

External conditions drive optimal planting configurations for salt marsh restoration

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Abstract

1. Coastal salt marshes are threatened by erosion from storminess and sea level rise, with resulting losses in flood protection, wildlife and recreational space. Although more than \$1 billion has been spent to reconcile losses, restoration has had varying success because of poor survival of planted patches in challenging wave and current conditions. Marsh expansion after colonization or replanting is regulated by positive and negative feedbacks between vegetation density and sediment capture. Dense vegetation stimulates sediment capture and vertical patch growth, but negatively constrains patch expansion by concentrating hydrological energy into erosion gullies along patch edges. Conversely, low-density vegetation may not simulate enough sediment capture, which increases plant dislodgement mortality. The strengths of positive and negative feedbacks will vary with wave exposure, but this has never been tested in natural conditions.
2. We observed density-dependent sediment feedbacks, survival and lateral expansion by *Sporobolus anglicus* patches (0.8 × 0.8 m) planted at three levels of vegetation density, at each of three levels of wave forcing (three sites).
3. We found interactive effects of plant density and forcing on the strength of positive and negative feedbacks. Density-dependent feedbacks only emerged in moderate and exposed conditions: classic marsh tussock patch shapes, which arise due to combined positive (vertical growth) and negative (gullies) feedbacks, were only associated with high density vegetation under exposed conditions. At high exposure, survival was enhanced by dense planting, which diverted energy away from the vegetation. In sheltered conditions, expansion was the greatest at medium density, while dense patches had high mortality and erosion.
4. *Synthesis and applications.* Success of wetland restoration clearly hinges on considering interactions between environmental stress and planting density. In challenging high-exposure settings, dense planting in large patches should maximize success, as plant facilitation boosts sediment capture and negative edge effects (gullies) will represent a diminished proportion of larger patches. Yet, benefits of dense planting will switch from positive (facilitation) to negative (competition) with reduced environmental stress, when moderate-density planting might be optimal. Switches along stress gradients between positive and negative feedbacks

are common across ecosystems. We call for wider integration of facilitation and stress–gradient principles into restoration design to safeguard restoration successes.

KEYWORDS

planting, positive and negative feedbacks, restoration, saltmarsh, sediment, *Sporobolus anglicus*, stress–gradient hypothesis, survival and expansion

1 | INTRODUCTION

Fifty percent of global salt marsh habitat was lost in the last century (Silliman et al., 2015). Loss of salt marsh habitat is a concern since they offer important ecosystem services, such as being important nursery habitats for fisheries species (Kneib, 1997), sequestering rich stores of ‘blue carbon’ (Himes-Cornell, Pendleton, & Atiyah, 2018) and acting as effective natural flood protectors along global coastlines (Möller et al., 2014). Salt marshes are now facing increased pressure from emergent sea level rise, increased storminess and diminishing sediment supply (Kirwan & Megonigal, 2013; Leonardi, Ganju, & Fagherazzi, 2016; Mariotti & Fagherazzi, 2010) and it is likely that irreversible erosional switches from marshland to unvegetated mudflats will become more frequent. To date, over 1 billion US \$ has been spent on restoration to tackle worldwide salt marsh losses (Silliman et al., 2015). Despite this investment, the majority of restoration projects either fail completely (Cunha et al., 2012; Tanner & Parham, 2010) or result in only partial recovery of the ecosystem (Rey Benayas, Newton, Diaz, & Bullock, 2009; Suding, 2011). This could be due to poor restoration designs and justifies the need to re-consider planting strategies (Derksen-Hooijberg et al., 2017; Silliman et al., 2015).

Current restoration designs for seagrasses, mangroves, corals and salt marshes focus on maintaining empty spaces between out-planted propagules (dispersed design), to minimize negative intra-species interactions, such as competition (Gedan & Silliman, 2009; Silliman et al., 2015). Yet, these practices ignore current ecological theory that positive species interactions can facilitate organism success (Crotty & Bertness, 2015; Renzi, He, & Silliman, 2019; Stachowicz, 2001). They also neglect that species interactions (i.e. positive and negative) vary across environmental gradients, as implied by the stress–gradient hypothesis (Bertness & Callaway, 1994; Callaway & Walker, 1997), and hence that restoration designs need to be tailored to the environmental conditions at the site. Discussions about wetland planting configurations call for a switch to clumped designs to facilitate positive species interactions (Gedan & Silliman, 2009; Silliman et al., 2015). Here we combine observations of sediment feedbacks, plant survival and vegetation expansion to assess how optimal planting configurations vary across gradients in physical stress.

The key to successful salt marsh establishment and expansion is to promote positive interactions between the vegetation and the surrounding sediment at the pioneer stage (Balke, Herman, & Bouma, 2014). *Sporobolus anglicus* is a dominant pioneer species in the lower intertidal zones of western European salt marshes,

owing to its ability to tolerate harsh environmental conditions, such as frequent tidal inundation (Bouma et al., 2009). *Sporobolus* is therefore a model species to study mechanisms of marsh establishment and expansion (Balke et al., 2012). Initial development of *Sporobolus* patches has the consequence of dissipating wave energy. This can have both positive and negative feedbacks on marsh development. While energy dissipation stimulates vertical sediment build-up (‘accretion’) inside the vegetation canopy (Figure 1), thus enhancing plant survival at higher elevations, it can also lead to erosion gullies forming immediately outside the vegetation, resulting in a restriction of lateral patch expansion (Figure 1) (Bouma et al., 2009; van Hulzen, van Soelen, & Bouma, 2007; van Wesenbeeck et al., 2008).

Plant density determines switches between positive and negative sediment feedbacks, which ultimately affects the potential for the vegetation to develop into a bigger marsh (Bouma et al., 2005, 2007). High density *Sporobolus* vegetation encourages greater sediment deposition by reducing hydrological energy inside the canopy, leading to higher plant survival (Bouma et al., 2005, 2009; van Hulzen et al., 2007; van Wesenbeeck et al., 2008). At the same time, deeper erosion gullies form immediately outside dense vegetation as the energy is deflected and concentrated, which limits the opportunity for lateral patch expansion (Bouma et al., 2009; van Hulzen et al., 2007; van Wesenbeeck



FIGURE 1 Positive within-canopy and negative outside-canopy sediment effects of marsh vegetation on a tidal flat. Green arrow represents positive vertical sediment accretion, whilst the red arrow represents the formation of expansion-restricting erosion gullies next to the vegetation patch

et al., 2008). At low vegetation densities, less sediment deposition occurs inside the vegetation canopy as the plants deflect less energy, leaving the plants prone to mortality via dislodgement (Bouma et al., 2009; van Hulzen et al., 2007; van Wesenbeeck et al., 2008). Yet, low density patches have less gully formation at the vegetation boundary, thus retaining the potential for lateral expansion (Bouma et al., 2009; van Hulzen et al., 2007; van Wesenbeeck et al., 2008). Plant density-linked feedbacks are likely to vary with the amount of wave forcing in the system (Bouma et al., 2009; Bruno, Rand, Emery, & Bertness, 2017). For example, dense vegetation in low wave forcing might encourage sediment deposition without generating erosion gullies, because wave forcing is too low to scour the substrate along the patch perimeter. Presently, gully formation is known to be current generated (Wesenbeeck et al., 2008). Yet, waves also create erosional shear stresses on the seabed, which can match or exceed those of currents (Shi et al., 2017; Shi, Yang, Wang, Bouma, & Zhu, 2012). We argue that waves have the potential to generate gullies and restrict the lateral expansion of marsh patches, contributing to the effect of currents. We propose that an interaction between wave forcing and plant density regulates switches from positive feedback conditions of marsh vertical growth and plant survival to negative feedback constraints on lateral expansion.

Here we ask whether density-dependent sediment feedbacks, plant survival and vegetation lateral expansion vary with the amount of wave forcing in the system to affect the success of replanted patches of *S. anglicus*. We hypothesize that (a) wave forcing will affect density-dependent sediment feedbacks in *Sporobolus* patches, with effects such as sediment vertical accretion (positive feedback) and gullying (negative feedback) becoming more prominent as both vegetation density and wave forcing increase. (b) Plant survival will be highest under sheltered wave forcing conditions, and in the densest patches. (c) Patch lateral expansion will be lowest under exposed wave forcing conditions, and in the densest patches, due to accentuated scouring around the patch perimeter.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

A manipulative field experiment was conducted in Red Wharf Bay (53°19'03.1"N and 4°11'03.0"W) on the south east coast of the isle of Anglesey, North Wales (United Kingdom) (Figure S1). Red Wharf Bay is characterized by broad sand flats and low-lying sandy beaches. The spring tidal amplitude of the bay reaches 7.6 m, with water levels ranging from 0.4 to 7.6 m (relative to chart datum). Waves are generally wind generated. Experiments were performed at three sites within the bay, to represent a wave-forcing gradient; a wave exposed site in the east, a sheltered site in the west and a moderately exposed site in the middle (Figure S1). The three sites were located c. 1 km apart and 5.25–5.85 m above chart datum, with average inundation periods of 3, 2:40 and 2:30 hr per day, respectively. Wave observations (September–October 2018)

confirmed significant differences in wave heights between the three sites (Figure S2, $p < .001$). Wave heights during average days and stormy days were 0.2 and 0.4 m respectively at the exposed site in the east, 0.1 and 0.3 m at the moderate site and 0.02 and 0.1 m at the sheltered site in the west (Figure S3). Tidal current speeds did not vary significantly between the three sites with average flows of 0.44, 0.37 and 0.61 m/s at the exposed, moderate and sheltered sites respectively (Figure S4, $p = .23$). The sediment was predominantly fine sand at all three sites, with some differences in silt-clay and medium-coarse sand contents (Table S1).

Experimental plots were placed on the sandflat c. 10 m in front of the seaward limit of the main, eroding marsh. This planting area represented a potential marsh expansion area, as indicated by intermittent clumps of pioneer *S. anglicus*. Between June and August 2016, *Sporobolus* was transplanted to create plots of three density treatments (low, medium and high) (Figure 2a) at each of the three wave exposure sites. Each density treatment was replicated five times at each of the three exposure sites, giving a total of 45 plots (3 sites \times 3 densities \times 5 replicates) (Figure 2b). Replicates were blocked and treatments were allocated randomly within the blocks. Clumps of *Sporobolus* consisting of 15–20 shoots and associated roots and each covering approximately 0.1 \times 0.1 m were dug up from the marsh at each site and transplanted into 0.8 \times 0.8 m plots spaced >5 m apart. Five clumps were used to create low density treatments (c. 80–100 shoots per plot), 16 clumps for medium density treatments (c. 240–320 shoots per plot) and 32 clumps for high density treatments (c. 480–640 shoots per plot) (Figure 2a).

2.2 | Cross-plot sediment elevation profiles

Net change in sediment elevation was measured inside and immediately outside the planted plots using Sedimentation–Erosion–Bars (SEB's) (Nolte et al., 2013) (Figure 2c). For each vegetated plot, four 1 m long wooden posts were inserted into the sediment with 0.5 m above ground: two posts on the landward side of the vegetation and two on the seaward side (Figure 2c). Posts were placed 1 m away from the vegetation to avoid scouring effects. These posts marked the boundaries of the measured 'SEB areas' (Figure 2c). During observations of sediment elevation, a horizontal beam was temporarily clamped onto the seaward and the landward posts to make two trestles (Figure 2c); a straight-edge beam was then placed from the landward to the seaward trestles, and sediment elevation was quantified as the vertical distance from straight-edge beam to the sediment surface. Sediment elevation was measured at five points, referred to as measurement points A1, A2, B, C1 and C2, to create a cross-shore profile of the SEB area (Figure 2d): points were in the centre of the vegetation, and at 0.4 and 0.8 m away from the centre of the vegetation in both directions (Figure 2d). SEB measurements were taken in September 2016 and August 2017. Net sediment elevations were calculated by subtracting the initial height measurements (September 2016) from the final measurements in August 2017, a year after

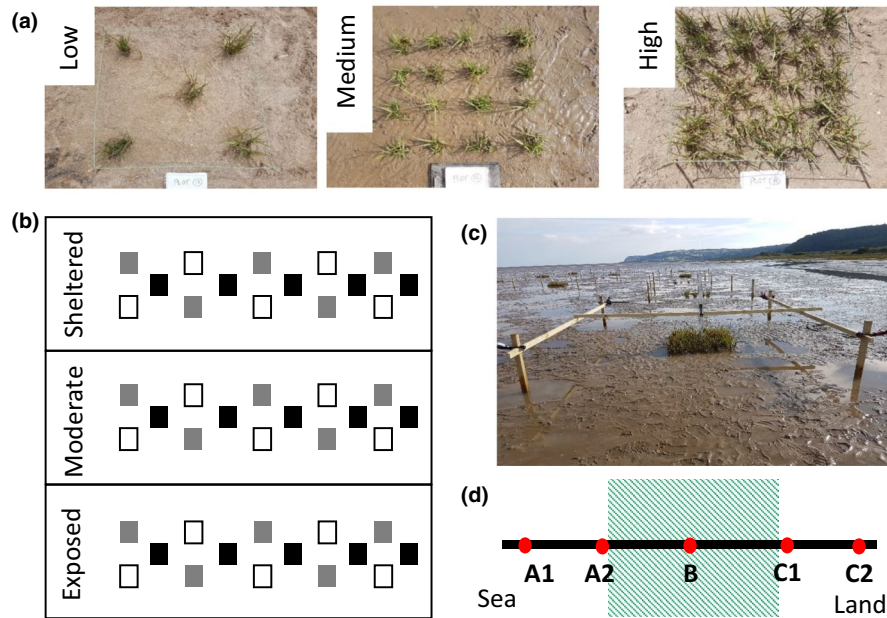


FIGURE 2 (a) Three vegetation density plots (0.8×0.8 m) created from clumps of *Sporobolus* consisting of 15–20 shoots and associated roots, giving 80–100 shoots (Low density), 240–320 shoots (Medium) and 460–640 shoots (High). (b) Layout of plot distribution (5/treatment) at a Sheltered, Moderately exposed and Exposed site. Grey, black and white squares represent Low, Medium and High density plots. (c) Four wooden posts (Sedimentation–Erosion–Bars, SEBs), one per corner, framed each experimental plot, and delineated the boundaries of the SEB observation area. The three horizontal bars were only in place whilst taking sediment elevation measurements. Observations of sediment elevation were made by measuring down from the horizontal bar centrally in the photo. (d) Vertical view of the position of the horizontal bar (black line) over the vegetation patch (green square), with the five positions (A1–C2: seaward to landward direction) where sediment elevations were measured to generate the cross-plot sediment elevation profile

the experiment started, and after a full growing season in 2017. August–September marks the peak of the salt marsh biomass in the UK. August–September was, therefore, an adequate time of the year to start and complete the experiment.

2.3 | Sediment digital elevation models

Before the initial and final measurements, photographs were taken of each SEB area by walking around the outside of the posts and pausing to take a photograph every 0.5 m along the SEB periphery. AGISOFT Photoscan Professional software was used to recover three-dimensional scene geometry from the photos, using a technique called structure from motion (Ullman, 1979). Ground control was achieved in the field with a Differential Global Positioning System (Leica dGPS GS08 GNSS) to an accuracy of ± 0.1 cm. Ground control points (GCPs) were taken from the tops of the SEB posts, ensuring an even distribution of GCPs across the modelled area (Betts & DeRose, 1999). Digital elevation models (DEMs) were constructed from the triangulated imagery in AGISOFT Photoscan Professional software by matching pixels or patterns of pixels (as in Betts & DeRose, 1999). The five replicates at each of the three sites were combined to create mean DEMs for each treatment, per site. This was done using the RASTER package in R (Hijmans, 2015). DEMs were then imported into ARCGIS (10.4) for further analysis. In ARCGIS (10.4), contour lines were superimposed onto the DEMs at 0.02 m intervals

to calculate a percentage of the SEB areas that had a net increase in sediment elevation (i.e. sediment deposition), a net decrease in sediment elevation (i.e. surface erosion) or had no change in sediment elevation (i.e. remained stable) at the end of the measurement period (August 2017).

2.4 | Plant survival

Plant survival was quantified using two approaches. For low and medium density plots, the number of clumps remaining at the end of the experiment (August 2017) were observed in the field and survival was equated to change in clump abundance (September 2016 minus August 2017, %). For high density plots, survival was determined using the DEMs: vegetated areas were identified by pixel classification and outlined by polygons, and survival was quantified as percent change of vegetated areas (September 2016 minus August 2017, %). We did not use the same approach to quantify survival in low/medium and high density plots because (a) vegetation was too dense in high-density plots to permit clump counting, and (b) DEM pixel resolution at the margin of individual clumps was sometimes insufficiently sharp to accurately delineate clump edges (wind moving plants: blurred edges in photos). Our mixing of approaches could lead to overestimation of survival in low/medium densities relative to high density plots. We recommend the reader treats our survival results with some caution.

2.5 | Patch lateral expansion

Lateral patch expansion was quantified in ARCGIS (10.4) using the DEMs. Polygons were drawn around vegetated areas at the beginning (September 2016) and at the end (August 2017) of the observation period. Vegetated areas at the end of the experiment were subtracted from areas at the beginning of the experiment to calculate a net change in the vegetated area (August 2017 minus September 2016, %).

2.6 | Data analysis

The response variable net change in sediment elevation was analysed using a linear mixed effects model with the fixed factors: wave forcing (three levels: sheltered, moderate and exposed), vegetation density (three levels: low, medium and high) and position of the sample across the cross-plot elevation profile (five levels: A1, A2, B, C1, C2). This model included the random effect of plot (45 levels, the 45 plots) on the intercept and on the slope, which allowed for a random shift around the intercept for each plot, but also allowed for different slopes for each position within the plot. The random intercept and slope model was clearly better than any other model with random effects, and was also better than the plain linear model according to the Akaike information criterion and likelihood ratio tests (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

The response variables percentage of plot areas that accreted, percentage of plot areas that eroded, percentage of plot areas that remained stable, percentage of plant survival and percentage of lateral patch expansion were analysed using linear models to test for the effects of the fixed factors wave forcing (three levels: sheltered, moderate and exposed) and vegetation density (three levels: low, medium and high).

Normality and homogeneity of variances were checked graphically by inspecting residuals and fitted values. All response variables followed the assumption of normality without need for data transformation. However, in some cases, there were obvious signs of heteroscedasticity in the residuals, and therefore the variance structure of the model was specified with weights using the NLME package (Pinheiro, Bates, DebRoy, & Sarkar, 2011; Zuur et al., 2009). Tukey HSD post hoc tests were performed on the data to determine treatment-specific differences within significant model variables. All statistical analyses were performed in the open-source statistical software R (R Core Team, 2017).

3 | RESULTS

3.1 | Net changes in surface elevation

Wave forcing had a significant effect on the net change in sediment elevation within and around *S. anglicus* patches (Figure 3; Table S2). With increase in wave forcing, the cross-shore profile changed

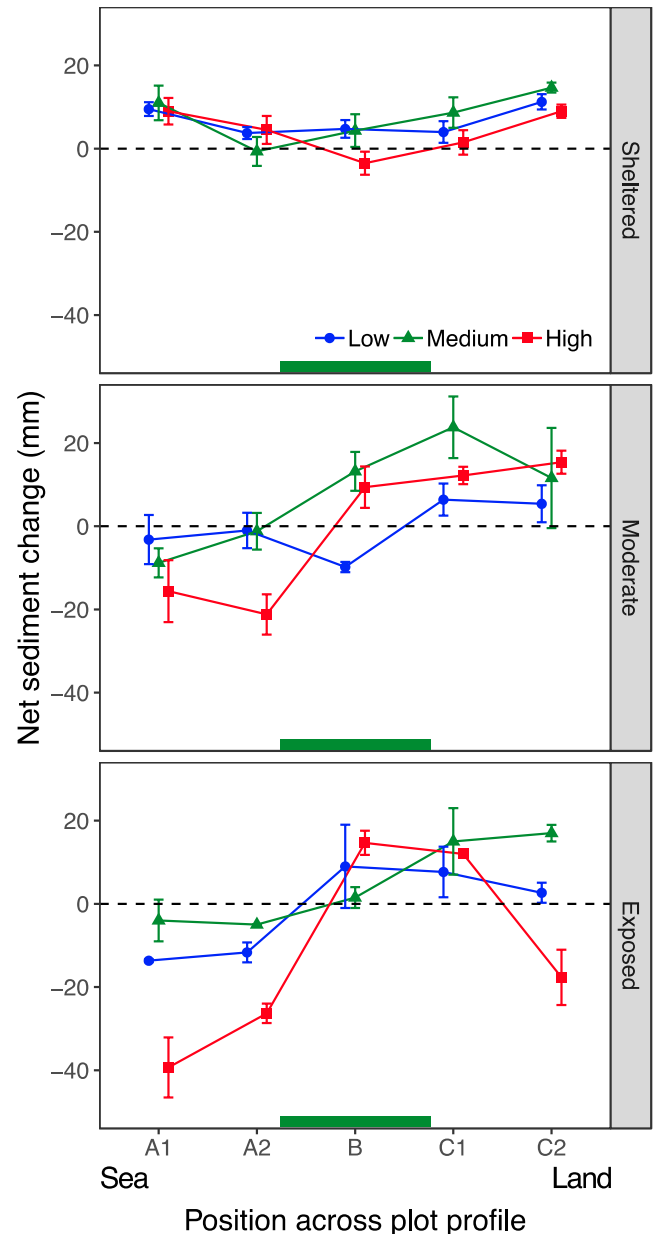


FIGURE 3 The mean \pm SE net change in sediment elevation, from the first (September 2016) to the last observation (August 2017) across cross-plot profiles within low, medium and high density vegetation at the sheltered, moderate and exposed sites ($n = 225$). X-axis codes: A1 and A2 represent measurements taken in front of the patch (seaward side), B in the middle of the patch, and C1 and C2 behind the patch (landward side). Green rectangle on x-axis represents the vegetated area of the plot

from relatively flat (sheltered), to sloping (moderate exposure) to humped (exposed), with the landscape dipping on the seaward side of patches and lifting over the vegetation itself (Figure 3). Sediment erosion always occurred on the seaward side, facing the waves, whilst accretion mainly occurred in the middle and on the landward side sheltered from waves (Figures 3 and 4; Table S3). While the seaward to landward lift in the landscape tended to steepen with increasing plant density (Figure 3; Table S2), it was wave forcing that determined plant density effects, highlighting the existence

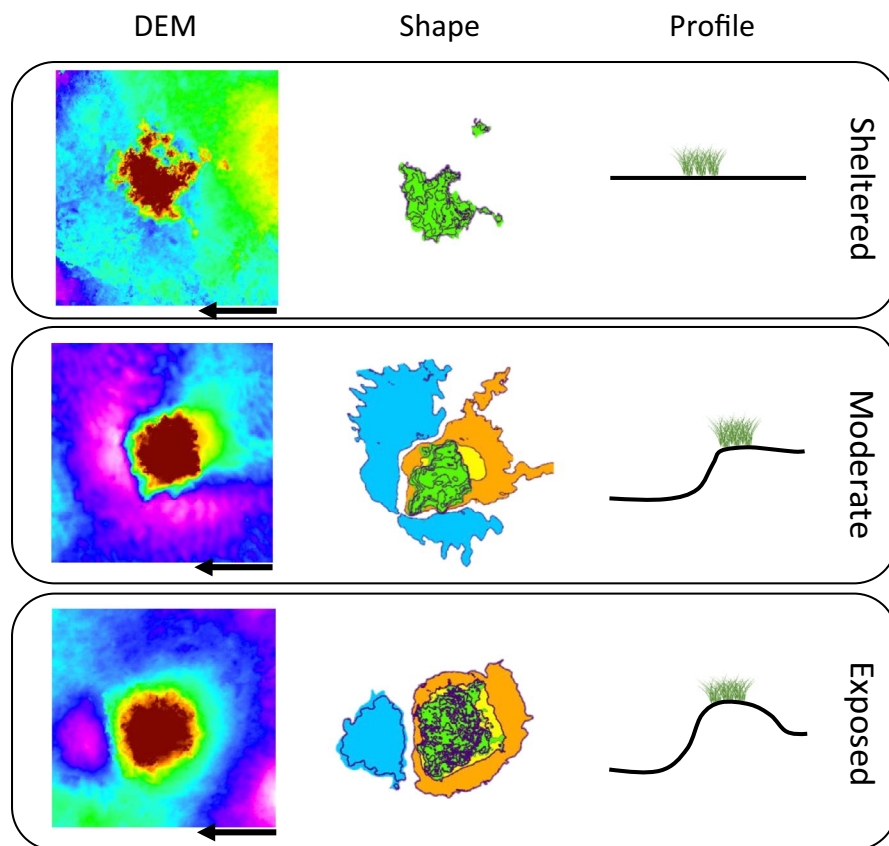


FIGURE 4 Schematic representation of the tussock shapes and profiles formed by high density vegetation at the sheltered, moderate and exposed sites ($n = 15$). The mean digital elevation models (DEM) represent sediment bed elevations (blue to red colouring = low to high elevations) in the 2×2 m DEM areas. The black arrow below the DEMs points towards the sea. Tussock shapes drawn from the percentage of vegetated (green), deposited (yellow and orange), and eroded (blue) areas calculated from the mean DEMs. Schematic profiles represent cross-sections of the tussock shapes

of a wave forcing \times plant density interaction (Figure 3; Table S2). Specifically, the cross-plot elevation profiles remained relatively flat at the sheltered site, regardless of vegetation density, whilst medium and high density patches caused strong sedimentation and erosion patterns at the moderate and exposed sites, leading to the formation of dome-shaped tussocks (Figures 3 and 4). Tussock formation was especially marked in high density patches at the moderate and exposed sites (Figures 3, 4 and S5; Table S3). Patch shape formation as a result of sediment deposition and erosion gully formation was therefore most consistent around the densest patches at the most exposed sites (Figures 4 and S5). The influence of wave forcing, vegetation density the position of the sampling points across the cross-plot elevation profile and their interactions explained 51% of the variance of the net sediment elevation change within the plots. Including the random effect of plots (on the intercept and slope of the response variable) into the model increased its predictive power to 95% (Table S2).

3.2 | Plant survival

Wave forcing, vegetation density and their interaction had a significant effect on plant survival (Figure 5; Table S3). As with net sediment elevation change, density-dependence only became obvious as wave forcing increased: low, medium and high density plots in the sheltered and moderate sites all had similar plant survival, while survival at the high density plots in the exposed site

was 25% and 50% higher than in the low and medium density plots respectively (Figure 5; Tables S3 and S4). The influence of wave forcing, vegetation density and their interaction explained 45% of the variance in plant survival (Table S3).

3.3 | Patch lateral expansion

Wave forcing, vegetation density and their interaction had a significant effect on patch lateral expansion (Figure 5; Table S3), with greater expansion at the sheltered than the moderate and exposed sites. Vegetation density also affected patch growth, overall generating significantly higher expansion in medium than high and low density patches (Figure 5; Table S3). Yet, density effects were moderated by wave exposure: they were only significant at the sheltered site, where medium density patches expanded more (221%) than other density patches (Figure 5; Table S3), again showing that wave forcing is a determinant of density effects. The influence of wave forcing, vegetation density and their interaction explained 77% of the variance associated with patch lateral expansion (Table S3).

4 | DISCUSSION

This study shows that wave forcing regulates the strength and direction of plant density-dependent feedbacks on sediment distribution

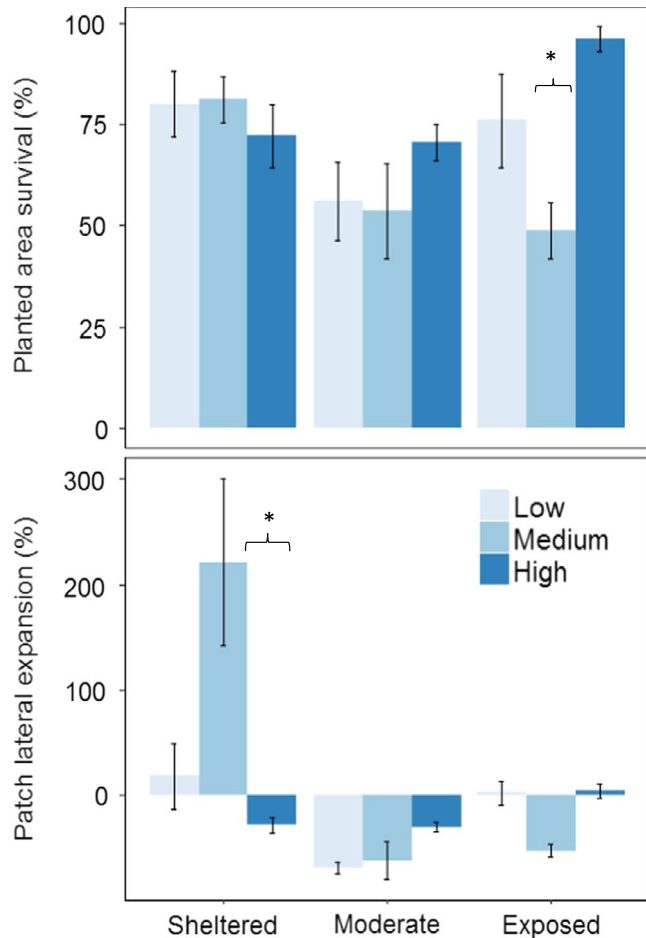


FIGURE 5 The mean \pm SE survival (of the originally planted area) and expansion (area cover of plants outside the planted areas) of low, medium and high density *Sporobolus* patches at the sheltered, moderate and exposed sites ($n = 45$). Significant differences between the sites are indicated as resulting from post hoc tests ($*p < .05$)

(positive sediment trapping and negative gully formation)—a process that ultimately determines whether vegetation patches in fluvial systems and coastal wetlands expand or erode (Corenblit, Steiger, Gurnell, Tabacchi, & Roques, 2009; Duarte, Losada, Hendriks, Mazarrasa, & Marba., 2013; van Maanen, Coco, & Bryan, 2015; Zong & Nepf, 2009). Whilst previous studies have demonstrated plant density effects on sediment feedbacks in flume settings (e.g. Bouma et al., 2009), this study goes further to show, for the first time in a natural setting, and over much longer time scales than previous studies, that hydrodynamics affect the strength of density-dependent sediment feedbacks across a forcing gradient, and that waves are a main contributor to this pattern. In the present study, feedbacks became more prominent with increasing vegetation density, but only under the highest wave force conditions. High density vegetation patches behaved as a solid unit in exposed conditions, deflecting wave energy away and encouraging sediment build-up, leading to the formation of classic dome-shaped tussocks (van Wesenbeeck et al., 2008). While the deflection of wave energy boosted plant survival, it also generated erosion gullies around

the vegetation, discouraging patch lateral expansion. High density patches in sheltered wave conditions had no major sediment accretion and no gully formation, but had high mortality and smaller finishing patch sizes than high-density treatments at higher levels of wave exposure, possibly as a result of increased within-patch plant competition.

Similar density-dependence has been described in other systems where scale-dependent (i.e. within and outside the vegetated patch) positive and negative effects fluctuate with density or biomass (Rietkerk et al., 2002; van de Koppel, Rietkerk, Dankers, & Herman, 2005). For example, diatom-aggregated biofilms trap fine sediments on mudflats to create hummocks that prevent them from being eroded away, but simultaneous erosion gullies form around the hummocks preventing the diatoms from aggregating outside (Ysebaert, Hart, & Herman, 2009). Mussels aggregate to protect themselves from erosion by waves and currents, but this has a simultaneous negative effect as algal food resources are depleted, thus reducing their survival inside the aggregations (van de Koppel et al., 2005). The strength of these feedbacks are strongly dependent on the amount of stress in the system (e.g. waves, currents, light, temperature) and our findings validate, in a wave forcing context, the stress-gradient hypothesis, which predicts a switch in the relative importance of positive and negative feedbacks between individuals along gradients in abiotic conditions (Bertness & Callaway, 1994; Bruno & Bertness, 2001).

Under high wave force conditions, wetland plants benefit from the additional protection provided by neighbouring individuals within high-density patches, thus promoting a positive (facilitative) interaction between individuals (Bertness & Shumway, 1993; Callaway & Walker, 1997; He, Bertness, & Altieri, 2013). In contrast, under lower wave force conditions, the benefits of neighbouring plants absorbing hydrological energy are outweighed by the negative effects of plant-plant competition for light, water and nutrients (Bertness & Callaway, 1994; Callaway & Walker, 1997; He et al., 2013). Species interactions may shift from competitive to facilitative with increasing environmental stress (Bertness & Callaway, 1994; He et al., 2013), as observed across a number of ecosystems (Bertness & Callaway, 1994; Bertness, Leonard, Levine, Schmidt, & Ingraham, 1999; Choler, Michalet, & Callaway, 2001). For example, in alpine forests, growth facilitation between individual trees increases at stressful higher altitudes, whilst competition is the dominant interaction at more benign lower altitudes (Choler et al., 2001). On rocky shores, species interactions switch from positive to negative with decreasing elevation, as individuals compete for space on the more frequently tidal-inundated low shore (Bertness et al., 1999).

Vegetation patchiness that arises from the feedback processes described here is frequently seen in salt marsh pioneer zones under natural conditions (Wang & Temmerman, 2013; van Wesenbeeck et al., 2008). The formation of dome-shaped tussocks was thought purely the outcome of plant engineering, and to be particularly pronounced in high density vegetation (Bouma et al., 2009; van Hulzen et al., 2007). Here, we show that tussocks arise from an interaction between vegetation density and hydrodynamics. Under lower wave

forcing conditions, *Sporobolus* should be able to exist at higher densities as the competitive interactions observed here, and the absence of erosional sediment feedbacks at the sheltered site is likely to permit the expansion of high density tussocks, as observed elsewhere (Bouma et al., 2009).

The study shows that wave exposure is the main cause of vegetation–sediment feedbacks that lead to the formation of vegetation tussocks and erosion gullies. This is new; previous studies have focused on currents as the main cause for tussock formation (Bouma et al., 2009, 2013; van Wesenbeeck et al., 2008). Waves are shallow in marsh areas, typically <0.5 m as in this study; yet they create erosional shear stresses on the seabed that match or exceed those of currents (Shi et al., 2017, 2012). For currents, dense vegetation diverts forcing around patches, causing acceleration of hydrological energy at the patch perimeter, which increases shear stress to form erosion gullies (Bouma et al., 2009, 2013; van Wesenbeeck et al., 2008). Here, we had a natural situation with both waves and currents, where only wave forcing differed between the three exposure sites, suggesting that wave–current interactions generated the observed differences in tussocks and gully formation between sites. The physics behind wave–current interactions on erosion processes are complex and not well understood (Maza et al., 2015; Shi et al., 2012, 2017; Yang & Irish, 2018). We propose a few simple principles that might explain the observed wave–current induced sediment patterns around the vegetation patches (Figure S6). We think flow deflection around the patch is key to gully formation (Figure S6a). Having waves in addition to current flow will likely strengthen the flow deflection effect around the patch (Figure S6b) and bring more sediment into motion through augmenting shear stress (Shi et al., 2017). This effect should be strengthened by wave refraction, by creating stronger waves alongside vegetation patches (Figure S6b). Wave reflection by (dense) vegetation is also likely to boost turbulence and erosion at the seaward side of the tussock (Figure S6c), putting sediment into temporary suspension only to settle out over the patch, when the vegetation attenuates the hydrological energy, causing patches to grow vertically into tussock shapes. These explanations of the patterns we observed require further testing. Obtaining a full understanding of the physical processes associated with wave–current–vegetation interactions require dedicated hydrodynamic research in controlled experimental conditions that is beyond the scope of this study.

4.1 | Implications for management: restoration

Our study findings are helpful for choosing planting configurations in salt marsh restoration. Principally, they highlight the need to consider wave forcing conditions before deciding on planting designs, particularly where marshes are located on open coasts and/or where the fetch in front of the marsh is sufficient to generate wave heights similar to those encountered here at the moderately exposed and exposed sites (>0.1 m). Figure 6 summarizes the outcomes of low, medium and high density transplanting of *Sporobolus* on sediment feedbacks (Figure 6a) and patch survival and expansion (Figure 6b). It illustrates, for instance,

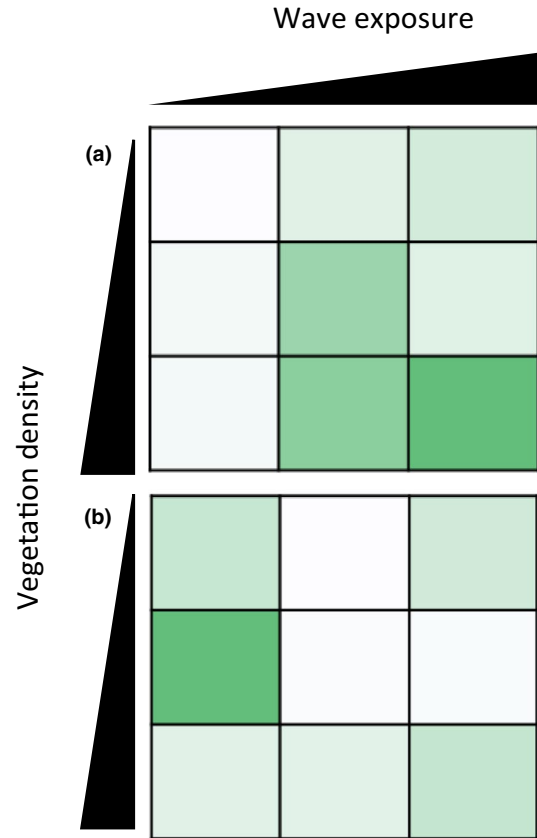


FIGURE 6 Conceptual representation of the effects of vegetation density and wave exposure on (a) sediment feedbacks (sediment deposition/erosion, gully formation), and (b) the survival and expansion of planted areas. The colour gradient from dark green to white signifies a decrease in the strength of plant sediment feedbacks. For example, for the low-density/low-exposure combination in figure (a) the white box implies minimal plant feedback on sediment deposition and erosion, with no gully formation. In figure (a) the high density/exposure box is dark green, signifying strong plant feedback on sediment, including negative effects like gully formation. In (b) colour changes from dark green to white indicate a switch from high to low patch survival and expansion. Thus, for medium-density planting in sheltered conditions the box is dark green, as the potential for survival and expansion is maximal

that planting low density vegetation at sheltered sites results in little or no sediment deposition (signified by light coloured box in top-left corner of Figure 6a), with only moderate plant survival and patch lateral expansion (indicated by a medium shade of green in the top-left box of Figure 6b), despite lack of gully formation. Medium density planting might be a better option in sheltered conditions, as it should maximize survival and patch expansion. At exposed sites, planting low-density vegetation results in modest sediment deposition and mild erosion gully formation outside patches (Figure 6a, top-right box), offering only moderate scope for plant survival and patch expansion (Figure 6b, top-right box). Planting high density patches in wave exposed conditions will maximize plant survival (Figure 6b, bottom-right box) and sediment capture (Figure 6a, bottom-right box); however, patch expansion will be constrained by erosion gullies (Figure 6b). Here we have considered

wave forcing as the main stressor for young patches of *Sporobolus*. We do not know whether the documented feedbacks to wave forcing will persist in multi-stressor contexts (salinity, temperature, nutrients, etc.), and whether patch size and planting density will determine patch survival in a similar way then. Larger patches of *Sporobolus* do recover better from drought conditions (Angelini & Silliman, 2012) and increased inundation (Gittman et al., 2018) than smaller patches, but it is not known how wave forcing affects such stress to patch-size relationships.

Tussock formation in wetlands is influenced by sediment characteristics and is most pronounced in erosion-prone sandy substrates, which are more likely to form gullies than erosion resistant silty substrates (Balke et al., 2014; van Hulzen et al., 2007). Here, the sediments were coarsest at our most exposed site. Arguably, gullies, and their restrictions on patch expansion, might not have emerged at the exposed site if the sediments had been finer-grained. We therefore cannot dismiss that fine sediments would moderate plant-sediment feedbacks to accommodate lateral expansion of high-density plantations in high energy settings. In natural conditions, it is difficult to disentangle the effects sediments and hydrology on gully and tussock formation, as sediment coarseness is positively correlated with hydrological energy (Komar, 1976). Future research may consider factorial experiments in laboratory/flume conditions or across multiple sites with different sediment-hydrology characteristics to disaggregate the effects of hydrology, planting density and sediment characteristics on planting success.

Overall, our study confirms that within or between species facilitation is an important and simple ecological process to accommodate for enhanced restoration success (Derksen-Hooijberg et al., 2017; Silliman et al., 2015). However, the study here shows facilitation is not a pervasively positive force to capitalize on in restoration projects: it depends on the level of stress encountered at the restoration site, with the positive effects of facilitation switching to negative interactions of competition in low-stress situations, in alignment with the stress-gradient hypothesis (Gedan & Silliman, 2009; Silliman et al., 2015). In plant systems, the simple route to getting this right is through setting planting density in accordance with the level of environmental stress encountered at the restoration site: higher stress, higher planting density for boosted facilitation. A significant proportion of wetland restoration projects have failed in the past, because interactions between plant ecology and environmental stresses were not sufficiently taken into consideration. We call for wider integration of facilitation and stress-gradient principles into restoration design to safeguard restoration successes in a diversity of ecosystems.

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AUTHORS' CONTRIBUTIONS

M.F.D.-E., M.W.S. and S.R.J. conceived the ideas and designed the methodology; M.F.D.-E. conducted the fieldwork and analysed the

data. J.F.P. provided statistical guidance; M.F.D.-E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via Figshare and Bangor University's repository <https://doi.org/10.6084/m9.figshare.10312550> (Duggan-Edwards, Pagès, Jenkins, Bouma, & Skov, 2019).

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SUPPORTING INFORMATION

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

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