

# Early Warning Signals for Rate-induced Critical Transitions in Salt Marsh Ecosystems

Floris K. Neijns, <sup>1</sup> Koen Siteur, <sup>2</sup> Johan van de Koppel, <sup>2,3</sup> and Max Rietkerk <sup>1\*</sup>

<sup>1</sup>Department of Environmental Sciences, Copernicus Institute, Utrecht University, PO Box 80115, 3508 TC Utrecht, The Netherlands;

<sup>2</sup>Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research, PO Box 140, 4400 AC Yerseke, The Netherlands; <sup>3</sup>Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

## ABSTRACT

Intertidal ecosystems are important because of their function as coastal protection and ecological value. Sea level rise may lead to submergence of salt marshes worldwide. Salt marshes can exhibit critical transitions if the rate of sea level rise exceeds salt marsh sedimentation, leading to a positive feedback between reduced sedimentation and vegetation loss, drowning the marshes. However, a general framework to recognize such rate-induced critical transitions and predict salt marsh collapse through early warning signals is lacking. Therefore, we apply the novel concept of rate-induced critical transitions to salt marsh ecosystems. We reveal rate-induced critical transitions and new geomorphic early warning signals for upcoming salt marsh collapse in a spatial model. These include a de-

crease in marsh height, the ratio of marsh area to creek area, and creek cliff steepness, as well as an increase in creek depth. Furthermore, this research predicts that increasing sediment capture ability by vegetation would be an effective measure to increase the critical rate of sea level rise at which salt marshes collapse. The generic spatial model also applies to other intertidal ecosystems with similar dynamics, such as tidal flats and mangroves. Our findings facilitate better resilience assessment of intertidal ecosystems globally and identifying measures to protect these ecosystems.

**Key words:** Salt marsh dynamics; Sea level rise; Spatial pattern formation; Intertidal ecosystems; Indicators.

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\*Corresponding author; e-mail: M.G.Rietkerk@uu.nl

## HIGHLIGHTS

- Salt marshes will collapse when the rate of sea level rise is too high.
- Generic early warning signals predict when the system is close to rate-induced tipping.
- A decrease in cliff steepness and marsh area are useful predictors for marsh collapse.

## INTRODUCTION

Salt marshes are ecosystems which form in the intertidal coastal zone and provide important ecosystem services, including water-quality improvement, shore protection and opportunities for recreation (Morris and others 2013; Reed and others 2018). A variety of plants can grow in salt marshes, adapted to both a high salinity and the partial inundation of the marsh by sea water. Salt marsh vegetation forms spatial patterns consisting of alternating vegetation patches entrenched by creeks through which seawater can flow (Bertness and Ellison 1987). These patterns form by increased sedimentation by vegetation, because plants decrease water flow. Sedimentation in turn decreases the inundation time of the plant, which feeds back into increased vegetation productivity. Vegetation growth also leads to the divergence of water flow, thereby increasing erosion and causing creeks to form between patches of vegetation (van Wesenbeeck and others 2008). Eventually, these processes lead to the characteristic vegetation patterns which are observed in tidal marsh ecosystems (van der Wal and others 2008).

Human activities put increasing stress on salt marshes, including pollution and exposure to high rates of sea level rise (Kirwan and Megonigal 2013). Sea level is expected to increase for most parts of the world, and this will lead to increased inundation of salt marshes when it is not met with a proportional rate of sedimentation (Roman 2017). Sea level rise causes the salt marsh to move away from a static equilibrium, because it is exposed to continuous change. How the balance of sea level rise and sedimentation will affect both plant growth as well as species composition may be an important determinant for the resilience of salt marshes in the near future.

Ecosystems that contain positive feedback mechanisms and that display spatial patterns may exhibit critical transitions when exposed to changing environmental conditions (Rietkerk and others 2004). Critical transitions are characterized by a dramatic change in the ecosystem state, resulting from sometimes minor changes in environmental conditions beyond some critical threshold value (Scheffer and others 2001). Critical transitions are often hard to foresee, making it particularly difficult to manage ecosystems that are vulnerable to tipping behaviour. Evidence is accumulating, however, that statistics of time series and changes in spatial patterning can potentially be used to assess the proximity of ecosystems to critical transitions (Rietkerk and others 2002; Scheffer and others 2009; Bastiaansen and others 2018).

Model studies suggest that salt marshes may undergo a critical transition if a certain critical rate of sea level rise is exceeded, beyond which vegetation-induced sedimentation cannot keep up with sea level rise (Temmerman and others 2004; Kirwan and Guntenspergen 2010). Hence, salt marsh degradation can be described as a so-called rate-induced critical transition. Rate-induced critical transitions occur beyond a certain critical rate of change, rather than a critical magnitude of change (Scheffer and others 2008; Siteur and others 2016). This novel concept is different from the classical theory on critical transitions because it describes ecosystems that are not in a static equilibrium, but instead are subject to continuously changing external conditions (Ashwin and others 2012). If environmental conditions change too rapidly for the ecosystem to cope with, the system may collapse even though a slower change in environmental conditions may have prevented this collapse. Current environmental changes are increasingly rapid due to anthropogenic activities, which makes studying these rate-sensitive systems (and the possible collapse) informative for managing these ecosystems.

A theoretical framework that applies the concept of rate-induced critical transitions to salt marshes and their resilience to sea level rise is currently still lacking. The fact that coastal ecosystems are not only exposed to a change in the magnitude of sea level, but also to a change in the rate of sea level rise, makes these systems particularly suitable for applying the concept of rate-induced tipping points. Furthermore, salt marshes can serve as a useful case study for applying the theoretical concept of rate-induced critical transitions to a specific ecosystem. In this paper, we present a theoretical framework to identify critical thresholds for salt marsh collapse and assess the resilience of salt marshes under increasing rates of sea level rise through early warning signals. The early warning signals consider both changes in temporal statistics as well as spatial patterning, and are based on numerical analysis and analytical treatment of a well-established spatial model for salt marsh dynamics (Morris and others 2002; Kirwan and Murray 2007).

## METHODS

### Model Description

To analyse salt marsh behaviour under increasing rates of sea level rise, a partial differential equations (PDE) model is proposed based on Morris and

others (2002) and Kirwan and Murray (2007). This model considers two spatial dimensions, that is, the elevation of the marsh platform (the marsh height) and the distance from the marsh platform to outlet along the water flow direction. The model describes salt marsh height development and encompasses three processes: sedimentation during inundation due to vegetation sediment capture, erosion due to water flow over the salt marsh surface, and sediment dispersal, which is implemented in the model as diffusion. Our model closely follows the model by Kirwan and Murray (2007), with the difference that only one spatial dimension is considered, that is water flow path, allowing for more detailed numerical analysis and yielding analytical tractability.

The model consists of two differential equations that describe the development over time of the salt marsh height ( $z_{SM}$ ) and the mean high tide ( $z_{HT}$ ), both in millimetres. The rate of change in mean high tide is assumed to be equal to the rate of sea level rise  $r$  in  $\text{mm year}^{-1}$ , which in turn is assumed to be constant. The rate of change of the marsh platform depends on the depth of the marsh below the mean high tide, as well as the amount of biomass. This can be summarized in the following equations:

$$\frac{dz_{HT}}{dt} = r \quad (1)$$

$$\frac{dz_{SM}}{dt} = S - E + F \quad (2)$$

in which  $S$  is the sedimentation rate,  $E$  is the erosion rate, and  $F$  is a diffusion term, all with the unit  $\text{mm year}^{-1}$ . The full model description is given in online Appendix 1.

To analytically study the model described above, the salt marsh height can be considered at the centre of the marsh platform. At this place, there will be no water flowing over the marsh (the centre of the marsh is analogous to the water divide) which allows us to set the erosion and diffusion terms to zero. With combining Eqs. (1) and (2), we can determine the critical depth  $D_c$  and the critical rate of sea level rise  $r_c$  above which the marsh will go through a rate-induced critical transition and drown. The mathematical analysis can be found in online Appendix 2. Furthermore, analysing the model at the water divide allows for the analytical calculation of the perturbation growth rate of the system, which indicates the stability of the system given a specific rate of sea level rise  $r$ . The calculation of the perturbation growth rate can be found in online Appendix 3.

Despite the apparent simplicity of the model, it does show an important characteristic of salt marshes, that is, the marsh will become submerged when exposed to a rate of sea level rise too high for the system to cope with (Morris and others 2002). This is due to a maximum biomass productivity, which corresponds to a maximum sediment capture ability at an optimal rate of sea level rise. When the rate of sea level rise in the model exceeds this optimum, the productivity decreases again, which leads to a lower sediment capture ability of the marsh vegetation, which in turn leads to a slower increase in marsh height with less available sediment. Furthermore, this model forms a cliff edge between the marsh and the submerged area, when made spatially explicit.

## Numerical Implementation

When the sedimentation, erosion and diffusion terms are all included, the full model represents a transect through a salt marsh. The model is discretized into one row of  $n = 600$  cells which have a length  $\Delta x = 5$  m, hereby modelling a water flow path of  $L = 3000$  m. Within each cell, deposition and erosion of sediment are governed as described above; sediment diffusion occurs every time step by redistributing the sediment driven by gravitation, with  $\Delta t = 10$  years. The rate of sea level rise  $r$  in the model is varied to study how the system will respond to rising sea level with a continuous rate. In the one-dimensional salt marsh model, a rate-induced critical transition will occur when sea level rise is higher than the rate of sediment deposition in equilibrium. The model parameterization used in this study is based on Kirwan and Murray (2007) and Kirwan and Guntenspergen (2010). An overview of the values used in the numerical simulations is given in Table 1.

## Early Warning Signals

We tested several approaches to examine how proximity to a rate-induced critical transition could be signalled by changes in the salt marsh height. If the system state is far away from this rate-induced critical transition, the system will quickly return to its equilibrium state after a perturbation. However, as the rate of sea level rise approaches its critical value, the perturbation growth rate of the system approaches zero. As a consequence, the system will become increasingly slow in recovering from perturbations in the system (Wissel 1984; Scheffer and others 2009; Ritchie and Sieber 2016). This can be demonstrated by analytically calculating the return time from perturbations, the temporal autocorre-

**Table 1.** Parameter Values Used in This Study.

Parameter	Value	Units	Description
<i>a</i>	28	$\text{g m}^{-2} \text{ year}^{-1} \text{ mm}^{-1}$	Scaling parameter for $B(D)$ relationship
<i>b</i>	- 0.093	$\text{g m}^{-2} \text{ year}^{-1} \text{ mm}^{-2}$	Scaling parameter for $B(D)$ relationship
<i>c</i>	- 270	$\text{g m}^{-2} \text{ year}^{-1}$	Scaling parameter for $B(D)$ relationship
<i>q</i>	0.00009	$\text{m}^3 \text{ g}^{-1} \text{ year}^{-1}$	Suspended sediment concentration proportionality constant
<i>k</i>	0.000015	$\text{m}^2 \text{ g}^{-1}$	Sediment trapping ability of vegetation
$C_{ss}$	20	$\text{g m}^{-3}$	Suspended sediment concentration above marsh platform
<i>m</i>	0.0014	$\text{kg m}^{-2} \text{ s}^{-1}$	Proportionality constant for erosion rate
$\tau_c$	0.4	$\text{N m}^{-2}$	Bed shear stress threshold for erosion
$\epsilon$	$4.38 \times 10^8$	-	Conversion constant from $\text{m s}^{-1}$ to $\text{mm year}^{-1}$
$\rho_s$	450	$\text{kg m}^{-3}$	Sediment density
$\rho_w$	997	$\text{kg m}^{-3}$	Water density
$f_c$	0.02	-	Friction parameter
$t_{rf}$	10,800	s	Reflux time after high tide
$\alpha$	3.65	$\text{m}^2 \text{ year}^{-1}$	Diffusion coefficient without vegetation growth
$\beta$	0.0019	$\text{m}^4 \text{ g}^{-1}$	Sediment stabilization by vegetation growth

Based on Kirwan and Murray (2007) and Kirwan and Guntenspergen (2010).

lation and the temporal variance when noise is applied to the salt marsh height state variable (Siteur and others 2016). These early warning signals are related to the perturbation growth rate  $\lambda$  via the following formulae:

$$t_r = -\frac{1}{\lambda} \tag{3a}$$

$$ac1 = e^{\lambda \Delta t} \tag{3b}$$

$$var = \frac{\sigma^2}{1 - ac1^2} \tag{3c}$$

in which  $t_r$  is the return time,  $ac1$  is the lag-1 autocorrelation,  $var$  is the variance,  $\Delta t$  is the time interval with which noise is applied on the state variables, and  $\sigma$  is the standard deviation of the applied noise.

If the perturbation growth rate of a system cannot be determined analytically, the autocorrelation and the variance can still be calculated numerically, as is done for the numerical model simulations. We calculate the numerical autocorrelation  $AC1$  with the following formula:

$$AC1 = \frac{\sum_{i=1}^N (z_{SM}(t) - \overline{z_{SM}})(z_{SM}(t + \Delta t) - \overline{z_{SM}})}{\sqrt{\sum_{i=1}^N (z_{SM}(t) - \overline{z_{SM}})^2 \sum_{i=1}^N (z_{SM}(t + \Delta t) - \overline{z_{SM}})^2}} \tag{4}$$

in which  $N$  is the number of time steps  $\Delta t$  during which noise is applied to the state variable and  $-\overline{z_{SM}}$  is the average salt marsh height over time. In

the same manner, the numerical variance  $VAR$  is calculated using the formula:

$$VAR = \frac{1}{N} \sum_{i=1}^N |z_{SM}(t) - \overline{z_{SM}}|^2 \tag{5}$$

Three additional early warning signals were identified which are specific for tidal marsh ecosystems (based on the results of Kirwan and Guntenspergen 2010), that is, the marsh vs the water channel depth with rising sea level, the creek cliff steepness, and the ratio of total marsh area to creek area. The depth  $D$  of the marsh and channel is calculated as the difference between the salt marsh height ( $z_{SM}$ ) and the mean high tide ( $z_{HT}$ ). The creek cliff steepness is calculated by taking the highest value of the slope of the salt marsh height  $z_{SM}$  with respect to the distance  $x$  (that is,  $\Delta z_{SM}/\Delta x$ , analogous to the derivative of the marsh height  $z_{SM}$  over the distance  $x$ ). The creek area is calculated by calculating the percentage of the salt marsh which has a depth  $D$  lower than the critical depth  $D_c$  through the marsh transect; this is then compared to the total marsh area (the modelled transect through the marsh  $x$  is taken representative of marsh and creek area).

## RESULTS

### Rate-Induced Critical Transition

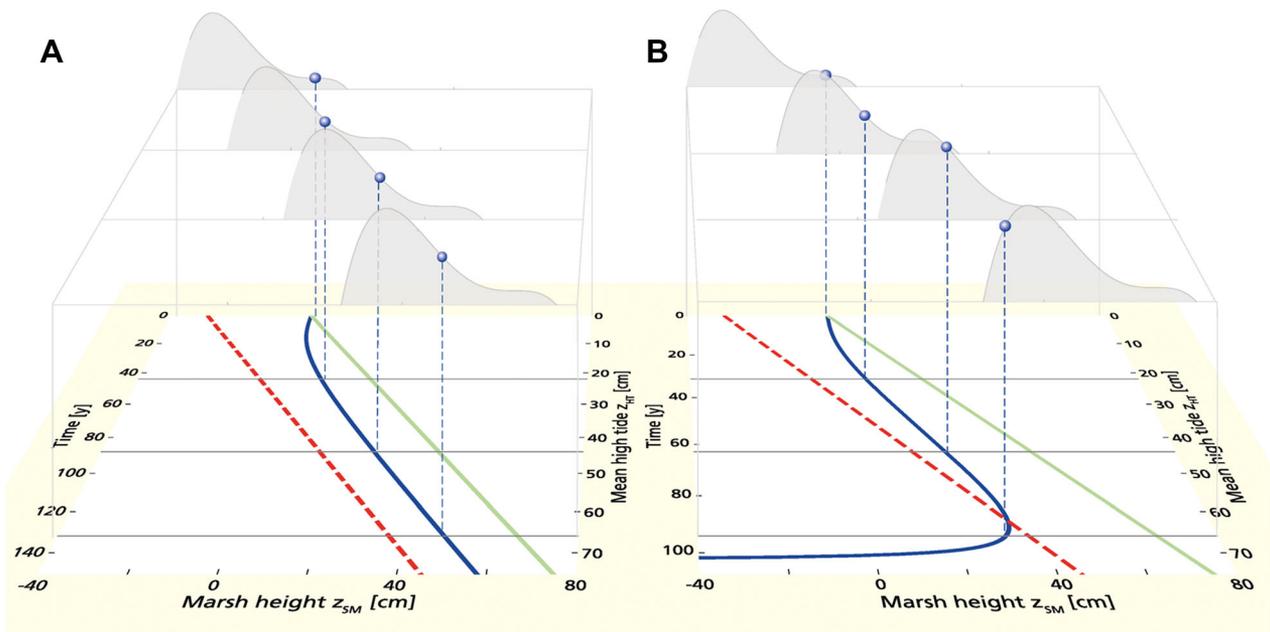
Our model analysis reveals that salt marsh resilience is directly affected by the rate of sea level rise. This is visualized by plotting the marsh height

development over time, as well as the system state in the potential landscape as a function of the marsh height, for two different rates of sea level rise (Figure 1). At rates of sea level rise below a critical threshold, the marsh will persist due to the presence of vegetation, which is crucial to maintain a sufficient rate of sedimentation (Figure 1A). However, for rates of sea level rise above a critical threshold, sea level rise will outpace the rate of sedimentation, and the marsh platform will collapse (Figure 1B). A rate of sea level rise beyond the critical threshold will move the system state over the hill in the potential landscape, which implies the system moves to a basin of attraction in which the marsh is stably submerged. Striking is that the marsh could persist if it were given sufficient time to adapt and accumulate sufficient sed-

iment even at a high absolute sea level rise. Based on the parameter values as given in Table 1, the critical rate of sea level rise  $r_c$  is  $5.19 \text{ mm year}^{-1}$ . If the rate of sea level is higher than this critical rate, the marsh will become stably submerged. Even though the critical rate  $r_c$  will show significant regional differences in marshes around the world and in this study heavily depends on the chosen parameter values (see the *Sensitivity analysis* section), the model shows a rate-induced tipping point in salt marshes exists which should not be crossed to prevent marsh collapse.

### Generic Early Warning Signals

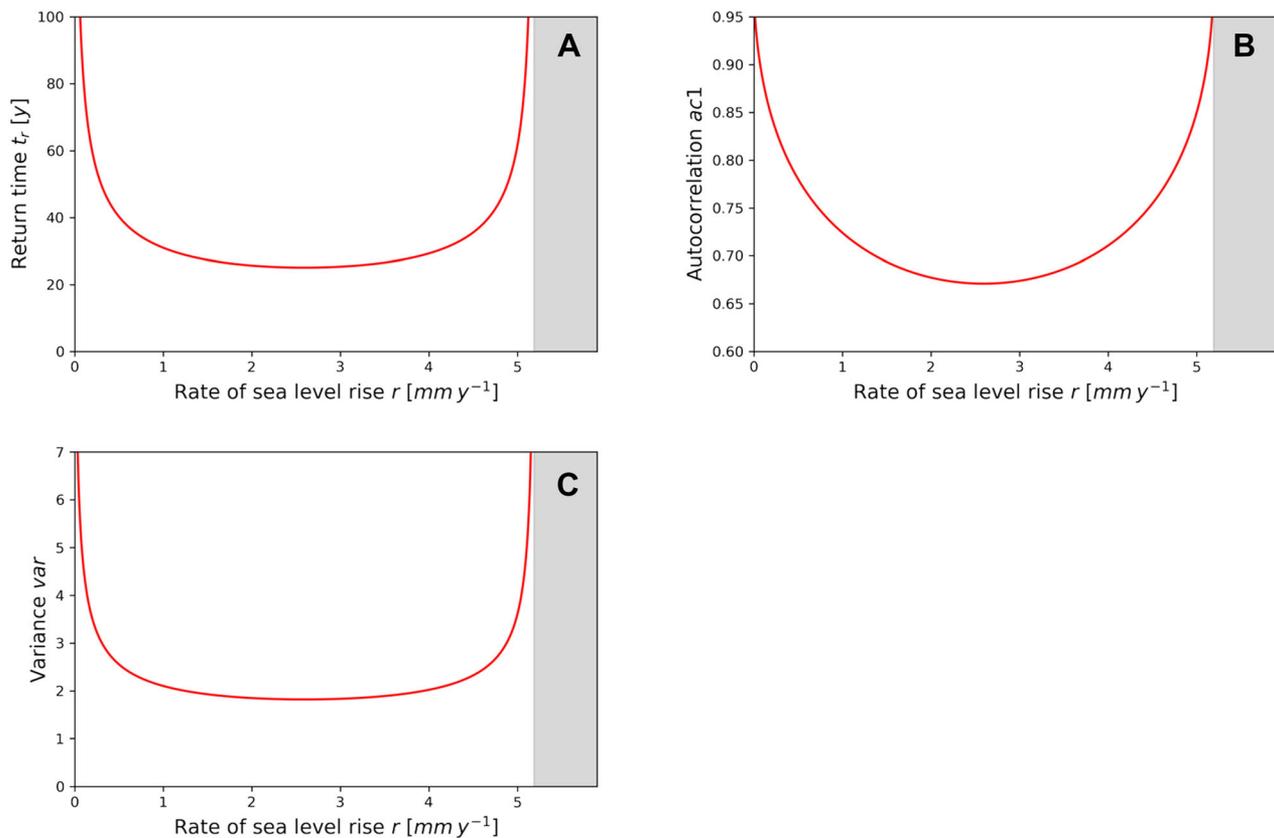
We examined three generic early warning signals, based on Scheffer and others (2009). At the water



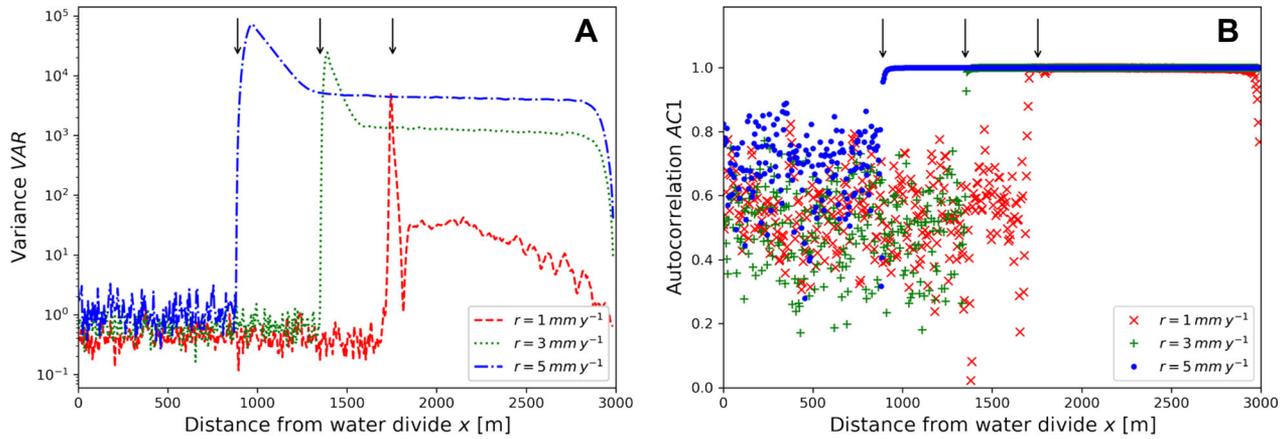
**Figure 1.** The development of marsh height  $z_{SM}$  (cm; blue lines) as a function of time (years; left axes) and mean high tide  $z_{HT}$  (cm; right axes), for two rates of sea level rise (moving potential landscapes to the right): left hand side **A**  $r = 5 \text{ mm year}^{-1}$  and right hand side **B**  $r = 7 \text{ mm year}^{-1}$ . Note that the scales of the time axes differ. Equilibrium states of the system are depicted in green (stable) and red (unstable). In the absence of sea level rise, the salt marsh would converge to the stable equilibrium at  $z_{SM} = z_{HT}$ . This is also the initial salt marsh height at  $t = 0$ , where  $z_{SM} = z_{HT} = 0$ . Trajectories of the model runs are depicted in blue. The green lines equal  $z_{HT}$ , and the difference between the green lines and the blue lines is  $z_{HT} - z_{SM} > 0$ . The corresponding blue marbles show the position of the system in the potential landscape at different moments in time. **A** If the rate of sea level rise is below a critical value (for  $r = 5 \text{ mm year}^{-1}$ ), the blue ball remains on the slope of the mountain and the salt marsh remains stable. In other words, the blue ball moves upslope initially, because of the changing conditions, but a “steady lag” sets in. This “steady lag” is measured by the equal distance over time between the stable equilibrium in the valley (green line), and the blue ball on the slope of the moving mountain (blue line). Would sea level rise halt, the mountain would stop moving, and the ball would roll back to the stable equilibrium, increasing marsh height. **B** If the rate of sea level rise is above a critical value (for  $r = 7 \text{ mm year}^{-1}$ ), the blue ball keeps moving upslope and crosses the black striped line, and the system will become unstable (the blue ball rolls over the top of the mountain) and hence the salt marsh will submerge. In other words, a rate-induced critical transition occurs. Would sea level rise stop, the mountain would stop moving to the right; however, the system now remains submerged, because the ball cannot roll back to the stable equilibrium.

divide, the return time, the temporal autocorrelation and the variance of the marsh height  $z_{SM}$  all show an increase close to the critical rate of sea level rise  $r_c = 5.19 \text{ mm year}^{-1}$  (Figure 2). Close to the critical transition, the marsh depth is high, implying perturbations will take a longer time to recover from the high inundation stress. Furthermore, all early warning signals show a minimum for intermediate values of the rate of sea level rise  $r$ , at which the system is most stable. Lastly, all early warning signals also show an increase when the rate of sea level rise  $r$  comes close to  $r = 0 \text{ mm year}^{-1}$ . This can be explained by noticing that both the vegetation productivity and the salt marsh depth become zero, which in turn causes the salt marsh not to be inundated anymore during floods. Consequently, perturbations in the system cannot be restored anymore. Therefore, a decrease in statistical early warning signals can imply the system is moving towards the rate-induced tipping point, as well as moving away from it.

We also investigated two generic early warning signals as a function of the distance  $x$  from the water divide, for different rates of sea level rise  $r$ . Both the autocorrelation and the variance of the marsh height  $z_{SM}$  are calculated for each cell in the marsh model for the last 500 years of the model run (Figure 3). The autocorrelation ranges between high and low values on the marsh (that is, between 0.2 and 0.8) and increases to 1 in the channel. Besides this, the autocorrelation on the marsh increases when the rate of sea level rise  $r$  is higher. The variance varies with a factor of 10 on the salt marsh. Just before the cliff, variance steeply increases, and shows a maximum at the cliff. In the water channel, the variance is much higher compared to the salt marsh. For high values of the rate of sea level rise  $r$ , the autocorrelation and variance are both considerably higher compared to lower values of  $r$ . These statistical early warning signals seem to show a considerable increase close to the critical transition and could potentially predict salt marsh collapse.



**Figure 2.** Generic early warning signals for marsh collapse at the water divide. **A** The return time  $t_r$ , **B** the autocorrelation  $ac1$  and **C** the variance  $var$  as a function of the rate of sea level rise  $r$ , with  $\Delta t = 10$  years. All early warning signals show a sharp increase close to  $r = 0 \text{ mm year}^{-1}$  and close to  $r = r_c = 5.19 \text{ mm year}^{-1}$ , the critical rate at which the salt marsh collapses.



**Figure 3.** The variance  $VAR$  (**A**) and the autocorrelation  $ACI$  (**B**) of the marsh height  $z_{SM}$  numerically calculated as a function of the distance from the water divide of the marsh for  $r = 1 \text{ mm year}^{-1}$ ,  $r = 3 \text{ mm year}^{-1}$ , and  $r = 5 \text{ mm year}^{-1}$ . Both are calculated for the last 500 years of the model run ( $t = 3000$  years), with  $\Delta t = 10$  years. The variance and the autocorrelation are lower on the marsh platform compared to the cliff and the water channel. Furthermore, the variance is highest at the location of the marsh cliff. Both the variance  $VAR$  and the autocorrelation  $ACI$  increase on the marsh platform with an increasing rate of sea level rise. The variance also shows an increase at the marsh cliff and the water channel with increasing  $r$ , contrary to the autocorrelation at the marsh cliff, which is the same regardless of  $r$ . The arrows indicate the location of the marsh cliff at which the variance peaks for the different values of  $r$ .

### Marsh-Specific Early Warning Signals

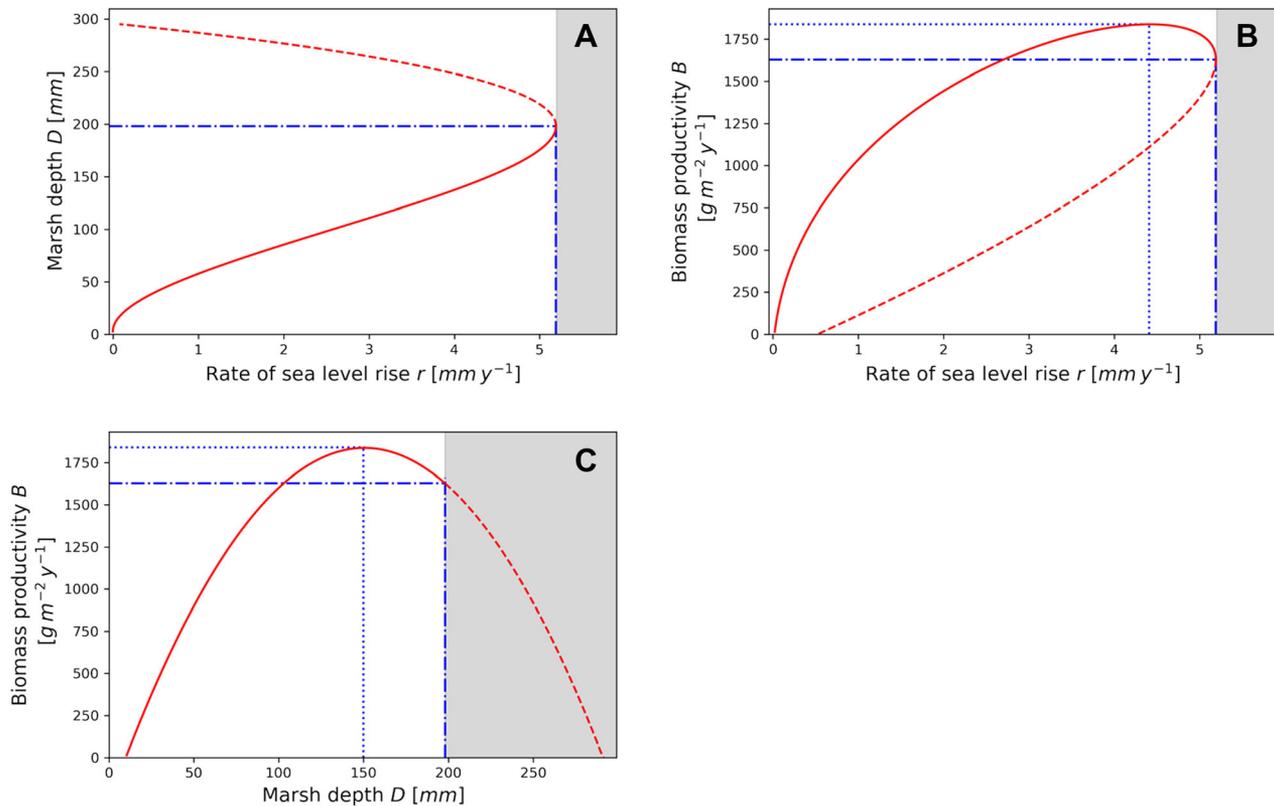
To investigate whether the marsh depth  $D$  and the biomass productivity  $B$  at the water divide are suitable early warning signals, these variables are plotted as a function of the rate of sea level rise  $r$  (Figure 4A, B). The marsh depth  $D$  continuously increases with increasing rates of sea level rise  $r$ , whereas for the biomass productivity  $B$  there is a maximum value after which the productivity slightly decreases towards the tipping point. Consequently, a decrease in marsh productivity over time could mean that the system is moving towards the tipping point, but it could also mean that it is moving away from the tipping point; this causes the marsh productivity to be a somewhat ambiguous early warning signal (*sensu* Morris and others 2002). At the critical marsh depth  $D_c$ , the system goes through a rate-induced critical transition and both the equilibrium depth and equilibrium biomass productivity become unstable. The biomass productivity  $B$  slightly decreases for high values of the marsh depth  $D$ , after which the marsh becomes unstable (Figure 4c).

Three additional early warning signals, that is, the marsh and water channel depth with rising sea level, the creek cliff steepness, and the total salt marsh vs channel area, were investigated (Figure 5). Firstly, the relative height difference between the salt marsh and the channel network increases with a higher rate of sea level rise. A higher  $r$  causes the marsh depth to increase less

compared to the depth in the water channels. Secondly, the salt marsh area is plotted as a function of the rate of sea level rise  $r$ . When  $r = 0 \text{ mm year}^{-1}$ , the salt marsh area is maximal, and no water channels or creek edge is present. With an increasing rate of sea level rise, the salt marsh area is monotonically decreasing, as well as the distance from the water divide to the cliff edge of the water channel. Close to the rate-induced tipping point, the sensitivity of the salt marsh area to an increase in  $r$  increases, because the salt marsh area more quickly decreases in the vicinity of  $r_c$ . When  $r > r_c$ , no salt marsh area is present. Lastly, the cliff steepness is plotted as a function of the rate of sea level rise  $r$ . The cliff steepness is highest at intermediate values for  $r$  (in the range of  $r = 2 \text{ mm year}^{-1}$  to  $r = 3 \text{ mm year}^{-1}$ ) and approaches zero when the rate of sea level rise  $r = 0 \text{ mm year}^{-1}$  and when  $r > r_c$ . When the system is approaching the rate-induced tipping point, the cliff steepness is considerably lower compared to values at intermediate sea level rise. Both the salt marsh area and the creek cliff steepness decrease when approaching the rate-induced tipping point and may therefore potentially serve as useful early warning signals for marsh collapse.

### Sensitivity Analysis

A sensitivity analysis has been performed for the salt marsh height model at the water divide to determine the effects of the suspended sediment



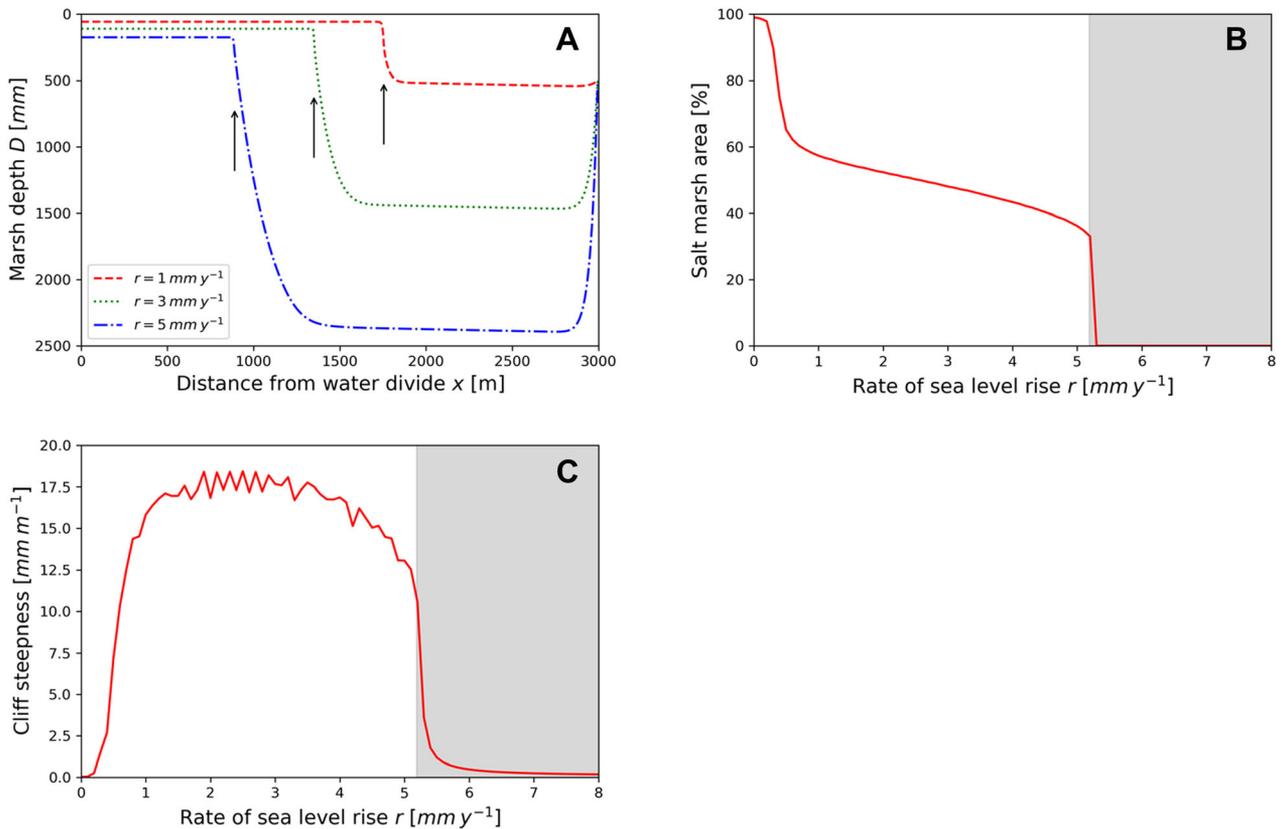
**Figure 4.** The influence of the rate of sea level rise  $r$  on the marsh depth  $D$  and the biomass productivity  $B$  (figures adapted from Morris and others 2002). **A** Marsh depth  $D$  as a function of the rate of sea level rise  $r$ . The marsh depth increases with a higher rate of sea level rise, until the critical rate of sea level rise  $r_c$  is reached. The critical rate of sea level rise  $r_c = 5.19$  mm year $^{-1}$  corresponds to the critical marsh depth  $D_c = 198$  mm. This graph is the inverse function of Equation (B.3), so marsh depth  $D$  is described by a third-order algebraic equation. **B** Biomass productivity  $B$  as a function of the rate of sea level rise  $r$ . The biomass productivity  $B$  shows an optimum of  $B_{opt} = 1837$  g m $^{-2}$  year $^{-1}$  at a rate of sea level rise of  $r_{opt} = 4.41$  mm year $^{-1}$ . The critical rate of sea level rise  $r_c = 5.19$  mm year $^{-1}$  corresponds to the critical biomass productivity  $B_c = 1628$  g m $^{-2}$  year $^{-1}$ . **C** Biomass productivity  $B$  as a function of the marsh depth  $D$ . The critical marsh depth  $D_c = 198$  mm corresponds to the critical biomass productivity  $B_c = 1628$  g m $^{-2}$  year $^{-1}$ . The optimal marsh depth  $D_{opt} = 150$  mm corresponds to a critical biomass productivity  $B_{opt} = 1837$  g m $^{-2}$  year $^{-1}$ . This graph is described in Equation (A.4), so the relationship is described by a second-order algebraic equation.

concentration  $C_{ss}$ , the saltmarsh biomass productivity  $c$ , and the sediment trapping ability  $k$  on when the rate-induced critical transition occurs at the salt marsh (Figure 6). The critical depth  $D_c$  increases when there is an increase in suspended sediment concentration  $C_{ss}$  and decreases when plant sediment capture  $k$  is higher and when biomass productivity  $c$  is higher. The effects of these parameter variations are in the order of millimetres, so the critical depth  $D_c$  in the model is not particularly sensitive to these parameter changes. The critical rate of sea level rise  $r_c$  increases with an increase in plant sediment trapping  $k$  and suspended sediment concentration above the marsh  $C_{ss}$  but decreases with an increase in the marsh productivity  $c$  (Figure 6B). We note that changing either the suspended sediment concentration  $C_{ss}$  or

the marsh productivity  $c$  has the same effect on both the critical depth and the critical rate of sea level rise, whereas changing the sediment trapping ability  $k$  has an opposite effect on the critical depth  $D_c$  and the critical rate of sea level rise. The critical rate of sea level rise is most susceptible to changes in parameter  $k$ , meaning that if vegetation is less able to capture sediment during flooding (for example, caused by a lower biomass productivity or a change in plant species composition), this will considerably lower marsh stability.

## DISCUSSION

Climate change is imposing unprecedented rates of environmental change upon ecosystems over the world (Vitousek and others 1997). Whether



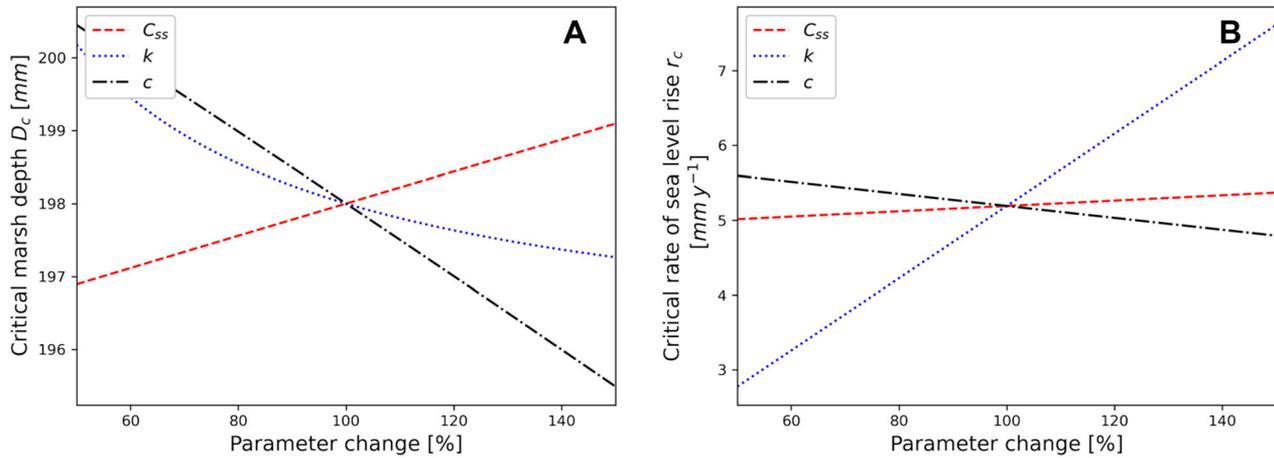
**Figure 5.** Salt marsh-specific early warning signals for rate-induced ecosystem collapse. **A** The marsh depth  $D$  as a function of the distance from the water divide for  $r = 1 \text{ mm year}^{-1}$ ,  $r = 3 \text{ mm year}^{-1}$ , and  $r = 5 \text{ mm year}^{-1}$ . Note the y-axis is reversed to indicate that a higher marsh depth corresponds to a lower salt marsh height. Both the salt marsh depth and the water channel depth increase with higher sea level rise. The arrows indicate the location of the channel cliff for different values of  $r$ . **B** The salt marsh area as a percentage of the total modelled area, graphed as a function of the rate of sea level rise  $r$ . The marsh area relative to the total area decreases with higher sea level rise. At the tipping point, the salt marsh area decreases to zero and the marsh disappears. **C** The channel cliff steepness as a function of the rate of sea level rise  $r$ . Cliff steepness decreases towards the tipping point. Notice that the value for the critical rate of sea level rise  $r_c$  corresponds well with the analytically derived value for  $r_c$ .

ecosystems can keep track and adapt to these changes is one of the major scientific challenges that ecologists are facing. In this paper, we highlight that salt marsh ecosystems may face rate-induced critical transitions in response to sea level rise, irrespective of the absolute sea level, when the feedback between plant growth and sedimentation is insufficient to allow salt marshes to follow the rate of sea level rise. This is conceptually different from the classical view of “change-induced” critical transitions (Scheffer and others 2001; Rietkerk and others 2004), where system stability depends on parameter values per se instead of the rate of change in parameter values (Siteur and others 2016). However, analysis reveals that several aspects of these types of critical transitions remain the same, that is, (1) a critical threshold needs to be exceeded for the transition to occur, and (2) close

to the threshold, early warning signals appear (Scheffer and others 2009; Siteur and others 2016).

Our study closely agrees with observations of drowning marshes across the world, and provides a conceptual framework for these observations (Rizzetto and Tosi 2011; Schepers and others 2017). The marsh ecosystems described in these studies have low sediment availability, making it difficult for the vegetation to concentrate sufficient sediment, and making them particularly susceptible to rate-induced critical transitions. Hence, despite the simplicity of our model formulation, it captures the essential dynamics of a wide range of salt marsh and mangrove systems.

The conceptual framework that we propose allows for the development of two different categories of early warning signals, that is, generic statistical early warning signals (an increase in re-



**Figure 6.** Sensitivity analysis for the point model considering salt marsh height at the water divide, for the suspended sediment concentration  $C_{ss}$ , sediment capture ability  $k$  and biomass productivity  $c$  parameters. **A** A higher suspended sediment concentration  $C_{ss}$  causes the critical depth  $D_c$  to increase, whereas a higher vegetation growth  $c$  or a higher plant sediment capture  $k$  leads to a lower critical depth. **B** A higher plant sediment capture  $k$  leads to a higher critical rate of sea level rise  $r_c$ , whereas an increase in vegetation growth  $c$  leads to a lower critical rate of sea level rise. For a higher suspended sediment concentration  $C_{ss}$ , the effect on the critical rate of sea level rise is also positive, even though the effect is marginal and possibly not significant.

turn time, autocorrelation and variance (Scheffer and others 2009; Siteur and others 2016)) and marsh-specific early warning signals (decreasing biomass productivity, increasing marsh depth, an decrease in salt marsh area, decreasing cliff steepness and increasing channel cliff height). The generic early warning signals show a similar pattern compared with earlier studies (Siteur and others 2016), which reinforces the idea that the early warning signals identified by Scheffer and others (2009) can also serve to predict a rate-induced critical transition. However, in this specific model the generic early warning signals all have a minimum value at intermediate values of  $r$ , so an increase in these early warning can signal that the system is moving towards the tipping point, but it could also imply the system is moving away from it. Despite the apparent ambiguity of these generic early warning signals, they can play a useful role in assessing proximity to marsh collapse for ecosystems which are known to be under high stress already. Besides this, analysing the generic early warning signals in a spatial context reveals a much clearer picture, with all generic signals increasing with a higher rate of sea level rise  $r$ . Our results are further supported by van Belzen and others (2017) who note that tidal marshes show an increase in return time when inundation stress increases. Furthermore, our results suggest that the variance is most useful for determining the proximity close to the tipping point, since the variance increases on both the marsh platform, the cliff and the water

channel. Concerning the marsh-specific early warning signals, the biomass productivity is first increasing with the rate of sea level rise, but decreasing close to the tipping point, so can as such serve as a useful indicator for marsh collapse. The marsh depth shows a clear increase towards the tipping point and could therefore probably even better help to identify a critical transition. The decrease in cliff steepness and marsh area are early warning signals which are potentially easier to measure (for example, with remote sensing). It is important to note that in order to determine whether a system is moving *towards* a tipping point and not *away* from it, early warning signals that show an optimum or minimum should always be combined with early warning signals that show a one-directional change towards the tipping point. In our case, the latter are decreasing salt marsh area, increasing marsh depth, increasing channel area and increasing channel depth. Further research in the field would be required to determine whether the early warning signals identified in this paper will also be present in real ecosystems, and which combination of early warning signals best predicts marsh collapse.

Our model results lead to several management implications. Our sensitivity analysis suggests that increasing the sediment capture ability in combination with increasing sediment concentration is useful for increasing salt marsh resilience. The sediment concentration in the sea water is influenced by the sediment input from nearby rivers or

can be artificially brought in; this additional sediment will lead to a greater stability under stress from sea level rise. Next, the sediment capture ability can be influenced by the type of vegetation growing on the marsh platform (for example, cord grasses as opposed to reed species), which in turn is influenced by climatic conditions (Kirwan and others 2009). The type of vegetation which grows on the marsh platform can be influenced by management of the marsh and can even be mimicked by artificial material (Temminck and others 2020).

Given its simplifications, there are several limitations to the applicability of the model used in this paper. For instance, the exact geomorphology of marshes in tree dimensions cannot be simulated with this model. These simplifications implicate the model cannot be used to make quantitative predictions for salt marsh development and collapse (Fagherazzi and others 2012). However, the model does give an overview of the processes and parameters most important for salt marsh dynamics, as well as the sensitivity of the system to parameter changes. Furthermore, the model helps to understand the susceptibility of salt marsh ecosystems to sea level rise in the context of rate-induced critical transitions. This has resulted in several proposed early warning signals, which should now be verified in field observations.

The dynamics used in this paper to simulate salt marsh dynamics could also be applied to other intertidal ecosystems. Tidal flats are also known to be prone to critical transitions (van de Koppel and others 2001), with similar sediment dynamics compared to salt marshes. Furthermore, mangroves behave in much the same way compared to salt marshes when exposed to sea level rise and are also vulnerable for collapse in the future (Lovelock and others 2015). Human activities cause lower sediment delivery to mangrove ecosystems, and many mangroves currently have a higher rate of sea level rise compared to the rate of soil elevation (Lovelock and others 2015). Modelling studies show a higher rate of sea level rise in these systems causes increased channel network branching and erosion (van Maanen and others 2015), possibly causing a rate-induced critical transition.

Coastal communities worldwide are facing an increasing danger of losing the intertidal ecosystems on which they depend for wave impact buffering, food provisioning, and other crucial ecosystems services (Morris and others 2013). To maintain a healthy and save coastal environment, managing these ecosystems is crucial in a way they can persist in a future with increasing rates of sea level rise (Meire and others 2005). For this, indi-

cators that can signal impending collapse of coastal ecosystems can play a crucial role. Here, we demonstrated how theoretical models can play an important role both in providing rate-sensitive indicators as well as a framework to understand how the resilience of salt marshes and other intertidal systems is affected by the rate of sea level rise.

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