

Abiotic origins of self-organized ridge-runnel patterns on tidal flats

Gregory S. Fivash^{1b, 1,2*} Marte M. Stoorvogel^{1b, 2,3} Jaco C. de Smit⁴ Floris van Rees^{2,3,5}
Jeroen van Dalen² Tim J. Grandjean^{2,3} Roeland C. van de Vijzel^{1b, 6} Tjeerd J. Bouma^{2,3,4}
Stijn Temmerman¹ Jim van Belzen^{2,7}

¹Ecosphere Research Group, Department of Biology, University of Antwerp, Antwerp, Belgium

²Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research, Yerseke, The Netherlands

³Earth Surface Processes, Coastal Dynamics, Fluvial Systems & Global Change, University of Utrecht, Utrecht, The Netherlands

⁴HZ Building with Nature, Middelburg, The Netherlands

⁵Deltares, Delft, The Netherlands

⁶Hydrology and Environmental Hydraulics Group, Wageningen University, Wageningen, The Netherlands

⁷Wageningen Marine Research, Wageningen University and Research, Yerseke, The Netherlands

Abstract

Striking large-scale spatial patterns in ecosystems, generated by self-organization through biotic and abiotic feedback processes, influence ecosystem functioning and response to global environmental change. A remarkable example of this are the regular ridge-runnel patterns found on tidal flats, which play an important role in mudflat-marsh transitions. Yet the mechanisms driving their formation, and whether they are abiotic or biotic in origin, have not been elucidated. The underlying mechanisms are unraveled in this study through a combination of field measurements and targeted laboratory experiments. In the field, we find that on the ridges of the pattern, the sediment bed level is less dynamic and more resistant to erosion than in the runnels. In laboratory flume experiments, we find that erosion-resistant surfaces, like those found on the ridges, can arise on time scales of hours to days due to the drying of the cohesive sediment bed, while this is prevented in waterlogged sediments in runnels. A disturbance-recovery experiment on benthic algae then confirms that biological processes require a longer developmental period than the time scale at which we have observed drying-induced erosion resistance to develop. Together, these results demonstrate that ridge-runnel patterns begin from an abiotic initiation point that can subsequently provide a template for further biological establishment and self-organization. Recognition of abiotic processes as catalysts of self-organization can improve our understanding of ecosystem responses to environmental changes.

Theoretical research on spatial patterns in ecosystems has demonstrated that the spatial structure of patterned environments enhances an ecosystem's resilience amidst hostile environmental conditions (Rietkerk et al. 2002; Gilad et al. 2004; Rietkerk et al. 2021). Regular spatial patterns commonly achieve this through the process of “stress divergence,” where hostile conditions are mitigated locally by diverting them into

neighboring areas. Biotically mediated stress divergence is a common theme in ecological spatial patterning (Rietkerk and van de Koppel 2008) that can be underpinned by any number of diverse mechanisms from (1) the re-allocation of resources, for example, by vegetation in arid systems (Rietkerk et al. 2002; Meron 2012) or shellfish in intertidal reefs (van de Koppel et al. 2005) to (2) the redirection of the stress of high

*Correspondence: greg.fivash@uantwerpen.be

Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: GFS designed, planned, and performed the field campaigns, lab experiments, analyzed the data, lead the writing of the manuscript, and is accountable for the integrity of the data, analysis and presentation of the findings as a whole. MMS participated in lab experiments, contributed new tools and methods to the study, and assisted in writing of the manuscript. JCS participated in lab experiments, contributed new tools and methods to the study, and assisted in analysis of the data and writing of the manuscript. FR planned and participated in field campaigns and lab experiments, contributed new tools and methods

to the study, assisted in analysis of the data and writing of the manuscript. JD planned and participated in field campaigns, contributed new tools and methods to the study. TJG participated in field campaigns, contributed new tools and methods to the study, and assisted in the writing of the manuscript. RCV participated in field campaigns, contributed new tools and methods to the study, and assisted in the writing of the manuscript. TJB acquired funding for the research, contributed to designing and planning of the study and supervised the writing of the manuscript. ST acquired funding for the research, contributed to designing and planning of the study and supervised the writing of the manuscript. JB contributed to designing and planning of the study, contributed new tools and methods to the study, assisted in lab experiments, and supervised the writing of the manuscript.

tidal flow rates around patches of marsh vegetation (Bouma et al. 2007, 2009; van Wesenbeeck et al. 2008). In principle, the act of redistributing stress or resources unevenly allows some regions to remain habitable at the cost of making adjacent areas even more uninhabitable. When environmental conditions become harsher, further reorganization of the system's spatial structure allows it to adjust the total habitable area to fit the new set of conditions, allowing habitation under conditions that would be impossible in a non-patterned environment. Hence, by dividing the landscape into habitable and uninhabitable regions, the productivity and the resilience of the system benefit overall (Rietkerk et al. 2021).

Most canonical work on ecosystem patterns focuses on biota-driven feedbacks responsible for their emergence (Rietkerk and van de Koppel 2008), thereby suggesting that when biota is absent, patterns cannot form to ameliorate harsh conditions and facilitate new establishment (e.g., Rietkerk et al. 2002; Scheffer et al. 2009). Yet, there are innumerable spatial patterns that arise out of abiotic feedback loops. Some examples include tidal creeks, under-sea sand waves, cracks caused by soil desiccation (unvegetated) eolian dunes, and longshore bars, all of which self-organize into patterned systems because of dynamic feedback processes that do not depend on biota. Furthermore, many of these patterns are likely to be capable of enacting stress divergence and consequently facilitate the establishment of organisms resulting in state transitions (Cheng et al. 2021; van de Vijzel et al. 2023; Zhang et al. 2023). In those cases, biotically mediated feedbacks are not the first to initiate the development of a self-organized landscape.

Recent studies demonstrate that the formation of “ridge-runnel” regular patterns in the tidal flat bathymetry can trigger a rapid transition to a vegetated state (van de Vijzel et al. 2020, 2021; Fivash et al. 2023; Fig. 1). Ridge-runnel patterns are strongly linearized dendritic drainage patterns that form on tidal flats (Carling et al. 2009). They are characterized by an alternating pattern of raised sediment ridges and lower drainage “runnels” where pooling water is commonly retained throughout the low tide interval. These alternating features form a regular pattern with a typical wavelength between 2 and 6 m (Supporting Information Fig. S1), and a maximum vertical relief of no more than 10 cm. The linear drainage features commonly run shore normal, parallel to the direction of the steepest slope. These patterns mainly occur high in the tidal frame, where twice daily tidal inundation does not always occur, and on tidal flats of very shallow slope, below 0.3° (Fivash et al. 2023). The formation of ridge-runnel patterns on the tidal flat facilitates the expansion of marsh vegetation in successive years to areas lower in the tidal frame, where hydrodynamic conditions are harsher, due to the stress-amelioration by the patterned topography (Fivash et al. 2020, 2023). Unlike more canonical patterned environments, tidal flat “ridge-runnel” patterns are not created by the marsh vegetation itself, but form either through physical or biophysical mechanisms on the tidal flat that marsh seedlings then merely

take advantage of (Fivash et al. 2020, 2021; Cao et al. 2021). Yet, we still lack a clear process-based explanation of (1) why and (2) how fast these patterns can develop.

In this study, we combine field measurements and flume experiments to investigate the processes driving ridge-runnel pattern formation, and whether they are biotic or abiotic in origin. We first compare the dynamics and erosivity of the ridges and runnels of a patterned tidal flat. We then determine experimentally the speed at which differences in erosivity can develop in cohesive sediment as a consequence of drying and water logging of the sediment surface. The speed of these changes is compared to the rate at which benthic algae can recolonize a sediment surface. Based on these findings, we argue that spatial patterns form as a result of physical changes in cohesive sediment strength that begin before the impacts of biota can be felt. Later colonization of the patterned tidal flat by algal mats, and then finally by vegetation both appear to further reinforce the feedbacks first initiated by this physical process.

Methods

Field measurements—Site characteristics

To quantify the sediment characteristics typical of patterned areas, we collected surface sediment samples (3 cm depth) at four tidal flat field sites in the Scheldt estuary (the Netherlands and Belgium) harboring ridge-runnel patterns (Baarland: 51.358647°N, 4.100534°E; Hoofdplaat: 51.372527°N, 3.677952°E; Keetenisse: 51.285044°N, 4.312248°E; and Zuidgors: 51.390763°N, 3.856090°E). These sites span a geographical range from 10 to 65 km from the river mouth. Across the sites, the average salinity ranges from 20 to 5 psu (Damme et al. 2005), with a tidal range that varies from 4 to 5.2 m (Wang et al. 2019; see Supporting Information Table S1 for site details). Sediment characteristics were surveyed at each site on the ridge and runnel of the pattern. Paired samples ($n = 3$) were taken to investigate differences in median grain size (μm) and mud fraction (%), $< 63 \mu\text{m}$) between these microenvironments (using a Mastersizer 2000; Malvern Panalytical). All four sites were characterized as cohesive sediment environments (Supporting Information Fig. S2). The mud fraction was typically between 70% and 90% on the ridges (mud fraction: $76.7\% \pm 2\%$, median grain size: $35.3 \pm 1.8 \mu\text{m}$; mean $\pm$ standard error), and was consistently coarser in the runnels (mud fraction: $67.3\% \pm 3.1\%$, median grain size = $43.5 \pm 3.4 \mu\text{m}$; mean $\pm$ SE).

Field measurements—Daily sediment bed-level dynamics

A pair of optical SED sensors (Hu et al. 2015; Willemsen et al. 2018) were installed at Keetenisse for 280 d to measure differences in daily changes in bed level between the ridge and runnel of the pattern. These sensors are composed of a vertical array of 200 light sensors spaced at 2-mm intervals along a shaft that is stuck into the tidal flat so that the 400-mm length array is partially underground. At the



Fig. 1. Photos of a large-scale vegetation expansion event over a ridge-runnel pattern on the tidal flat “Zuidgors” in the Western Scheldt between 2021 (top) and 2022 (bottom), as seen from the air (left) and the ground (right). Note the wooden reference pole (highlighted with a white triangle) visible in the ground perspective in both 2021 and 2022 marks that the two photos are of the same location.

sediment surface, the sensor array detects a transition from light to dark, which is used to determine the position of the bed. Measurements were repeated every 30 min, but only those taken during low tide, daytime conditions were considered accurate (for details, see Hu et al. 2015). The raw measurements selected during daytime, low tide periods were averaged to produce daily estimates of the bed level. Hu et al. 2015 reported SED sensors to have an accuracy of 5.0 ± 3.9 mm (mean $\pm$ SD). We used this daily bed-level time series to compare the intensity of sediment dynamics between the “ridge” and “runnel” microenvironments by calculating the average return time of daily bed-level changes of different magnitudes (as described in Grandjean et al. 2023; Fig. 2). The return time of accretion and erosion events (positive and negative bed-level change) were calculated separately. Linear

regressions were fit to the result ($\log y$) to estimate the scale of the exponential function for each environment. The inverse of the scale exponent is then equal to the average magnitude of daily bed-level change.

Field measurements—Sediment erodibility

To look for differences in the sediment’s capacity to resist erosion between the ridge and runnel of the pattern, nine sediment samples were extracted ($20 \times 12.5 \times 10$ cm [length $\times$ width $\times$ height] metal rectangular box) from the tidal flat at Keetenisse. In total, six samples were taken from the ridge and three from the runnel. Three of the six ridge samples had 1 cm of surface sediment removed before their resistance to erosion was measured. The erosion threshold of

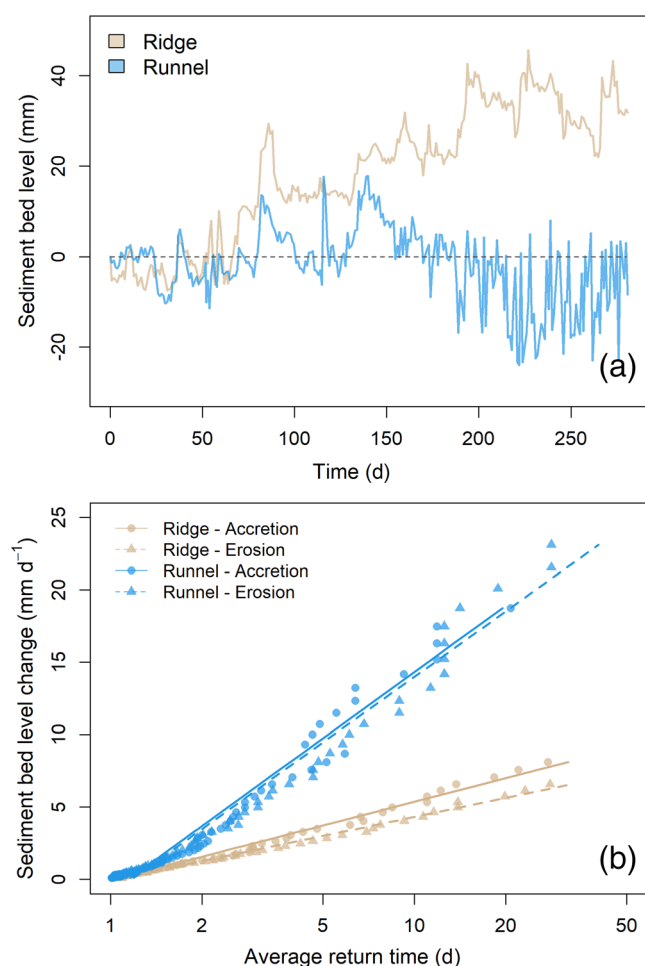


Fig. 2. Differences in daily sediment bed-level dynamics between ridge and runnel of the pattern on the tidal flat of Keetenisse in the Scheldt estuary. Panel (a) displays the raw bed-level time series data produced by the SED sensor. In panel (b), the likelihood of successively larger daily bed-level changes are compared between the two microenvironments using return time analysis on the time series. This reveals that bed-level dynamics are, on average, three times greater in magnitude in the runnels than on the ridges.

these three treatment groups ($n = 3$) was measured in the Oscillatory Flow Channel (OsCar; de Smit et al. 2021). OsCar is a flume that imposes shear stress at the surface of a sediment core by accelerating water back and forth over the sediment surface, mimicking the orbital shear stresses at the seafloor imposed by waves. In these trials, the peak flow velocity experienced at the sediment surface was gradually increased every 60 s in 15 steps from an initial 5 cm s^{-1} to a final 75 cm s^{-1} . The peak flow velocity was measured using a 25 Hz pressure sensor (Druck 1800 series; Druck) placed in one of the flume's two vertical water columns to measure vertical water movement. The flow velocity in the channel was calculated as the first derivative (in time) of this water movement signal. Critical bottom shear stress (τ_{cr}), that is, the bottom shear stress at which sediment resuspension begins to occur, was then calculated according

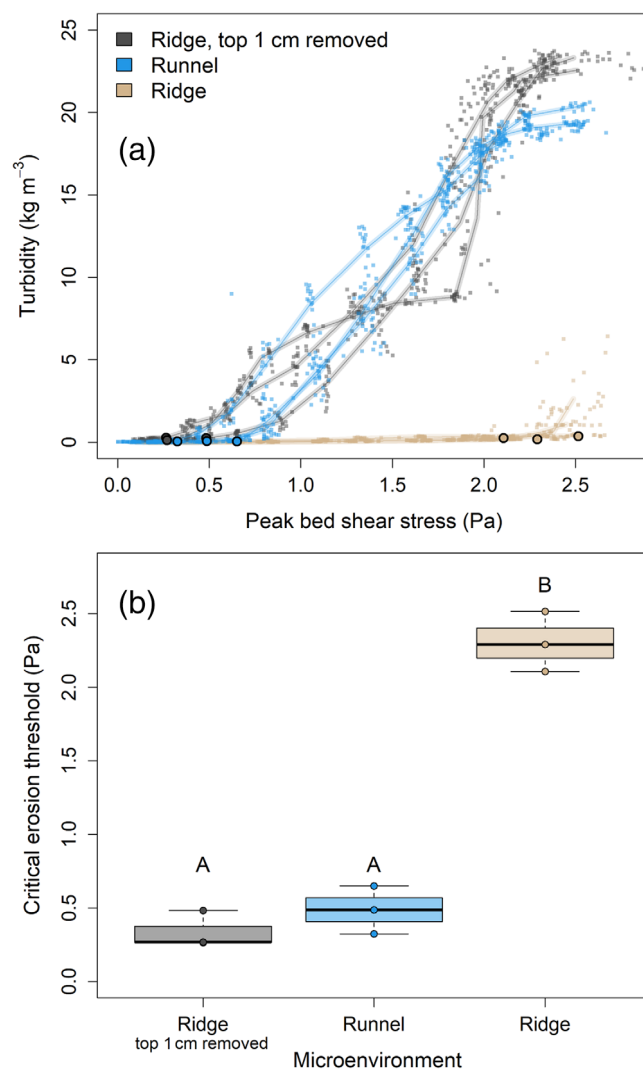


Fig. 3. Oscillatory Flow Channel (OsCar) erosion trials comparing the erosion resistance of ridge and runnel sediment field samples from the patterned tidal flat at Keetenisse in the Scheldt estuary. In panel (a), the colored points show the average turbidity and peak shear stress exerted during each individual wave in the flume trials. The colored lines are splines fitted to the points to aid in visualization. The larger colored circles represent the estimated erosion threshold for each trial ($n = 3$), and correspond to data points in the panel (b) used in the statistical analysis. The erosion threshold of the sediment is considered to have been passed once the rate of turbidity change in time overcomes a threshold value (see Methods for details). These results show that ridge sediment is much more resistant to erosion than runnel sediment, but that this difference disappears if the surface of the sediment (top 1 cm) is removed.

to the method of Le Hir et al. (2007) as described in de Smit et al. (2021), following Eq. 1:

$$\tau_{\text{cr}} = \frac{1}{2} \rho f_w u_{\text{cr}}^2. \quad (1)$$

Here, ρ represents the density of seawater (1027 kg m^{-3}), u_{cr} is the critical flow velocity at which sediment resuspension

begins to occur, and f_w is a dimensionless friction factor estimated within the OsCar flume setup by de Smit et al. (2021), described as:

$$f_w = aA_{\max}^{-0.52} \quad (2)$$

where f_w is calculated from $A_{\max}$, which is the maximum variation in the water level (in m) during a single oscillation, and $a = 0.0076$, a constant value estimated for the OsCar flume (see de Smit et al. 2021 for details). The peak flow velocity and the maximum variation in the water level were calculated for every oscillation in the experimental time series to produce a time series of peak bed shear stress values over the experiment.

Sediment resuspension within the flume was measured using a turbidity sensor (Cyclops 7; Turner Designs) placed 20 cm to the side of the sediment surface. Turbidity measurements were calibrated with a series of known concentrations of an 80% mud–20% sand mixture. The erosion threshold of the sediment core was identified from the turbidity readings. We estimated the moment at which the erosion threshold was exceeded by inspecting the rate of change of the turbidity over 60-s windows (as also seen in de Smit et al. 2021). The erosion threshold was said to be exceeded when the turbidity's rate of change exceeded a threshold value (in this case, $(0.015 \text{ kg m}^{-3})/(\text{cm s}^{-1})$, see Figs. 3a, 4b). To achieve this, we fitted a linear regression to a moving window of 60 s of turbidity data and identified the average rate of change over that interval (i.e., the slope of the regression). The 60-s moving window frame was shifted over the entire dataset by an interval of 4 s. Statistical comparisons of the erosion threshold between the treatments were performed via one-way ANOVA.

Lab experiment—Development of shear stress resistance

On ridge-runnel patterns in the field, prolonged water retention and pooling are typically observed in the runnels during low tide. Surface water run-off from ridges into the runnels potentially enhances drying of the sediment bed on the ridges while the pooling surface water hinders drying in the runnels. We performed an experiment in the lab to test how sediment drying and pooling surface water affect the development of an erosion-resistant surface layer in cohesive sediment. In this experiment, sediment collected from the field site at Zuidgors was remobilized by mixing it with filtered seawater from the Eastern Scheldt estuary in the Dutch delta (30 ppt), using a cement mixer. The unconsolidated mud was then poured into six sediment sample boxes ($20 \times 12.5 \times 10 \text{ cm}$; length $\times$ width $\times$ height) and allowed to settle in intertidal conditions in a tidal tank (Cao et al. 2018) for 24 h. Tidal tanks simulate periodic tidal inundation by pumping water from a reservoir chamber into an experimental chamber at programmable intervals. Inside this chamber, the sediment boxes experienced inundation by seawater from the Eastern Scheldt for 2 h every 12 h cycle. The six sample

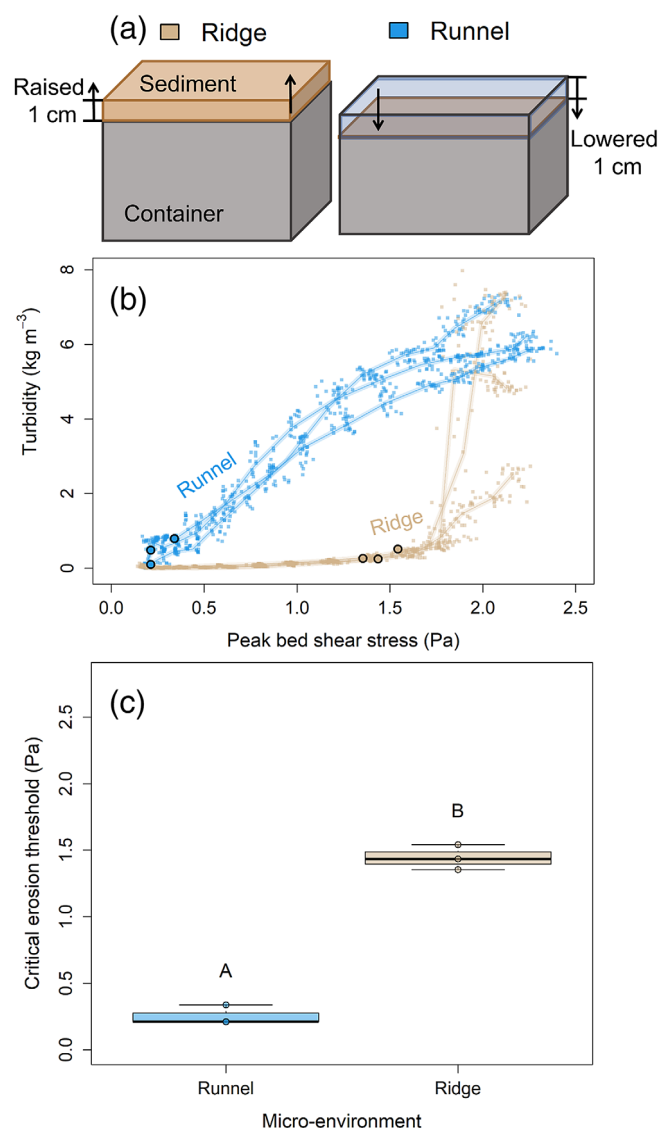


Fig. 4. Development of erosion resistance in a consolidating bed of cohesive sediment left in intertidal conditions for 24 h. Very large differences in erodibility developed between sediment cores that were able to dewater during low tide (ridge, **a**—left), and sediment left beneath a shallow pool of water (runnel, **a**—right). Panel (**b**) shows the raw results of the OsCar erosion trials. The larger colored circles represent the estimated erosion threshold for each trial ($n = 3$), and correspond to data points in panel (**c**) used in the statistical analysis.

boxes were split into two experimental groups ($n = 3$), imitating the conditions experienced on (1) runnels and (2) ridges. In runnel treatments (1), the surface of the sediment was left 1 cm below the top of the box so that pooling water would always remain over the sediment. In the ridge treatment (2), the sediment surface instead protruded 1 cm above the edge of the sediment core (see Fig. 4a for visual representation). To prevent the growth of microphytobenthos, which can affect sediment erodibility (Le Hir et al. 2007; Stal 2010), the tank

was wrapped in a layer of thick black plastic sheeting to keep the interior completely dark. The absence of microphytobenthos was verified in each replicate using an imaging-PAM Chlorophyll Fluorescence System (MINI Version IMAGING-PAM M-Series; WALZ). The temperature of the climate chamber where the experiment was performed was 18°C. After 24 h the sediment samples were then placed in the OsCar flume to determine their critical erosion threshold, following the same procedure as explained above. Statistical comparisons between the treatments were performed via one-way ANOVA, as seen in the earlier OsCar trials.

Field measurements—Development of sediment shear strength

To determine the time scale over which differences in sediment erosion resistance develop in cohesive sediments in the field, we performed a 1-d field campaign in which we repeatedly measured shear strength at the sediment surface via a Torvane test using a Gilson HM-504A Handheld Shear Vane (Gilson Company) with a 47.6 mm diameter vane size. Repeated measures were taken at intervals of 30 to an hour during the low-tide interval, over a period of roughly 4.5 h. These measurements were performed at the patterned tidal flat of Zuidgors in the Dutch Western Scheldt. In total five measuring locations were selected along an 800 m transect ranging from the foot of the dike to the low water line at low tide (a vertical range of 3.5 m, see Supporting Information Fig. S3 for details). Of the five measuring locations, the two nearest the dike were within a ridge-runnel pattern. To compare shear strength development between ridge and runnel microenvironment, paired measurements were taken at the highest measuring location both on ridge sediment and within an adjacent runnel, which remained submerged in a shallow layer of pooling water over the entire sampling period. At all other locations, measurements were taken on the ridge of the pattern if differences in microtopographic relief were present. Two replicate Torvane measurements were taken at each measuring moment. A linear regression was fit between shear strength and time to estimate the rate of change in the shear strength over the measured period, to characterize both differences between the ridge and runnel (Fig. 5), and differences over the elevation gradient (Supporting Information Fig. S3).

Lab experiment—Regeneration time of benthic algae after sediment surface disturbance

Benthic algae are commonly associated with ridge-runnel patterns, and much work has gone into demonstrating their role in sediment shear strength development (MacIntyre et al. 1996; Le Hir et al. 2007; Stal 2010). Therefore, we lastly designed a mesocosm experiment with the aim of distinguishing the role of physical sediment strength development (through sediment drying or waterlogging) from biological effects (algal growth). To do so, we compared the time scales of (1) the sediment strength development observed

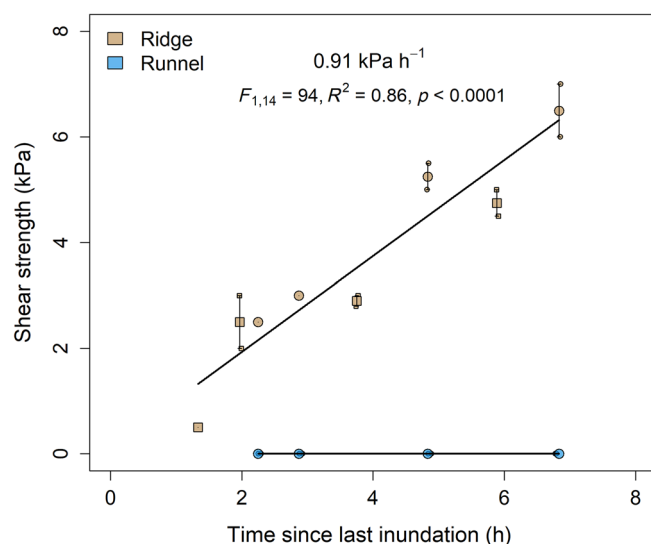


Fig. 5. Development of sediment shear strength during a single low tide interval on the tidal flat at Zuidgors in the Scheldt estuary within a ridge-runnel pattern. The small points represent replicate measured values ($n = 2$), while the large points represent the mean value at a given measurement moment. Error bars indicate standard error. The shape of the point indicates the location at which the measurement was taken (location 1: circle, location 2: square; see Supporting Information Fig. S3 for details). Both locations were within 200 m of each other. Paired ridge and runnel measurements at location 1 (circles) were less than 5 m apart.

in the field and in the lab experiment described above and (2) the development period required for benthic algae to recolonize the sediment surface in the aftermath of a small sediment disturbance (4 mm of artificial erosion or accretion).

To begin, sediment taken from the patterned tidal flat at Keetenisse was distributed amongst 28, 2.7-cm $\varnothing$ sediment pots. These replicate pots were placed in intertidal conditions (inundated for 2 h every 12-h cycle) in a tidal tank for 1 month, until a layer of fibrous green benthic algae (*Vaucheria* sp.) was fully developed over all replicates. Replicate pots were then divided into accretion and erosion treatment groups ($n = 14$). In the accretion treatment, the sediment surface was lowered to 4 mm below the lip of the pot by removing a 4-mm width disk from the bottom of the sediment pot. Unconsolidated sediment was then poured on top of each pot until the sediment surface was again flush with the top of the pot. In the erosion treatment, the sediment surface was instead pushed 4 mm above the top of the pot by adding a 4-mm width disk to the bottom. The protruding 4 mm of sediment was then removed so that the sediment surface was again level with the pot. Tidal tanks were filled with brackish water (5 ppt) created from mixing 30 ppt filtered Eastern Scheldt water and freshwater, fertilized with 10 g L⁻¹ of slow-release fertilizer pellets. The environment was set to 18°C, 1000–1500 lx, and a 16-h light, 8-h dark (summer) day–night cycle (as prescribed in van de Vijssel et al. 2021).

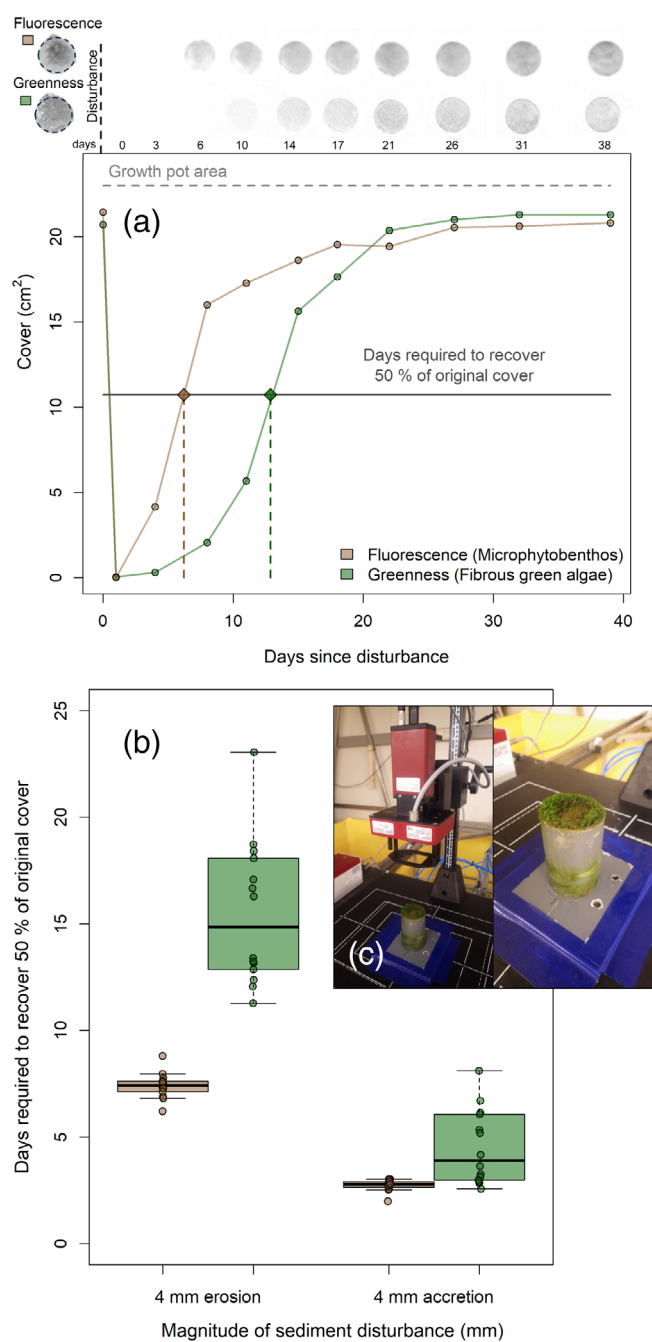


Fig. 6. Results of the benthic algae disturbance-recovery mesocosm experiment. The circular images above panel (a) show the raw fluorescence and greenness images corresponding to the cover values in the figure below them. The figure in panel (a) shows the recovery of fluorescent and green cover over a 40-d period for a single experimental replicate. The time required to reach 50% of the initial cover is estimated from this time series and used to compare recovery time between treatments across the experiment (as shown in panel b). In panel (c), the setup used to take standardized fluorescence images is shown beside an example of a sediment core partially recolonized by fibrous green algae and microphytobenthos.

The regeneration of benthic algae was monitored over a 40-d period with top-down images from a standardized

distance (Fig. 6a). Both fluorescence and the greenness index were monitored to differentiate between the development of (1) microphytobenthos, which are fluorescent but not green and (2) fibrous green algae, which are both fluorescent and green. Fluorescence was measured with an imaging-PAM Chlorophyll Fluorescence System (MINI Version IMAGING-PAM M-Series; WALZ). The greenness index was measured with an RGB (red–green–blue) camera according to Eq. 3.

$$\text{Greenness index} = (2 \times G) - R - B. \quad (3)$$

When the fluorescence or greenness index of a pixel in an image overcame a threshold value (fluorescence: 0.02, greenness index: 0.05), that pixel was considered to have recovered. These thresholds were set to be as low as practical to detect early recovery while remaining capable of distinguishing recovery from background noise. The total recovered area was then calculated as the proportion of recovered pixels within the circular region of interest (marked by the edges of the pot) in the image. We used this data to estimate the recovery rate of each replicate, defining it as the length of time required to return to half of its initial cover, prior to the disturbance (Fig. 6a). The recovery time was then compared between disturbance treatments for both fluorescent and green recovery using one-way ANOVA tests. All data analyses were performed in R version 2023.03.0+386 (R Core Team 2023).

Results

Sediment dynamics and erodibility

SED sensor records of the sediment surface on the patterned tidal flat at Keetenisse indicated that daily bed-level dynamics contrasted strongly between the ridge and the runnel of the pattern (Fig. 2). On the ridge, the average change in daily bed level was three times smaller ($2.17 \pm 0.03 \text{ mm d}^{-1}$) than in the adjacent runnel ($6.55 \pm 0.31 \text{ mm d}^{-1}$). Sediment samples taken from the ridges were also much more resistant to erosion (critical erosion threshold: $2.3 \pm 0.12 \text{ Pa}$) than the sediment in the runnels (critical erosion threshold: $0.47 \pm 0.08 \text{ Pa}$; $n = 3$, $p = 1.4 \times 10^{-5}$). However, once the top centimeter of the sediment surface was experimentally removed from the ridge, it became indistinguishable from runnel sediment in terms of its erodibility (critical erosion threshold: $0.34 \pm 0.07 \text{ Pa}$; $n = 3$, $p = 0.58$; Fig. 3), indicating that the source of ridge sediment's resistance to erosion is concentrated at its surface.

Development of shear-stress resistance

Abiotically incubated sediment samples revealed that a cohesive sediment bed can develop significant resistance to erosion (critical erosion threshold: $1.44 \pm 0.05 \text{ Pa}$) in as little as 24 h when the sediment surface remains above water for a significant portion of the tidal cycle (10 of every 12 h). However, erosion resistance does not develop if the sediment

remains permanently submerged under a thin layer of pooling water (critical erosion threshold: 0.25 ± 0.04 Pa; $n = 3$, $p = 7.3 \times 10^{-5}$; Fig. 4). Note that these experiments were performed in dark conditions to exclude any effects of benthic algae.

In addition to these laboratory tests, we were also able to measure the development of shear strength at the sediment surface on a patterned tidal flat in the field. During a single low tide window, the shear strength of ridge sediment on the tidal flat, captured within a range between 0.5 and 7 kPa, increased at a rate of 0.91 ± 0.11 kPa h⁻¹ ($F_{1,14} = 94$, $n = 24$, $R^2 = 0.86$, $p < 0.0001$; Fig. 5). Meanwhile in an adjacent runnel, where the sediment remained submerged in pooling water, the shear strength of the sediment remained consistently below measurable levels throughout the low tide interval.

Time scale of benthic algae reformation

The disturbance-recovery experiment on benthic algae reveals the mismatch in time scales between the abiotic rate of development of erosion resistance we observed, and the period required for benthic algae to recolonize a disturbed sediment bed (Fig. 6). The return of fluorescence to the sediment surface (indicating the presence of microphytobenthos) to at least 50% of initial levels required 2.7 ± 0.1 d after the accretion of 4 mm of sediment and twice that (7.4 ± 0.2) after 4 mm of erosion ($F_{1,26} = 716$, $n = 14$, $p < 2.2 \times 10^{-16}$). The return of fibrous green algae to the sediment surface took even longer (4 mm accretion: 4.5 ± 0.5 d, 4 mm erosion: 15.5 ± 0.9 d, $F_{1,26} = 117$, $n = 14$, $p = 4.2 \times 10^{-11}$). Although the timescales reported in this study are likely slower than what would occur in natural settings due to the use of artificial light, which has a lower intensity than natural sunlight, these results should be representative of the order of magnitude at which recolonization takes place. Overall, benthic algae recolonization required timescales on the order of several days to weeks, while we observed the development of sediment erodibility on the timescale of hours to a day in the lab and field.

Discussion

Resistant surface formation

In this study, we found that across ridge-runnel patterns, the sediment shear strength is much higher and erodibility lower on ridges than in runnels. Our lab incubation experiment demonstrates that these differences are caused by a thin, erosion-resistant surface layer that forms when cohesive sediment is able to dry-out on ridges during low tide; while pooling water in runnels prohibits the increase of erosion resistance. The development of the shear stress-resistant surface layer on ridges is likely caused by porewater loss at the surface via evaporation (Fagherazzi et al. 2017) and lateral porewater drainage into adjacent runnels (Anderson and Howell 1984; Fivash et al. 2020; Van Putte et al. 2020). The

loss of this porewater would increase sediment shear strength by decreasing its void ratio, thus increasing contact between particles, which is known to increase the cohesive bonds between electrostatically charged silt and clay particles (Amos et al. 2004; Bale et al. 2007; Fagherazzi et al. 2017). Conversely, in the high water-content sediment beneath pooling water, silt and clay particles are farther from each other, decreasing the strength of electrostatic bonds, and increasing erodibility (Winterwerp and van Kesteren 2004). However, it is also possible for cohesive sediment beds to gain shear strength over time, independent of water content, as long as they remain undisturbed due to the reorganization of sediment particles (Zreik et al. 1998). The combination of these effects could create conditions for the two microenvironments to substantially diverge due to both the initially lower erosion resistance in waterlogged sediments in the runnels, combined with the inability for the shear strength to develop via sediment reorganization because of frequent resuspension by water movement within the runnels.

Stress divergence within the ridge-runnel pattern

Fivash et al. (2023) demonstrated that the presence of ridge-runnel patterns on tidal flats increases the probability of vegetation establishment in future years. We expect that the suppression of erosion dynamics on the ridges, caused by the formation of this erosion-resistant surface layer, facilitates marsh establishment. Pioneer seedling establishment is normally disrupted by frequent, intense bed-level dynamics which either erode the root zone of the plants or bury them in sediment (Bouma et al. 2016; Cao et al. 2018; Willemsen et al. 2018). Since bed-level dynamics on ridges are reduced by around three times (compared to the runnels), this gives the pioneer seedlings an interval, on average, three times as long to develop a root zone sufficiently deep to withstand a given magnitude bed-level change (van Belzen et al. 2022). The reduced bed-level dynamics on the pattern ridges thus lead to a greater probability of seedling survival and facilitate the colonization of environments that would normally be too dynamic. This effect is observed to be strongest near the seaward limit of marsh extent (as defined in Balke et al. 2016), where conditions are, on average, more hostile for plant establishment. This aligns well with the theoretical notion of patterns as stress-redistributing features that have the greatest utility in more hostile environments (Rietkerk et al. 2004). Based on this evidence, we argue that ridge-runnel patterns perform a “stress divergence” function by restructuring the landscape into local refugia, that is, here ridges, where stress from erosion is reduced, allowing vegetation to expand into more hostile hydrodynamic environments.

Formation of ridge-runnel patterns via scale-dependent feedback

Scale-dependent feedback processes are known to produce patterned landscapes (Rietkerk and van de Koppel 2008) and

may help to explain how ridge-runnel patterns originally form (van de Vijssel et al. 2020, 2021). In a fully developed patterned landscape, pooling water is redistributed from the ridges into runnels, which promotes sediment drying and erosion-resistant surface development on the ridges while suppressing it in the waterlogged runnels. In addition to this, since runnels act as drainage conduits that concentrate water from a wide region, it follows that this greater discharge volume imposes greater shear stress in runnels during ebb tide (Williams et al. 2008). Together, these mechanisms create a self-reinforcing loop known as scale-dependent feedback (as defined in Rietkerk and van de Koppel 2008), that is (1) local positive feedback between the formation of ridges, sediment drying, and development of erosion resistance, which further sustains the ridge development; and (2) longer-distance negative feedback, where water drainage from the ridges into adjacent runnels leads to water pooling, which increases vulnerability to erosion in the runnels through both weaker sediment strength, and higher exposure to erosive forces. In its very earliest stages, ridge-runnel development on tidal flats can be considered an amplification of this scale-dependent feedback process, beginning from an irregular sediment surface with only very slight differences in bed level. Over such an irregular bed, surface water redistributes from marginally raised areas into their lower surroundings during low tide, which promotes erosion-resistant surface development locally on raised areas, and sustains erosion-vulnerable surfaces in small depressions. When erosive events occur, the spatial differences in erodibility intensify the topographic relief between erodible lower areas, and resistant higher areas, creating feedback that reinforces and self-organizes the ridge-runnel pattern (Fig. 7, see also the conceptual models of Weerman et al. 2010; van de Vijssel et al. 2021). Earlier field studies have proposed that a relationship between dewatering and soil strength development may underpin ridge-runnel pattern formation (Allen 1987; Blanchard et al. 2000; Williams et al. 2008). With this study, we provide the first clear experimental evidence to support this claim.

Time scale of disturbances mediates ecosystem state transitions

According to Fagherazzi et al. (2017), emerged mud flats maintain their acquired cohesive strength even when subjected to inundation. Yet, because of the thinness of the resistant surface layer and the frequency of erosion on the tidal flat, it seems that the layer itself must reform quickly and often in the wake of disturbances to have a persistent effect on its environment. Both our lab and field tests have shown that the reformation time of the layer takes place on the time scale of hours to a day. This intrinsic timescale appears to restrict ridge-runnel pattern formation to tidal flats situated high enough in the tidal frame where the high water level does not always inundate the site (Fivash et al. 2023), and

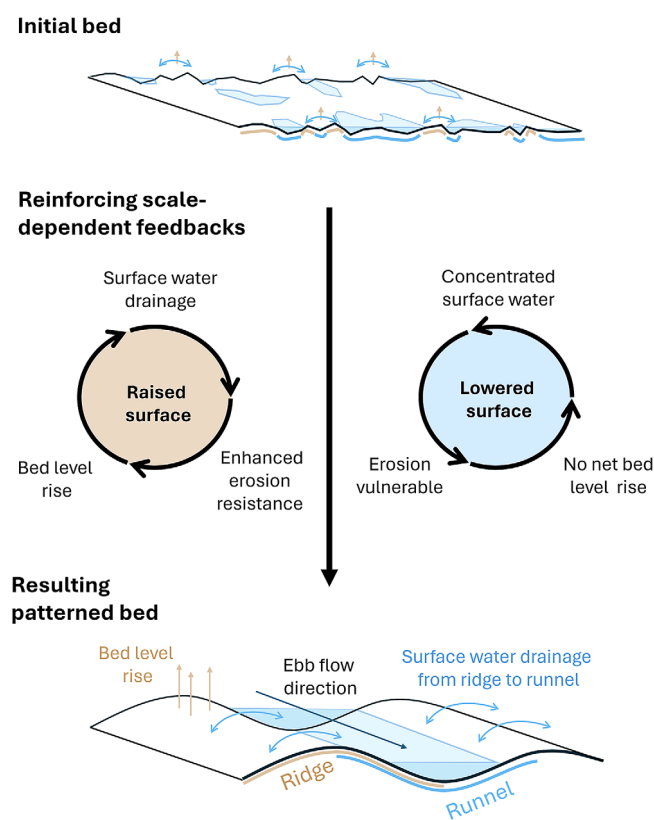


Fig. 7. Conceptual figure illustrating the formation of regular ridge-runnel patterns as a consequence of a scale-dependent feedback process. Here, small differences in bed level between adjacent areas cause surface water to flow into and concentrate in low regions, which allows higher areas to remain dry and develop cohesive sediment strength over a larger period during the low-tide interval. A reduction in erosion in slightly raised areas leads to an imbalance in accretion and erosion, causing bed-level rise, further intensifying local bed-level differences between high and low areas. Since raised ridges depend on the presence of nearby runnels to drain surface water to maintain their raised position, a periodic (regular) pattern develops. Through this process, initially random, small-scale variations in bed level are amplified into larger-scale variations and regularized into ridges and runnels of a characteristic length scale.

where hydrodynamic disturbances are more limited in impact (Willemsen et al. 2018).

There are other well-known biogeomorphic mechanisms that affect the erodibility of cohesive sediment on the tidal flat, such as the production of EPS by microphytobenthos (MacIntyre et al. 1996; Le Hir et al. 2007; Stal 2010), or the physical reinforcement of the sediment by fibrous algal mats (van de Vijssel et al. 2020, 2021). Benthic algae, which flourish on ridge-runnel patterns, have often been credited for having a major role in the development and stabilization of regular patterns (van de Koppel et al. 2001; Weerman et al. 2010; van de Vijssel et al. 2020). However, the results of our study suggest that their role in this process is secondary to the purely physical mechanisms of sediment drying and waterlogging, due to the shorter timescale on which the erosion-resistant layers

form in response to drying. It is worth noting that photosynthetic organisms are not the only organisms that can affect sediment properties. Many kinds of bacteria and fungi are also known to produce EPS (Mahapatra and Banerjee 2013; More et al. 2014), which affects sediment strength, and may also do so via other mechanisms. For instance, the cable bacteria present in tidal flats can also cause the migration of metals, for example, iron and calcium to the sediment surface, forming an armored surface layer (Geerlings et al. 2019). Within our experimental facilities sterilization of all microorganisms could not practicably be maintained. Therefore, the timescale at which soil properties develop as a consequence of these other groups and mechanisms remains an open question.

How generally do organisms leverage and amplify existing physical feedbacks?

On the tidal flat, there are other geomorphic structures, such as tidal creek networks and desiccation cracks, that restructure the stress and resource distribution in the environment in ways that benefit plants (van de Vijzel et al. 2020, 2023; Zhang et al. 2023). As with ridge-runnel patterns, these other features may yet be shown to act as critical initiation points for organisms piggybacking off the early physical feedbacks. But examples can also be found beyond the tidal flat of environments where organisms may be leveraging and amplifying existing physical processes to support their own growth. In deep-sea sand wave fields, tidal movement along the length of the sand wave decelerates around the lee face, concentrating the deposition of organic matter into the lee face of the wave. This represents a scale-dependent feedback that creates a locally richer environment from which a more abundant benthic infauna community can develop (Cheng et al. 2021), and potentially concentrate and re-circulate organic matter within the community thereafter. Deep-sea cold-water coral mounds drawdown organic matter through a similar means by acting as a vertical obstruction in the water column that enhances baroclinic tides (van der Kaaden et al. 2021). Here too, cold water corals may be initiated from structures on the seafloor that perform this role in a more limited manner before the coral mound begins to grow and amplify the feedback. These are just a few examples of potentially many more cases where physical feedbacks and environmental self-organization facilitate organisms that may then mimic and further amplify the pre-existing feedbacks.

Conclusion

In conclusion, we find that ridge-runnel patterns are likely created initially by abiotic self-organization of erosion-resistant regions that arise from the drying of cohesive sediment on spots that are initially slightly higher, while the pooling of water in the lower surroundings prevents the development of erosion resistance. These changes then impact the intensity of daily bed-level dynamics, leading to more stable

sediment on ridges and more erosion-vulnerable sediment in runnels. Through this process, erosion-resistant sediment beds can form deeper in the tidal frame, which can be more easily colonized by benthic algae, and pioneer vegetation. Based on these findings, we argue that spatial patterns facilitate state transitions in this system because they perform a stress divergence function that results from a physical process that begins long before biota—such as, algae and vegetation—become relevant. The abiotic initiation point acts as an essential stepping stone for biota to later gain control over the stress divergence feedback. We hence provide a clear example of how pure physical processes facilitate the formation of self-organized biogeomorphic landscapes. Given all of this, it may be worth considering whether other geomorphological patterns act similarly as the facilitators of ecological state shifts across other systems as well.

Data availability statement

The data that support the findings of this study are openly available in the research repository 4TU. Research Data, doi: [10.4121/b6c37815-dd5e-4cae-9776-9395ab0b3d9c](https://doi.org/10.4121/b6c37815-dd5e-4cae-9776-9395ab0b3d9c).

References

- Allen, J. R. L. 1987. Streamwise erosional structures in muddy sediments, Severn Estuary, southwestern UK. *Geogr. Ann. Ser. B* **69**: 37–46. doi:[10.1080/04353676.1987.11880195](https://doi.org/10.1080/04353676.1987.11880195)
- Amos, C. L., and others. 2004. The stability of tidal flats in Venice Lagoon—The results of in-situ measurements using two benthic, annular flumes. *J. Mar. Syst.* **51**: 211–241. doi:[10.1016/j.jmarsys.2004.05.013](https://doi.org/10.1016/j.jmarsys.2004.05.013)
- Anderson, F. E., and B. A. Howell. 1984. Dewatering of an unvegetated muddy tidal flat during exposure—Desiccation or drainage? *Estuaries* **7**: 225–232. doi:[10.2307/1352142](https://doi.org/10.2307/1352142)
- Bale, A. J., J. A. Stephens, and C. B. Harris. 2007. Critical erosion profiles in macro-tidal estuary sediments: Implications for the stability of intertidal mud and the slope of mud banks. *Cont. Shelf Res.* **27**: 2303–2312. doi:[10.1016/j.csr.2007.05.015](https://doi.org/10.1016/j.csr.2007.05.015)
- Balke, T., M. Stock, K. Jensen, T. J. Bouma, and M. Kleyer. 2016. A global analysis of the seaward salt marsh extent: The importance of tidal range. *Water Resour. Res.* **52**: 3775–3786. doi:[10.1002/2015WR018318](https://doi.org/10.1002/2015WR018318)
- Blanchard, G. F., and others. 2000. The effect of geomorphological structures on potential biostabilisation by micro-phytobenthos on intertidal mudflats. *Cont. Shelf Res.* **20**: 1243–1256. doi:[10.1016/S0278-4343\(00\)00021-2](https://doi.org/10.1016/S0278-4343(00)00021-2)
- Bouma, T. J., L. A. van Duren, S. Temmerman, T. Claverie, A. Blanco-Garcia, T. Ysebaert, and P. M. J. Herman. 2007. Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. *Cont. Shelf Res.* **27**: 1020–1045. doi:[10.1016/j.csr.2005.12.019](https://doi.org/10.1016/j.csr.2005.12.019)

- Bouma, T. J., M. Friedrichs, B. K. van Wesenbeeck, S. Temmerman, G. Graf, and P. M. J. Herman. 2009. Density-dependent linkage of scale-dependent feedbacks: A flume study on the intertidal macrophyte *Spartina anglica*. *Oikos* **118**: 260–268. doi:10.1111/j.1600-0706.2008.16892.x
- Bouma, T. J., and others. 2016. Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics. *Limnol. Oceanogr.* **61**: 2261–2275. doi:10.1002/lno.10374
- Cao, H., Z. Zhu, T. Balke, L. Zhang, and T. J. Bouma. 2018. Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration. *Limnol. Oceanogr.* **63**: 647–659. doi:10.1002/lno.10657
- Cao, H., and others. 2021. Salt marsh establishment in poorly consolidated muddy systems: Effects of surface drainage, elevation, and plant age. *Ecosphere* **12**: e03755. doi:10.1002/ecs2.3755
- Carling, P. A., J. J. Williams, I. W. Croudace, and C. L. Amos. 2009. Formation of mud ridge and runnels in the intertidal zone of the Severn Estuary, UK. *Cont. Shelf Res.* **29**: 1913–1926. doi:10.1016/j.csr.2008.12.009
- Cheng, C., B. W. Borsje, O. Beauchard, S. O'Flynn, T. Ysebaert, and K. Soetaert. 2021. Small-scale macrobenthic community structure along asymmetrical sand waves in an under-water seascape. *Mar. Ecol.* **42**: e12657. doi:10.1111/maec.12657
- Damme, S. V., E. Struyf, T. Maris, T. Ysebaert, F. Dehairs, M. Tackx, C. Heip, and P. Meire. 2005. Spatial and temporal patterns of water quality along the estuarine salinity gradient of the Scheldt estuary (Belgium and The Netherlands): Results of an integrated monitoring approach. *Hydrobiologia* **540**: 29–45. doi:10.1007/s10750-004-7102-2
- de Smit, J. C., M. G. Kleinhans, T. Gerkema, and T. J. Bouma. 2021. Quantifying natural sediment erodibility using a mobile oscillatory flow channel. *Estuar. Coast. Shelf Sci.* **262**: 107574. doi:10.1016/j.ecss.2021.107574
- Fagherazzi, S., T. Viggato, A. M. Vieillard, G. Mariotti, and R. W. Fulweiler. 2017. The effect of evaporation on the erodibility of mudflats in a mesotidal estuary. *Estuar. Coast. Shelf Sci.* **194**: 118–127. doi:10.1016/j.ecss.2017.06.011
- Fivash, G. S., J. van Belzen, R. J. M. Temmink, K. Dideren, W. Lengkeek, T. van der Heide, and T. J. Bouma. 2020. Elevated micro-topography boosts growth rates in *Salicornia procumbens* by amplifying a tidally driven oxygen pump: Implications for natural recruitment and restoration. *Ann. Bot.* **125**: 353–364. doi:10.1093/aob/mcz137
- Fivash, G. S., S. Temmerman, M. G. Kleinhans, M. Heuner, T. van der Heide, and T. J. Bouma. 2023. Early indicators of tidal ecosystem shifts in estuaries. *Nat. Commun.* **14**: 1911. doi:10.1038/s41467-023-37444-6
- Fivash, G. S., and others. 2021. Restoration of biogeomorphic systems by creating windows of opportunity to support natural establishment processes. *Ecol. Appl.* **31**: e02333. doi:10.1002/eap.2333
- Geerlings, N. M. J., E.-M. Zetsche, S. Hidalgo-Martinez, J. J. Middelburg, and F. J. R. Meysman. 2019. Mineral formation induced by cable bacteria performing long-distance electron transport in marine sediments. *Biogeosciences* **16**: 811–829. doi:10.5194/bg-16-811-2019
- Gilad, E., J. von Hardenberg, A. Provenzale, M. Shachak, and E. Meron. 2004. Ecosystem engineers: From pattern formation to habitat creation. *Phys. Rev. Lett.* **93**: 098105. doi:10.1103/PhysRevLett.93.098105
- Grandjean, T. J., J. C. de Smit, J. van Belzen, G. S. Fivash, J. van Dalen, T. Ysebaert, and T. J. Bouma. 2023. Morphodynamic signatures derived from daily surface elevation dynamics can explain the morphodynamic development of tidal flats. *Water Sci. Eng.* **16**: 14–25. doi:10.1016/j.wse.2022.11.003
- Hu, Z., W. Lenting, D. van der Wal, and T. J. Bouma. 2015. Continuous monitoring bed-level dynamics on an intertidal flat: Introducing novel, stand-alone high-resolution SED-sensors. *Geomorphology* **245**: 223–230. doi:10.1016/j.geomorph.2015.05.027
- Le Hir, P., Y. Monbet, and F. Orvain. 2007. Sediment erodability in sediment transport modelling: Can we account for biota effects? *Cont. Shelf Res.* **27**: 1116–1142. doi:10.1016/j.csr.2005.11.016
- MacIntyre, H. L., R. J. Geider, and D. C. Miller. 1996. Microphytobenthos: The ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. *Estuaries* **19**: 186–201. doi:10.2307/1352224
- Mahapatra, S., and D. Banerjee. 2013. Fungal exopolysaccharide: Production, composition and applications. *Microbiol. Insights* **6**: 1–16. doi:10.4137/MBI.S10957
- Meron, E. 2012. Pattern-formation approach to modelling spatially extended ecosystems. *Ecol. Model.* **234**: 70–82. doi:10.1016/j.ecolmodel.2011.05.035
- More, T. T., J. S. S. Yadav, S. Yan, R. D. Tyagi, and R. Y. Surampalli. 2014. Extracellular polymeric substances of bacteria and their potential environmental applications. *J. Environ. Manag.* **144**: 1–25. doi:10.1016/j.jenvman.2014.05.010
- R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rietkerk, M., and J. van de Koppel. 2008. Regular pattern formation in real ecosystems. *Trends Ecol. Evol.* **23**: 169–175. doi:10.1016/j.tree.2007.10.013
- Rietkerk, M., M. C. Boerlijst, F. van Langevelde, R. HilleRisLambers, J. V. de Koppel, L. Kumar, H. H. Prins, and A. M. de Roos. 2002. Self-organization of vegetation in arid ecosystems. *Am. Nat.* **160**: 524–530. doi:10.1086/342078
- Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**: 1926–1929. doi:10.1126/science.1101867

- Rietkerk, M., R. Bastiaanse, S. Banerjee, J. van de Koppel, M. Baudena, and A. Doelman. 2021. Evasion of tipping in complex systems through spatial pattern formation. *Science* **374**: eabj0359. doi:[10.1126/science.abj0359](https://doi.org/10.1126/science.abj0359)
- Scheffer, M., and others. 2009. Early-warning signals for critical transitions. *Nature* **461**: 53–59. doi:[10.1038/nature08227](https://doi.org/10.1038/nature08227)
- Stal, L. J. 2010. Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. *Ecol. Eng.* **36**: 236–245. doi:[10.1016/j.ecoleng.2008.12.032](https://doi.org/10.1016/j.ecoleng.2008.12.032)
- van Belzen, J., G. S. Fivash, Z. Hu, T. J. Bouma, and P. M. J. Herman. 2022. A probabilistic framework for windows of opportunity: The role of temporal variability in critical transitions. *J. R. Soc. Interface* **19**: 20220041. doi:[10.1098/rsif.2022.0041](https://doi.org/10.1098/rsif.2022.0041)
- van de Koppel, J., P. M. J. Herman, P. Thoolen, and C. H. R. Heip. 2001. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology* **82**: 3449–3461. doi:[10.1890/0012-9658\(2001\)082\[3449:DASSOI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3449:DASSOI]2.0.CO;2)
- van de Koppel, J., M. Rietkerk, N. Dankers, and P. J. M. Herman. 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. *Am. Nat.* **165**: E66–E77. doi:[10.1086/428362](https://doi.org/10.1086/428362)
- van der Kaaden, A.-S., and others. (2021). Feedbacks between hydrodynamics and cold-water coral mound development. *Deep Sea Research Part I: Oceanographic Research Papers*, **178**: 103641. <https://doi.org/10.1016/j.dsr.2021.103641>
- van de Vijssel, R. C., J. van Belzen, T. J. Bouma, D. van der Wal, V. Cusseddu, S. J. Purkis, M. Rietkerk, and J. van de Koppel. 2020. Estuarine biofilm patterns: Modern analogues for Precambrian self-organization. *Earth Surf. Process. Landforms* **45**: 1141–1154. doi:[10.1002/esp.4783](https://doi.org/10.1002/esp.4783)
- van de Vijssel, R. C., J. van Belzen, T. J. Bouma, D. Wal, and J. van de Koppel. 2021. Algal-induced biogeomorphic feedbacks lay the groundwork for coastal wetland development. *J. Geophys. Res.: Biogeosci.* **126**: e2021JG006515. doi:[10.1029/2021JG006515](https://doi.org/10.1029/2021JG006515)
- van de Vijssel, R. C., and others. 2023. Vegetation controls on channel network complexity in coastal wetlands. *Nat. Commun.* **14**: 7158. doi:[10.1038/s41467-023-42731-3](https://doi.org/10.1038/s41467-023-42731-3)
- Van Putte, N., and others. 2020. Groundwater dynamics in a restored tidal marsh are limited by historical soil compaction. *Estuar. Coast. Shelf Sci.* **244**: 106101. doi:[10.1016/j.ecss.2019.02.006](https://doi.org/10.1016/j.ecss.2019.02.006)
- van Wesenbeeck, B. K., J. van de Koppel, P. M. J. Herman, and T. J. Bouma. 2008. Does scale-dependent feedback explain spatial complexity in salt-marsh ecosystems? *Oikos* **117**: 152–159. doi:[10.1111/j.2007.0030-1299.16245.x](https://doi.org/10.1111/j.2007.0030-1299.16245.x)
- Wang, Z. B., W. Vandenbruwaene, M. Taal, and H. Winterwerp. 2019. Amplification and deformation of tidal wave in the Upper Scheldt Estuary. *Ocean Dyn.* **69**: 829–839. doi:[10.1007/s10236-019-01281-3](https://doi.org/10.1007/s10236-019-01281-3)
- Weerman, E. J., J. van de Koppel, M. B. Eppinga, F. Montserrat, Q. Liu, and P. M. J. Herman. 2010. Spatial self-organization on intertidal mudflats through biophysical stress divergence. *Am. Nat.* **176**: E15–E32. doi:[10.1086/652991](https://doi.org/10.1086/652991)
- Willemsen, P. W. J. M., and others. 2018. Quantifying bed level change at the transition of tidal flat and salt marsh: Can we understand the lateral location of the marsh edge? *J. Geophys. Res.: Earth Surf.* **123**: 2509–2524. doi:[10.1029/2018JF004742](https://doi.org/10.1029/2018JF004742)
- Williams, J. J., P. A. Carling, C. L. Amos, and C. Thompson. 2008. Field investigation of ridge–runnel dynamics on an intertidal mudflat. *Estuar. Coast. Shelf Sci.* **79**: 213–229. doi:[10.1016/j.ecss.2008.04.001](https://doi.org/10.1016/j.ecss.2008.04.001)
- Winterwerp, J. C., and W. G. M. van Kesteren [eds.]. 2004. Introduction to the physics of cohesive sediment in the marine environment. Elsevier.
- Zhang, K., J. Yan, Q. He, C. Xu, J. van de Koppel, B. Wang, B. Cui, and Q. Liu. 2023. Self-organized mud cracking amplifies the resilience of an iconic “Red Beach” salt marsh. *Sci. Adv.* **9**: eabq3520. doi:[10.1126/sciadv.abq3520](https://doi.org/10.1126/sciadv.abq3520)
- Zreik, D. A., B. G. Krishnappan, J. T. Germaine, O. S. Madsen, and C. C. Ladd. 1998. Erosional and mechanical strengths of deposited cohesive sediments. *J. Hydraul. Eng.* **124**: 1076–1085. doi:[10.1061/\(ASCE\)0733-9429\(1998\)124:11\(1076\)](https://doi.org/10.1061/(ASCE)0733-9429(1998)124:11(1076))

Acknowledgments

This research was financed through the German Federal Institute of Hydrology (BfG) in line with its R&D-Project Uferfunk (estuarine shoreline functions, M39630304077, Gregory S. Fivash). Gregory S. Fivash and Stijn Temmerman also acknowledge financial support from the Research Foundation Flanders (FWO grant nrs. G039022N and G031620N).

Conflict of Interest

The authors declare no conflict of interest.

Submitted 15 November 2023

Revised 28 March 2024

Accepted 10 April 2024

Associate editor: Ruth Reef