions and serve as measures of ecosystem resilience have been proposed for time series and spatial data (Kéfi et al., 2007; Guttal and Jayaprakash, 2009; Dakos, 2012; Dakos and Soler-Toscano, 2017; Eby et al., 2017). For systems with scale-dependent feedbacks, the most promising indicator has been the change in the shape of the spatial patterns near a critical transition, although other indicators such as spatial variance, correlation, and skewness have been considered (Guttal and Jayaprakash, 2009; Dakos et al., 2011; Kéfi et al., 2014; Dakos and Soler-Toscano, 2017).

While previous conceptual and numerical models of salt marsh dynamics focus on the interaction between wave activity, sediment fluxes and vegetation (Mariotti and Fagherazzi, 2010; Fagherazzi et al., 2012; Leonardi et al., 2016; Bernik et al., 2018), other ecosystem engineers, such as ribbed mussels, are capable of modifying their habitat and altering the hydrodynamic forces from waves and currents (Bouma et al., 2007). Through their interactions and positive feedbacks, they have a significant impact on marsh development, persistence and proliferation (Bertness, 1984; Bertness and Grosholz, 1985; Altieri et al., 2007; Watt et al., 2010; Angelini et al., 2016; Crotty et al., 2018; Crotty et al., 2020). Given the recent focus on the importance of facilitation in ecosystem dynamics and restoration efforts (van de Koppel et al., 2001; Halpern et al., 2007; Angelini et al., 2011; Silliman et al., 2015; Kéfi et al., 2016), it is important to consider the impact ecosystem engineers may have on marsh dynamics. Therefore, we investigate self-organization on the marsh edge as a result of interactions between sedimentation and two ecosystem engineers of salt marshes—ribbed mussels *Geukensia demissa* and smooth cordgrass *Spartina alterniflora*, which exhibit strong interspecific facilitation (Bertness, 1984). As sea-level rise continues to contribute to marsh deterioration by increasing wave energy on marsh boundaries, investigating the marsh system's response to such changes in erosion intensity is critical. Since a mathematical model combining the effect of mussels and vegetation on the evolution of marsh boundaries and their resilience to erosion has not yet been considered, our goal is twofold. First, we propose a mathematical framework for modeling self-organization of an eroding marsh shoreline, based on realistic assumptions of three-way interactions between sediment volume and two ecosystem engineers (smooth cordgrass and ribbed mussels). Second, using biologically reasonable parameter values, we perform a numerical investigation of the system to address questions of marsh stability and the role that spatial organization plays in the system's adaptation to varying erosion conditions. Given the presence of multiple positive feedbacks in our system, it is especially necessary to consider these questions as such feedbacks are commonly associated with alter-

native stable states, saddle-node bifurcations and consequently critical transitions (Dakos, 2012; Kéfi et al., 2016).

2. A model of marsh edge dynamics

We model the three-way interactions between ribbed mussels, smooth cordgrass, and sediment (Fig. 1). Mussels bind the sediment and stabilize the marsh edge, while their filtering activities and pseudofeces production stimulate the growth of cordgrass through soil enrichment, and significantly contribute to the sediment budget (Smith and Frey, 1985; Ysebaert et al., 2008; Angelini et al., 2016). Cordgrass enhances the growth and reproductive success of mussels by decreasing physical stress and providing attachment substrate (Bertness and Grosholz, 1985; Bertness et al., 2015; Honig et al., 2015). Our model did not incorporate relationships between belowground (roots and rhizomes) biomass and aboveground (shoots) biomass of cordgrass (Darby and Turner, 2008) because we have no data on belowground biomass, nor did we integrate marsh age (Allen, 2000) in our model because the shoreline marsh studied in Lipcius et al. (2021) is an established marsh that has persisted for over 8 decades. Cordgrass binds sediment with its rhizomes, further stabilizing the marsh edge and attenuating wave energy, which increases resistance to erosion (Gedan et al., 2011; Ysebaert et al., 2011; Silliman et al., 2012; Möller et al., 2014). As a consequence of reduced erosion, the increased sediment levels promote vegetation growth by decreasing tidal currents (Nyman et al., 1993; van de Koppel et al., 2005b; Van Wesenbeeck et al., 2007). These interactions highlight the important role of smooth cordgrass and ribbed mussels as ecosystem engineers, the positive feedbacks of which can be valuable in preventing degradation and loss of resilience (Bertness et al., 2015; Silliman et al., 2015; Angelini et al., 2016).

Along with these local interactions, cordgrass and mussels exhibit some scale-dependent (nonlocal) interactions that can change from positive to negative, depending on the spatial scale. Mussels tend to self-organize into dense aggregations as this configuration leads to greater survivorship due to protection from harsh winters, physical disturbances and predation (Bertness and Grosholz, 1985; van de Koppel et al., 2008; Liu et al., 2012). This interaction constitutes short-range activation. However, as mussel aggregations become large, intra-specific competition for resources intensifies, causing the aggregations to break up into smaller clusters, which constitutes long-range inhibition (Bertness, 1980; Bertness and Grosholz, 1985; van de Koppel et al., 2008; Liu et al., 2012; Liu et al., 2014). Cordgrass also displays scale-dependent effects as cordgrass enhances sediment accretion through attenuation of hydrodynamic energy at short distances, while forming erosion troughs farther away (Balke et al., 2012; Bouma, 2013; Bouma et al., 2007; Fivash et al., 2021; Schwarz et al., 2015; Van Wesenbeeck et al., 2008). In this case, the nearby accumulation of sediment constitutes short range activation, whereas erosion of adjacent patches reflects long-range inhibition. These scale-dependent interactions are important as their presence may lead to self-organization. In Lipcius et al. (2021), the authors provide empirical evidence that specific combinations of smooth cordgrass *Spartina alterniflora* shoot density and ribbed mussel *Geukensia demissa* density are associated with distinct spatial patterns along the shoreline of salt marshes.

To simplify our model, we consider the changes in cordgrass shoot density G (shoots m^{-2}), mussel density M (mussels m^{-2}) and the height of the sediment layer S (m) in a one-dimensional slice parallel to the marsh edge (Fig. 2A). Erosion and sedimentation dynamics change throughout the marsh as one moves landward. As erosion tends to be most severe at the edge of the marsh, this one-dimensional approach serves to provide intuition

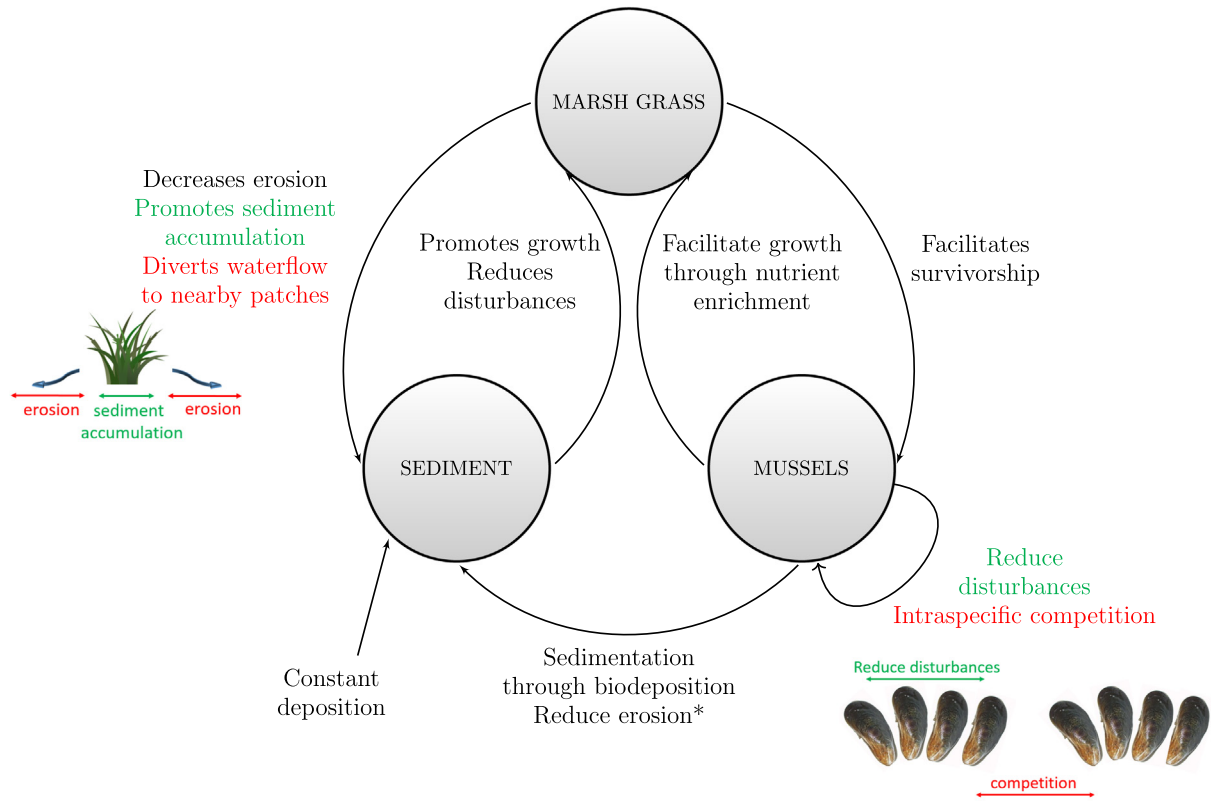


Fig. 1. Diagram of interactions between mussels, sediment, and marsh grass adapted from Bertness (1984). Photo credit: United States Geological Survey (2010). Non-local interactions are indicated in color, with green corresponding to short-range activation and red to long-range inhibition. The effect of mussels on reducing erosion is marked with an asterisk because while significant, it does not change the dynamics qualitatively and is modeled indirectly through grass for simplification.

and heuristic understanding of the species interactions and the pattern forming mechanism on the edge without introducing more complicated formulations. We include the interactions discussed above and propose the following set of reaction-diffusion equations:

$$\begin{cases} \partial_t G = D_G \partial_x^2 G + \underbrace{G(F(M, S) - cG)}_{\text{Logistic growth}}, \\ \partial_t M = D_M \partial_x^2 M + \underbrace{M(H(G) - aM)}_{\text{Logistic growth}} + \underbrace{\alpha M \int_{-\infty}^{\infty} N(x') M(x - x') dx'}_{\text{Scale-dependent mussel interactions}}, \\ \partial_t S = D_S \partial_x^2 S + \underbrace{dM + \eta - SL(G)}_{\text{Deposition Erosion}} + \underbrace{\lambda S \int_{-\infty}^{\infty} P(x') G(x - x') dx'}_{\text{Grass-dependent net deposition/erosion}}, \end{cases} \quad (1)$$

where

$$F(M, S) = \frac{p_1(M)(S - l_1)}{S + l_1^*}, \quad H(G) = \frac{r(G - l_2)}{G + l_2^*}, \quad L(G) = \frac{\psi(G + k_s g)}{G + k_s},$$

and

$$p_1(M) = \frac{pM + \omega_1}{M + \omega_2}.$$

Although the cordgrass rhizome structure stabilizes the marsh edge, we use shoot density as a measure of cordgrass vegetation abundance since shoot density is proportional to the root and rhizome structure (Darby and Turner, 2008; Mudd et al., 2009; Kirwan and Guntenspergen, 2015). Each equation includes a diffusion term with diffusion coefficients (D_G, D_M, D_S) to quantify spread

along the shoreline. The cordgrass diffusion coefficient D_G accounts for the spread of the rhizomes, while the diffusion coefficient for mussels D_M is close to zero, as ribbed mussels do not move much after settlement (Bertness, 1984). For both cordgrass and mussel equations, we use logistic-type growth terms with additional threshold parameters l_1, l_2 accounting for the obligatory nature of cordgrass-sediment and mussel-cordgrass interactions. The parameter l_1 specifies the minimum amount of sediment needed to allow the growth of cordgrass, while l_2 specifies the minimal cordgrass density needed for mussel persistence. We model the erosion of sediment as a decreasing function of cordgrass density with $g > 1$. The erosion rate is highest in the total absence of cordgrass (Mariotti and Fagherazzi, 2010; Silliman et al., 2012) and lowest at maximum grass abundance. The efficiency of mussels' filtering activity is controlled by parameter d , while the parameter η gives a constant baseline sediment deposition rate (van de Koppel et al., 2005a; Liu et al., 2012; Liu et al., 2014). Given the cooperative nature of this system and the number of positive interactions, the mussels' impact on reducing erosion is modeled indirectly through grass dynamics. While this is an important positive interaction, it does not change the dynamics qualitatively. This is consistent with previous literature which highlights the importance of having both positive and negative interactions occurring at different spatial scales as a necessary pattern forming mechanism in many ecological systems (Rietkerk and van de Koppel, 2008). Further, in both the mussel and sediment equations, we include a term accounting for the corresponding scale-dependent feedbacks. To model the mussel-mussel and cordgrass-sediment scale-dependent interactions, we use a Mexican hat influence kernel function (Fig. 2B) (Fuentes et al., 2003; D'Odorico et al., 2006; Borgogno et al., 2009; Siebert and Schöll, 2015) that quantifies both the strength and scale of the positive and negative feedbacks between neigh-

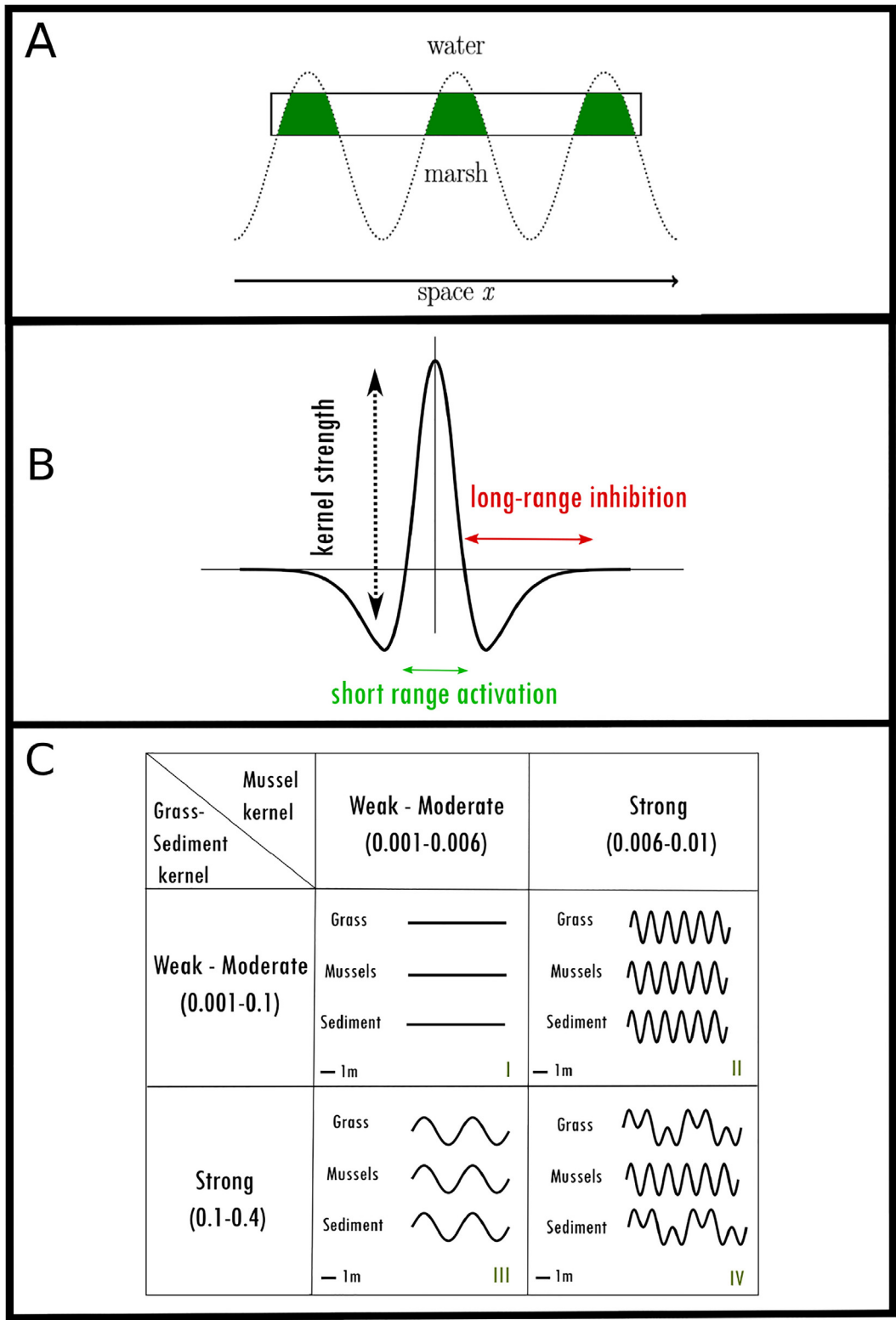


Fig. 2. (A) The cross-section of marsh edge used to model the marsh dynamics. (B) Diagram of Mexican hat kernel and scale-dependent feedback adapted from [Rietkerk and van de Koppel \(2008\)](#). (C) Schematic of types of patterns for various relative strengths of the scale-dependent interactions.

boring individuals. This approach has been previously used to model nonlocal interactions in vegetation in arid climates (D’Odorico et al., 2006; Borgogno et al., 2009; Merchant and Nagata, 2011) where it was limited to a single species case. We define the interaction kernels $N(x)$ and $P(x)$ as follows:

$$\begin{aligned} N(x) &= \frac{1}{\sqrt{2\pi}} \left[\frac{1}{\sigma_{11}} \exp\left(-\frac{x^2}{2\sigma_{11}^2}\right) - \frac{1}{\sigma_{12}} \exp\left(-\frac{x^2}{2\sigma_{12}^2}\right) \right], \\ P(x) &= \frac{1}{\sqrt{2\pi}} \left[\frac{1}{\sigma_{21}} \exp\left(-\frac{x^2}{2\sigma_{21}^2}\right) - \frac{1}{\sigma_{22}} \exp\left(-\frac{x^2}{2\sigma_{22}^2}\right) \right], \end{aligned} \tag{2}$$

with

$$\sigma_{11} < \sigma_{12}, \sigma_{21} < \sigma_{22}.$$

Both Mexican hat kernels $N(x)$ and $P(x)$ are functions of two normalized Gaussians, incorporating nonlocal excitatory and inhibitory interactions with variances $\sigma_{11}^2, \sigma_{21}^2$ and $\sigma_{12}^2, \sigma_{22}^2$ respectively. The parameters α, λ control the strength (or amplitude) of the mussel-mussel and cordgrass-sediment interactions. In this way, for our simulations, we can control both the width and the strength of the scale-dependent interactions to explore the system behavior. The functions $P(x)$ and $N(x)$ are symmetric and satisfy:

$$\int_{-\infty}^{\infty} P(x)dx = 0, \int_{-\infty}^{\infty} N(x)dx = 0.$$

For simulation, we consider $x \in (-\infty, \infty)$, looking for spatially periodic solutions of the system of Eqs. (1) (refer to Appendices A and B for details of parameter values and numerical methods). We investigate both the three-way (cordgrass-mussel-sediment) as well as the two-way (cordgrass-sediment) interactions to understand the self-organization taking place on the marsh edge.

3. Results

3.1. Cordgrass-mussel-sediment dynamics

We first investigate the full system based on the three-way interactions between cordgrass, mussels and sediment in the system of Eqs. (1). Biologically realistic parameters are used where possible to numerically simulate and study this system (see Table 1 and Appendix A for parameter values and details). While the scale of cordgrass-sediment scale-dependent interactions is generally longer than that of mussel scale-dependent interactions, the exact spatial scales (corresponding to the widths of the Mexican hat ker-

nels) and relative strengths of these interactions (corresponding to the amplitudes of the Mexican hat kernels given by α and λ , respectively) are difficult to estimate and can vary substantially. Harsh environmental conditions may impact the degree of aggregation by mussels (de Jager et al., 2017) while the nature and strength of the cordgrass-sediment scale-dependent interactions depend on the underlying hydrodynamics, sediment composition, patch size and interpatch distance (Vandenbruwaene et al., 2011; Balke et al., 2012; Bouma et al., 2013; Schwarz et al., 2015). For this reason, we choose from a range of values of the kernel strengths α and λ to investigate the system's dynamics in four different parameter regimes. The results of these simulations are presented in Figs. 2C and 3.

We observe four general types of model dynamics depending on the relative strengths of the scale-dependent interactions. Type I corresponds to a case where the scale-dependent interactions for both mussels and cordgrass-sediment are in the relative weak-to-moderate range (Figs. 2C and 3) and do not contribute significantly to the erosion of the shoreline, resulting in a flat, uniform marsh edge. This is expected as scale-dependent feedbacks are necessary for self-organization. Type II is characterized by relatively strong scale-dependent mussel interactions, and weak-to-moderate scale-dependent interactions between cordgrass and sedimentation (Figs. 2C, 3B). Given the stronger nature of mussel interactions, the spatial scale of their interactions related to the width of the mussel kernel drives the characteristic length scale of the emerging patterns and results in more narrow undulations. Type III is characterized by relatively strong scale-dependent interactions between cordgrass and sedimentation and weak-to-moderate mussel scale-dependent interactions (Figs. 2C, 3C). Here, the spatial scale of the protrusions on the marsh edge is driven by the cordgrass-sediment interactions and is more consistent with

Table 1
Parameters used for simulations.

Symbol	Meaning	Unit	Value	Source
D_G	cordgrass diffusion coefficient	$m^2 \text{ yr}^{-1}$	0.06–0.135	Adams et al. (2012)
D_M	mussel diffusion coefficient	$m^2 \text{ yr}^{-1}$	0.0	Liu et al. (2014)
D_S	sediment diffusion coefficient	$m^2 \text{ yr}^{-1}$	0.876	Liu et al. (2014)
c	self-limiting growth rate of cordgrass	$m^2 \text{ shoots}^{-1} \text{ yr}^{-1}$	0.0057	Yang et al. (2014)
a	self-limiting growth rate of mussels	$m^2 \text{ mussels}^{-1} \text{ yr}^{-1}$	0.0002	Bertness and Grosholz (1985) and Mykoniatis and Ready (2012)
ψ	minimum erosion rate	yr^{-1}	0.002–0.3	Rosen (1980) and Hardaway and Byrne (1999)
k_s	cordgrass density at which marsh erosion is half-maximal	shoots m^{-2}	30–50	Mariotti and Fagherazzi (2010)
g	erosion constant in the absence of cordgrass	non-dimensional	5	Mariotti and Fagherazzi (2010) and Sheehan and Ellison (2015)
η	sediment deposition rate	$m \text{ yr}^{-1}$	0.002–0.006	Stumpf (1983) and Goodman et al. (2007)
d	sediment deposition rate of mussels	$m^3 \text{ mussels}^{-1} \text{ yr}^{-1}$	0.00002	Bertness (1984) and Galimany et al. (2013)
p	intrinsic growth rate of cordgrass	yr^{-1}	2	Yang et al. (2014)
r	intrinsic growth rate of mussels	yr^{-1}	0.2–0.4	Mykoniatis and Ready (2012)
ω_1	controls the rate of increase of intrinsic cordgrass growth	mussels	1050	Bertness (1984) and Bertness et al. (2015)
ω_2	number of mussels at which cordgrass growth is half-maximal	mussels m^{-2}	700	Bertness (1984) and Bertness et al. (2015)
l_1	sediment threshold for cordgrass persistence	m	0.02	estimated
l_1'	sediment elevation at which cordgrass growth is half-maximal	m	0.06	estimated
l_2	cordgrass density threshold for mussel persistence	shoots m^{-2}	5	estimated
l_2'	cordgrass density at which mussel growth is half-maximal	shoots m^{-2}	50	estimated
α	strength of nonlocal mussel interactions	$m^2 \text{ mussel}^{-1} \text{ yr}^{-1}$	0.0002–0.0008	estimated
λ	strength of nonlocal cordgrass-sediment interactions	$m^2 \text{ shoots}^{-1} \text{ yr}^{-1}$	0.0004–0.3	Bouma et al. (2007)
σ_{11}	standard deviation of the excitatory feedback for mussels	m	0.25	van de Koppel et al. (2008)
σ_{12}	standard deviation of the inhibitory feedback for mussels	m	0.4	van de Koppel et al. (2008)
σ_{21}	standard deviation of the excitatory feedback for cordgrass	m	0.43	Bouma et al. (2007)
σ_{22}	standard deviation of the inhibitory feedback for cordgrass	m	0.68	Bouma et al. (2007)

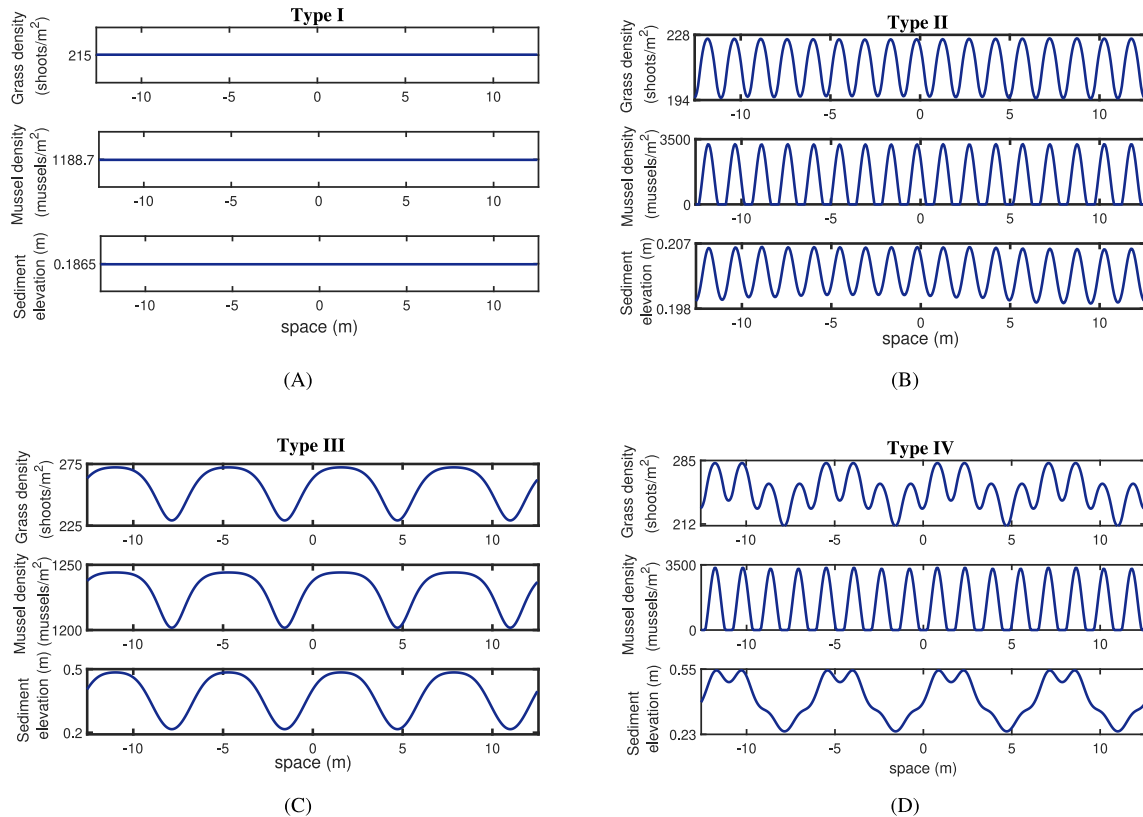


Fig. 3. Simulations for different strengths of mussel and cordgrass-sediment scale-dependent interactions α and λ , respectively corresponding to Type I (A), II (B), III (C) and IV (D) behaviors. The following values were used for simulation: Type I - $\alpha = 0.0002$, $\lambda = 0.01$, Type II - $\alpha = 0.00068$, $\lambda = 0.01$, Type III - $\alpha = 0.0002$, $\lambda = 0.2$, Type IV - $\alpha = 0.00068$, $\lambda = 0.2$. Other parameter values used in simulations: $D_G = 0.06$, $D_M = 0.0000001$, $D_S = 0.9$, $p = 2$, $l_1 = 0.02$, $l_1^* = 0.06$, $\omega_1 = 1050$, $\omega_2 = 700$, $c = 0.0057$, $l_2 = 5$, $l_2^* = 50$, $a = 0.0002$, $d = 0.00003$, $r = 0.3$, $\eta = 0.006$, $g = 5$, $k_s = 30$; $\phi = 0.15$, $\sigma_{11} = 0.25$, $\sigma_{12} = 0.4$, $\sigma_{21} = 0.43$, $\sigma_{22} = 0.68$. All simulations were run on a domain of size 7π or approximately 22 m.

the spatial scale of the cordgrass-sediment kernel. Type IV is characterized by relatively strong scale-dependent interactions for both mussels and cordgrass-sediment (Figs. 2C, 3D). As expected, the patterning of the marsh edge occurs on two spatial scales, driven by both the mussel and cordgrass-sediment kernels.

Next, for each of the four types, we explore the system's tolerance to erosion by investigating how much erosion the system is able to withstand before degrading (Fig. 4A). Here, degradation is characterized as marsh recession with little sediment remaining and no vegetation or mussels. To investigate this, we track the average equilibrium densities for cordgrass and mussels as well as sediment elevation as functions of the erosion rate ψ . In addition, spatial variance and wavelength (defined as the distance from peak to peak) of the spatial patterns are plotted as a function of erosion rate ψ in Fig. 4B to understand how the spatial characteristics of the patterns change as erosion worsens and the system approaches degradation (Dakos et al., 2011; Dakos, 2012; Kéfi et al., 2014; Dakos and Soler-Toscano, 2017).

We find that the system is able to cope with harsher erosion in patterned configurations (Type II, Type III, Type IV) than otherwise would be possible with a uniform shoreline (Type I). As Type I patterns are characterized by having weak scale-dependent feedbacks, it is not surprising that the dynamics of the system under this regime are consistent with those in the nonspatial ODE model. Cordgrass and mussels persist at erosion rates up to 0.34 yr^{-1} , 0.68 yr^{-1} , 0.68 yr^{-1} for type II, III and IV patterned regimes but fail to persist at erosion rates greater than 0.32 yr^{-1} for the type I uniform shoreline (Fig. 4A). While equilibrium densities decline with erosion rate in all cases, the decline is more gradual for the patterned regimes than in the uniform case. In addition, the equilibrium densities are higher in the patterned regimes than in the

uniform state, suggesting that the system is more productive and is able to sustain higher densities through self-organization. We also note that Type III patterns don't emerge until sufficient erosion is present in the system.

While the Type II regime does not display changes in the shape of the patterns for varying erosion rates, both Type III and IV regimes exhibit this phenomenon. We find that both Type III and Type IV regimes display overall decreases in pattern wavelength and increases in spatial variance as erosion is varied and the system moves towards degradation (Fig. 4B). In the Type II regime, the variance decreases as the system moves towards degradation. This is expected given that the spatial organization of the mussels does not change and the variance naturally decreases as the system degrades. Further, the Type III regime is the only one of the three patterned regimes that does not display spatial patterning for extremely weak erosion rates. This is explained by the fact that mussel interactions in the other two regimes (Type II and Type IV) are strong enough to contribute to spatial patterning even in the absence of significant erosional forces. In the Type III regime, the cordgrass-sediment scale-dependent interactions, which are responsible for the generation of spatial patterns, do not have significant impact for extremely low erosion rates and result in a uniform marsh edge with spatial patterns emerging for low-moderate erosion rates.

3.2. Cordgrass-sediment dynamics

While mussels and *Spartina alterniflora* often co-occur, it is not always the case as some marsh areas may not have mussels. Therefore, we investigate the nature of self-organization in the absence of mussels and consider the effect of erosion on the self-

organization on the marsh edge. Taking $M = 0$, the mussel-free subsystem becomes:

$$\begin{cases} \partial_t G = D_G \partial_x^2 G + G(F(S) - cG), \\ \partial_t S = D_S \partial_x^2 S + \eta - SL(G) + \lambda S \int_{-\infty}^{\infty} P(x') G(x - x') dx', \end{cases} \quad (3)$$

where $F(S)$ and $L(G)$ are defined as before. Given that the cordgrass-sediment feedback is the only scale-dependent feedback in this system, we find that as in the full system, the strength of this interaction dictates whether or not spatial patterning arises. The system displays Type I behavior in the absence of significant scale-dependent feedbacks and Type III behavior in the presence of significant scale-dependent interactions (same values of λ are chosen as

in the full system). We again investigate the spatial structure of the marsh edge under different erosion conditions by varying erosion rate ψ and calculating spatial variance and wavelength as the system approaches degradation, which is characterized by very little sediment and no grass. The results of the simulations are presented in Fig. 5 and are similar to the Type III behavior in the full system. Starting from a spatially uniform steady state, i.e., a flat shore line, a spatially heterogeneous shoreline develops as erosion becomes stronger. Eventually, erosion is too strong and the marsh collapses to a degraded unvegetated state consisting of low sediment elevations. As erosion increases, wavelength decreases while spatial variance increases before the system collapses. Again, the

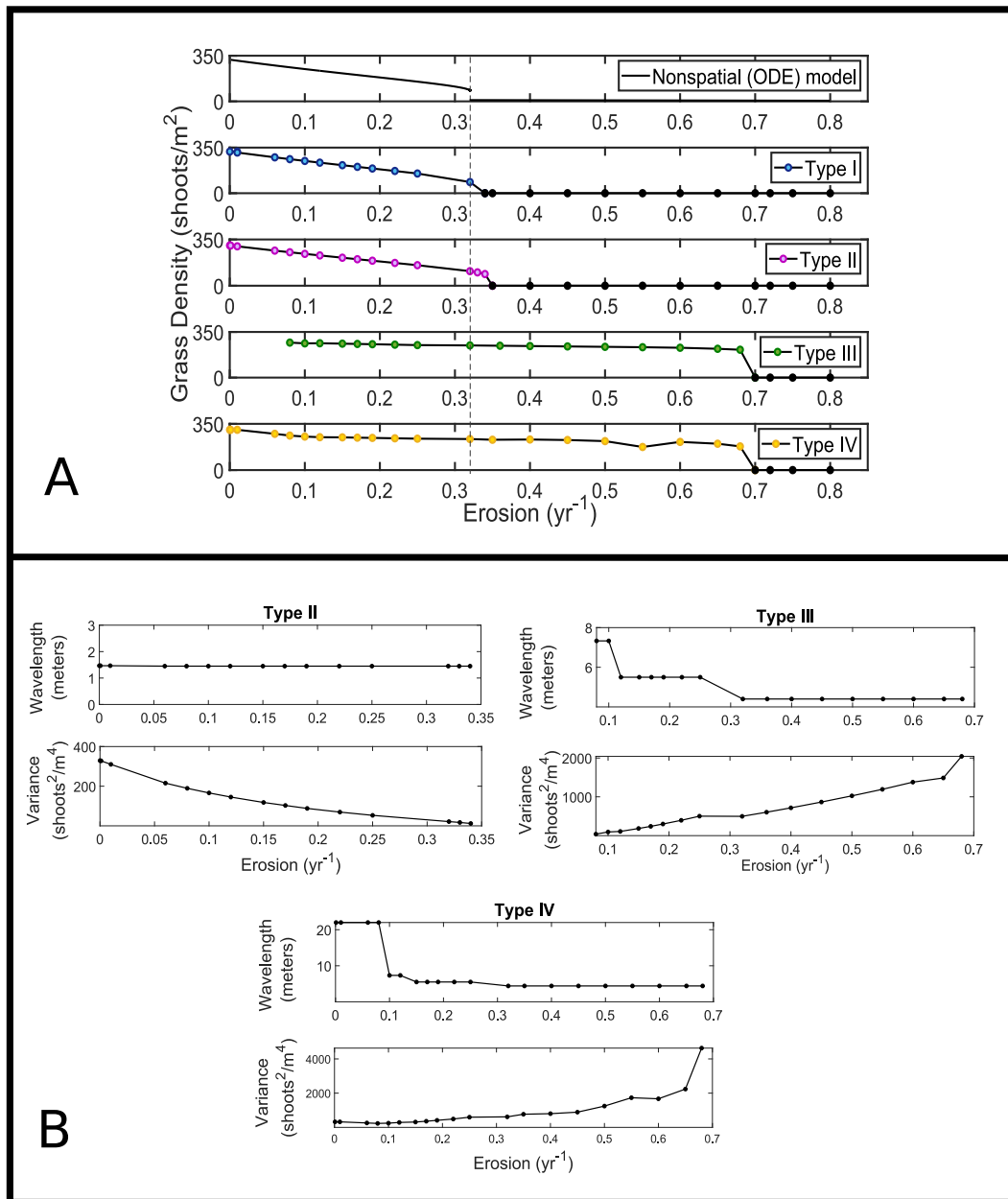


Fig. 4. (A) Average equilibrium cordgrass density from numerical simulations versus erosion rate ψ . While the plots only show cordgrass density, the behavior is the same for mussel density and sediment elevation. The first color point for each type corresponds to the erosion value at which patterns emerge. The final color point in each plot corresponds to the last erosion rate at which the system persists before degradation (shown in black). Dashed line corresponds to the erosion rate at which the system collapses in the uniform shoreline case. The behavior of the nonspatial (ODE) model is consistent with Type I regime. The system is able to persist for higher erosion rates in all three of the patterned states (Type II, III and IV). The average density is also higher in patterned states compared to uniform state. Parameters are the same as in Fig. 3. (B) Wavelength and variance of spatial patterns for Types II-IV regimes before onset of degradation.

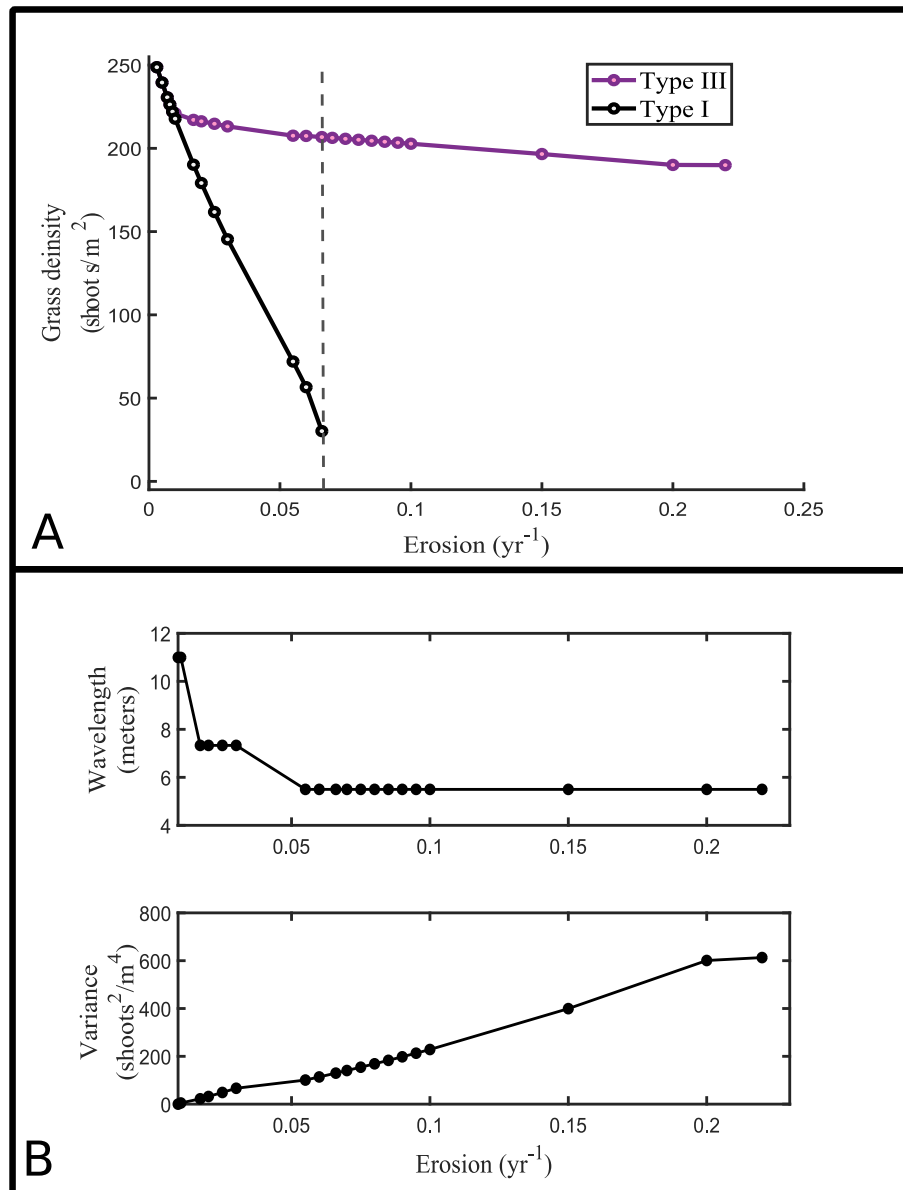


Fig. 5. (A) Average equilibrium cordgrass density versus erosion rate ψ for system 3 for Type I and III patterns. As in the full system 1, Type I corresponds to weak scale-dependent grass-sediment interactions with $\lambda = 0.01$ resulting in a uniform shoreline. Type III corresponds to moderate-strong scale-dependent grass-sediment interactions with $\lambda = 0.2$ resulting in spatial patterns. The first point for each type corresponds to the erosion value at which patterns emerge. The final point in each plot corresponds to the last erosion rate at which the system persists before degradation. The system is able to tolerate harsher erosion in a patterned Type III state than in a homogeneous Type I state which collapses shortly after the value marked by dashed line ($\psi = 0.066$). All simulations are performed on the domain of length 7π with $dx = 0.04\pi$, $dt = 0.2$. Parameters used for all simulations: $D_C = 0.06$, $D_S = 0.9$, $p = 2$, $l_1 = 0.02$, $l'_1 = 0.06$, $\omega_1 = 1050$, $\omega_2 = 700$, $c = 0.0057$, $\eta = 0.006$, $g = 5$, $k_s = 30$; $\psi = 0.15$, $\sigma_{21} = 0.43$, $\sigma_{22} = 0.68$. (B) Wavelength and variance of the spatial patterns are plotted as a function of ψ . As erosion increases, wavelength of the patterns decreases while variance increases.

system is able to tolerate harsher erosion in a patterned state than otherwise would be possible in the spatially uniform state.

When we compare Type III patterns in the full and the mussel-free system, we observe that the spatial patterns in the full system are characterized by shorter wavelengths than those in the subsystem. This indicates that the presence of mussels modulates the spatial scale of the spatial patterns, allowing for more narrow peaks to form than is possible in the absence of mussels. Further, given the positive feedback that mussels have on the marsh grass, it is not surprising that not only is the grass density lower in the absence of mussels but the system is not capable of tolerating the same level of erosion as it can when mussels are present. A more in-depth investigation into the cordgrass-sediment dynamics

and rigorous mathematical analysis can be found in Zaytseva et al. (2020).

4. Discussion

Ecogeomorphic models of marshes have focused primarily on plant-sediment interactions (van de Koppel et al., 2005b; Fagherazzi et al., 2012; Balke et al., 2012), despite evidence that ecosystem engineer species influence the productivity, trophic interactions and stability of the system (Jones et al., 1997; Altieri et al., 2007; Watt et al., 2010; Crotty et al., 2018; Crotty et al., 2020). Prior investigations of the interactions between two such

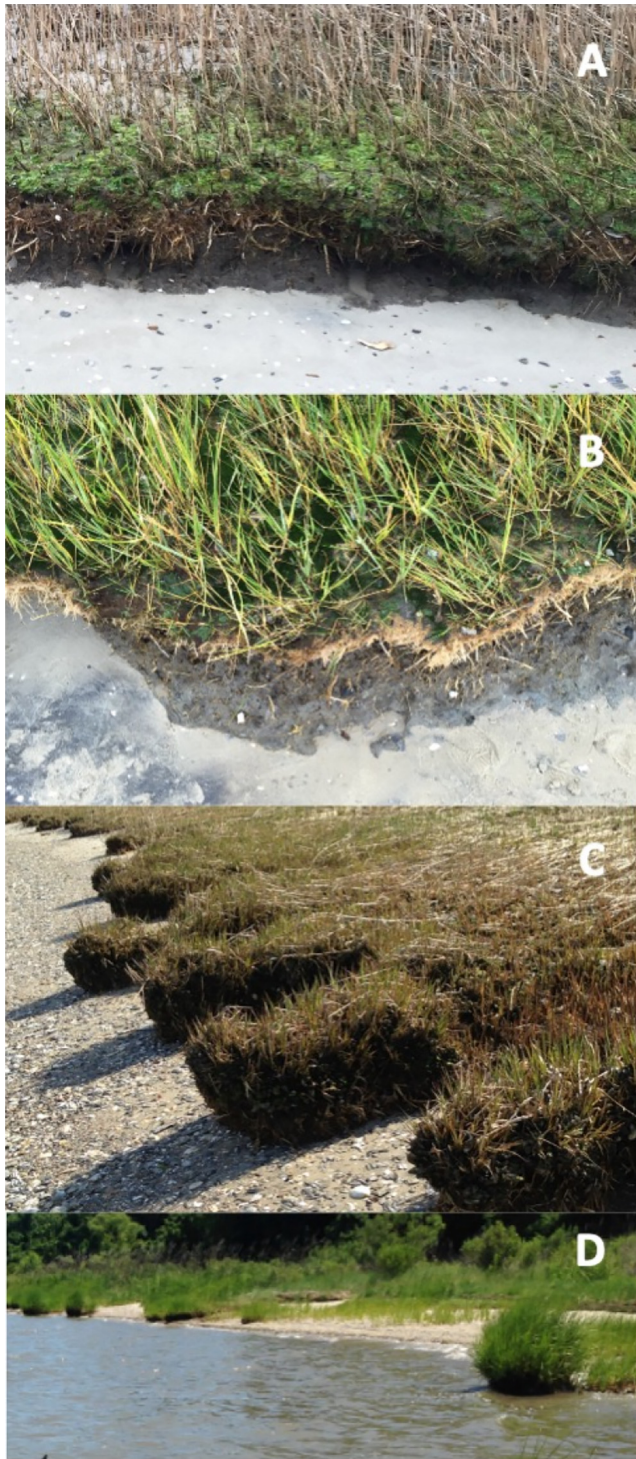


Fig. 6. (A) An example of a flat, uniform shoreline reminiscent of Type I behavior. (B) Wide “round” protrusions on the marsh edge. (C) Narrow “finger-like” protrusions on the marsh edge. (D) Landscape of the marsh, which appears to be a dynamic marsh (Reed et al., 2018), with finger-like protrusions on the far left, young grass growing on accumulated sediment in the center, and a remnant, disconnected portion of an eroded finger-like protrusion on the right with young grass growing behind it. All photos were taken at the same location (south shore of the York River, Virginia USA) where marsh types were quantified as to cordgrass and mussel density (Lipcius et al., 2021). The finger-like protrusions can be observed in Google Earth (earth.google.com/web/) at Latitude 37.255647°, Longitude −76.540809° at an eye altitude of 150 m. The other marsh types occur along the same shoreline from Latitude 37.257078°, Longitude −76.541776° to Latitude 37.255330°, Longitude −76.540749°. Photo credits: Romuald Lipcius.

ecosystem engineers, smooth cordgrass *Spartina alterniflora* and ribbed mussels *Geukensia demissa*, have focused on inter-specific facilitation in the field without consideration of spatial pattern formation (Bertness, 1984; Bertness et al., 2015; Angelini et al., 2016). Here we provide a mathematical framework of their interactions, which has not been proposed for any interacting ecosystem engineers, to our knowledge. Furthermore, the mathematical framework includes realistic scale-dependent positive and negative feedbacks between these two ecosystem engineers to investigate the resulting spatial pattern formation.

Despite the relatively simple dynamics of our one-dimensional model, it was able to capture the self-organization on the marsh edge as a result of scale-dependent feedbacks between vegetation, mussels and sediment accumulation. The model displays four general types of behavior dictated by the relative strengths of the scale-dependent mussel-mussel and cordgrass-sediment interactions. The resulting self-organization our model captures is similar to marsh configurations observed in nature (Lipcius et al., 2021), which range from a uniform shoreline as in Type I patterns (Fig. 6A) to patterns at varying spatial scales, with wide undulations as in Type III patterns (Fig. 6B) and narrow undulations as in Type II patterns (Fig. 6C). We note that the mixed mode Type IV patterns have not been characterized previously and further investigation is needed to determine if such undulations occur in nature. Portions of the shoreline investigated by Lipcius et al. (2021) are characterized by dynamic changes where cliffs develop at the seaward edge of the marsh, with sediment from collapsed blocks of consolidated marsh being retained in the upper bare flats, providing a foundation for vegetation colonization and renewed progradation. This has been previously described as a dynamic shoreline (Reed et al., 2018), which exhibits changes in the position and form of the seaward marsh margin over time (i.e., cycling between erosion and progradation). While our model cannot capture the progression of the patterns over time, it is able to capture the variety of undulations that have been observed in the field. The agreement between the model simulations and field observations (Lipcius et al., 2021) suggests that important pattern-generating processes have been captured in the model and non-local interactions between plants, mussels, and sediment can drive the formation of shoreline patterns. The model thus provides further evidence that the presence of scale-dependent interactions is essential for self-organization (Type II, Type III and Type IV). Although other models predict heterogeneous shoreline patterns in environments with plant trait diversity (Bernik et al., 2018) and limited wave power (Leonardi and Fagherazzi, 2014), our model results predict that shoreline heterogeneity cannot occur under weak or non-existent scale-dependent interactions (Type I). Further, the model was able to predict the formation of more regular spatial patterns with characteristic length scales, versus the jagged, rough marsh boundaries modeled previously (Leonardi and Fagherazzi, 2014). A key finding is that self-organization allows the system to delay degradation and withstand higher erosion rates than otherwise would be possible in the spatially uniform state. In addition, the system appears to be more productive and is able to sustain greater densities through self-organization. This is consistent with the recent findings in Rietkerk et al. (2021), which indicate that self-organization may be a way to evade tipping points in real ecosystems and is analogous to observations of mussel-marsh interactions that facilitate marsh function (Crotty et al., 2018) and survival during droughts (Angelini et al., 2016). Moreover, we find that the relative strengths of the mussel and cordgrass-sediment interactions drive the features of pattern formation. When the cordgrass-sediment feedback is strong and the mussel feedback is weaker, the resulting marsh

undulations are wide. In contrast, when the mussel feedback is strong and the cordgrass-sediment feedback is weaker, marsh undulations are much narrower. In addition, the presence of mussels allows for higher grass densities as well as the ability for the system to tolerate a greater level of erosion. Both types of undulations, as well as the linear shorelines, are reflected in field observations of marsh-mussel interactions (Lipcius et al., 2021).

As the model is meant to be phenomenological in nature, we omitted factors such as the effect and variation of hydrodynamics and wave action, more rigorously modeled previously (Fagherazzi et al., 2012). As a result, a number of refinements should be considered in the future. One limitation of our model is the lack of multiple spatial dimensions as only the dynamics on a one-dimensional cross-section of the marsh edge were considered. Hence, we were not able to observe the full geometry of the protrusions. The choice of a 2D Mexican-hat kernel for the mussel scale-dependent feedback is a natural extension and should be considered in the future. For grass-sediment interactions, most of the scale-dependent feedback still takes place in the lateral direction at the boundary of the marsh edge and the water, as erosion is strongest at the adjacent sites. Therefore, to extend the model to two dimensions, not only do we need to consider the shape of the grass-sediment kernel more carefully but we would also need high resolution data on the flow dynamics to accurately parameterize a 2D kernel. The current lack of flow data has made it difficult to capture the differences in scale-dependent feedback strengths due to the variation in flow conditions. As a result, the model only captures shorter-scale processes (on the scale of 10s of meters) and doesn't account for the presence of different types of patterns in the same area. A future refinement of the model should account for a larger scale redirection of water flow as well as flow-dependent differences in scale-dependent feedback strengths. Further, the model in its current form is not able to produce irregular patterns, which can also be observed in nature. A refinement of the model to allow for such patterns should be considered in the future. Finally, model calibration poses an additional challenge and a more thorough parameter fitting is needed in the future as more data become available.

Ecologists and geomorphologists have long sought to explain complex processes and rates through simple observations of pattern (Dietrich and Perron, 2006). For eroding marsh edges, undulating shorelines are generally associated with slow erosion rates (Leonardi and Fagherazzi, 2015; Leonardi et al., 2016), high soil shear strength relative to wave power (Leonardi and Fagherazzi, 2014) and increasing heterogeneity and organization of plant traits that influence shear strength (Bernik et al., 2018). Although it may be difficult to deduce exact erosion conditions from the nature of spatial patterns, our model can offer some insights. First, we find that spatial variation of marsh shorelines tends to emerge for low to medium erosion rates, whereas the marsh erodes uniformly for extremely low or severe erosion rates, consistent with previous findings (Leonardi and Fagherazzi, 2014). In addition, under low-moderate erosion rates, the model suggests that the spatial patterns become more sinusoidal with increasing wave action and erosion rates. This result is consistent with field observations indicating a significant positive correlation between small-scale marsh boundary sinuosity and erosion rate (Priestas et al., 2015), and modeling results that link erosion rates and shoreline roughness with increasing heterogeneity and organization of plant traits that influence soil shear strengths (Bernik et al., 2018). Finally, as erosion increases in our model, the wavelength of the spatial patterns of Type III and IV decreases, resulting in a transition from more wide "round" patterns to more narrow, finger-like patterns. This change in the wavelength as well as variance of the spatial patterns from wide to more narrow patterns at moderate to high erosion may provide useful insight into how the system can adapt to harsh

environmental conditions and its potential path towards degradation (Kéfi et al., 2014; Siteur et al., 2014).

While mussels are commonly found in tidal marsh communities, we previously found that self-organization of the marsh edge can occur in their absence due to the two-way feedback between vegetation and sediment accumulation (Zaytseva et al., 2020). The self-organization in this case is similar to Type III behavior that we found in our full system, in which the cordgrass-sediment scale-dependent interaction is relatively strong while the mussel-mussel scale-dependent interaction is relatively weak. We again find that self-organization allows the marsh edge to cope with harsher erosion than otherwise would be possible with a uniform shoreline. This highlights the importance of the cordgrass-sediment interaction in pattern formation, particularly since marsh mussels rarely exist independently of cordgrass. Apart from stabilizing the marsh edge, the presence of mussels in the system modulates the spatial scale of the resulting patterns and generates spatial patterns with shorter wavelengths.

Previous studies found that the balance between positive and negative feedbacks acting on different spatial scales may explain self-organization in mussel beds, semiarid ecosystems, and various estuarine communities (Klausmeier, 1999; van de Koppel et al., 2008; Weerman et al., 2010; van de Koppel et al., 2012) and help increase persistence and stability of these ecosystems (Liu et al., 2014; de Paoli et al., 2017). Our model extends these results to marsh ecosystems and the self-organization that occurs on the marsh edge. From previous experimental and observational evidence, self-organization on the marsh edge in the form of undulations with peaks and troughs has been suggested to improve the stability of the marsh edge on short timescales, while leading to degradation over longer time scales (Gleason et al., 1979; van de Koppel et al., 2005b; Fagherazzi et al., 2013). While our model cannot detect the long-term evolution of the spatial patterns, it suggests that spatial heterogeneity, particularly in the form of specific patterns, may increase the system's short-term stability and allow it to withstand conditions of harsher erosion than otherwise would be possible on a uniform shoreline. A refinement of the model, one that includes kernels extended to two spatial dimensions, incorporates additional data from field experiments and captures long-term evolution of the spatial patterns, is a natural next step and can help further elucidate how spatial heterogeneity affects the stability of the marsh system. As sea-level rise continues to contribute to worsening environmental conditions, our findings extend important results regarding the mechanisms and function of self-organization to wetland communities and demonstrate the potential value of self organization for wetland management and restoration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Parameterization of model

The erosion rate given by $L(G)$ in the sediment equation in system (1) represents a proportion of eroded sediment from the marsh edge. Since erosion rates are usually given for horizontal marsh erosion, we need to relate that to our measurement of pro-

portion of vertical sediment erosion. To calculate the total eroded volume of sediment, we multiply the value of horizontal marsh erosion by the erosion depth (referring to the height of sediment that gets eroded away, roughly equivalent to the height of the marsh above low tide) and the width of our box (since everything is considered per cubic meter, the width of the box is 1 m). Finally, we use this to calculate the total eroded volume of sediment. Erosion depth is usually about 0.5–1 m for the microtidal York River and the Chesapeake Region (Tonelli et al., 2010; Priestas et al., 2015), while typical erosion rates are on the order of 0.1–1 m/yr (Rosen, 1980; Hardaway and Byrne, 1999; Fagherazzi, 2013). In addition, studies following the BP oil spill have investigated the effect of marsh grass on erosion and concluded that erosion approximately doubles following a transition from average marsh grass values to a complete loss of marsh vegetation (Silliman et al., 2012), while being five times higher for no vegetation versus with maximum vegetation (Mariotti and Fagherazzi, 2010). We take this into consideration when choosing parameter values for ψ, g, k_s .

We refer to literature regarding the spatial effect of marsh vegetation on sedimentation dynamics (Bouma et al., 2007; Bouma et al., 2009) to estimate the width and strength of the cordgrass-sediment kernel. Less is known about the spatial interactions of ribbed mussels; therefore, the estimates of the mussel kernel are less accurate. The spatial scale of mussel aggregations is much smaller than that of the cordgrass-sediment interactions, and we choose the mussel kernel width according to this assumption.

Appendix B. Numerical simulations

All numerical simulations were performed using MATLAB. For the simulation of both the full system and the mussel-free subsystem, we used an implicit finite difference scheme to numerically integrate the equations. Although this scheme is more computationally intensive, it was chosen because it is numerically stable and convergent. The integration was done over a spatial domain of size 7π with $dx = 0.04\pi$, $dt = 0.1$ with periodic boundary conditions. Because domain size plays an important role in the system's ability to form patterns, a large enough domain has to be chosen to be able to fit patterns with their characteristic wavelength. We chose a domain of about 22 m for physical realism. Since the kernel widths and amplitudes influence the general scale of the patterns, we adjusted the domains accordingly to provide adequate space for patterns to develop. The integrals were evaluated using the *trapz* function in MATLAB, which performs numerical integration using the trapezoidal rule.

We applied Turing's idea of diffusion driven instability and used a spatially periodic perturbation of the stable positive steady state of the corresponding system of ODEs as the initial condition for our simulations. Figs. 4 and 5 are extended to erosion rates at which the constant steady state of the corresponding ODEs doesn't exist. At higher erosion rates, we take a numerical continuation approach: each new simulation uses a spatially periodic perturbation of the previous final state as the initial condition. This continues until the dynamics show a shift to a degraded state. The erosion rate is varied slowly enough in Figs. 4 and 5 to accurately locate the last erosion rate at which the system persists before degradation.

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