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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 $1billion 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 colonisation or re-planting 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 *Spartina anglica* patches (0.8×0.8m) 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 vegetation. In sheltered conditions, expansion was 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 maximise 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: Positive and negative feedbacks, Planting, Restoration, Saltmarsh, Sediment, *Spartina anglica*, Stress-gradient hypothesis, Survival and expansion

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 pressures from emergent sea level rise, increased storminess and diminishing sediment supply (Mariotti & Fagherazzi, 2010; Kirwan & Megonigal, 2013; Leonardi, Ganju, & Fagherazzi 2016) 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 *et al.* 2009; Suding, 2011). This could be due to poor restoration designs and justifies the need to re-consider planting strategies (Silliman *et al.* 2015; Derksen-Hooijberg *et al.* 2018).

Current restoration designs for seagrasses, mangroves, corals and salt marshes focus on maintaining empty spaces between out-planted propagules (dispersed design), to minimise 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 (Gedan & Silliman, 2009). 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 et al. 2014). *Spartina anglica* 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). *Spartina* is therefore a model species to study mechanisms of marsh establishment and expansion (Balke *et al.* 2012). Initial development of *Spartina* 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 (Fig. 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 (Fig. 1) (van Hulzen, van Soelen, & Bouma 2007; van Wesenbeeck *et al.* 2008; Bouma *et al.* 2009).

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 *Spartina* vegetation encourages greater sediment deposition by reducing hydrological energy inside the canopy, leading to higher plant survival (Bouma *et al.* 2005, 2009; van Hulzen, van Soelen, & Bouma 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 (van Hulzen, van Soelen, & Bouma 2007; van Wesenbeeck *et al*. 2008; Bouma *et al*. 2009). 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 (van Hulzen, van Soelen, & Bouma 2007; van Wesenbeeck *et al*. 2008; Bouma *et al.* 2009). Yet, low density patches have less gully formation at the vegetation boundary, thus retaining the potential for lateral expansion (van Hulzen, van Soelen, & Bouma 2007; van Wesenbeeck *et al.* 2008; Bouma *et al.* 2009). Plant density-linked feedbacks are likely to vary with the amount of wave forcing in the system (Bouma *et al.* 2009; Bruno *et al.* 2017). For example, dense vegetation in low wave forcing might encourage sediment deposition without generating erosion gullies, because wave energy is too low to scour the substrate along the patch perimeter. 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 *Spartina anglica*. We hypothesise that (1) wave forcing will affect density-dependent sediment feedbacks in *Spartina* 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. (2) Plant survival will be highest under sheltered wave forcing conditions, and in the densest patches. (3) Patch lateral expansion will be lowest under exposed wave forcing conditions, and in the densest patches, due to accentuated scouring around the patch perimeter.

Materials and methods

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 north east coast of the isle of Anglesey, North Wales (United Kingdom) (Fig. S1). Red Wharf Bay is characterised by broad sand flats and low-lying sandy beaches. The spring tidal amplitude of the bay reaches 7.6m, with water levels ranging from 0.4 to 7.6m (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 (Fig. S1). The three sites were located ~1km apart and 5.25 – 5.85m above chart datum. Wave observations (September - October 2018) confirmed significant differences in wave heights between the three sites (Fig. S2, p-value < 0.001). Wave heights during average days and stormy days were 0.2m and 0.4m respectively at the exposed site in the east, 0.1m and 0.3m at the moderate site and 0.02m and 0.1m at the sheltered site in the west (Fig. 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 (Fig. S4, p-value = 0.23). The sediment was predominantly fine sand at all three sites, with some differences in silt-clay and medium-coarse sand percentages (Table S1).

Between June and August 2016 *Spartina* was transplanted to create plots of three density treatments (low, medium and high) (Fig. 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 *3 densities *5 replicates) (Fig. 2b). Replicates were blocked and treatments were allocated randomly within the blocks. Clumps of *Spartina* consisting of 15-20 shoots and associated roots and each covering approximately 0.1 x 0.1m were dug up from the marsh at each site and transplanted into 0.8 x 0.8m plots spaced >5m apart. Five clumps were used to create low density treatments (~80-100 shoots per plot), 16 clumps for medium density treatments (~240-320 shoots per plot) and 32 clumps for high density treatments (~480-640 shoots per plot) (Fig. 2a).

Cross-plot sediment elevation profiles

Net change in sediment elevation were measured inside and immediately outside the planted plots using Sedimentation-Erosion-Bars (SEB's) (Nolte *et al.* 2013) (Fig. 2c). For each vegetated plot, four 1m long wooden posts were inserted into the sediment with 0.5m above ground: two posts on the landward side of the vegetation and two on the seaward side (Fig. 2c). Posts were placed 1m away from the vegetation to avoid scouring effects. These posts marked the boundaries of the measured 'SEB areas' (Fig. 2c). During observations of sediment elevation, a horizontal beam was temporarily clamped onto the seaward and the landward posts to make two trestles (Fig. 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 (Fig. 2d): points were in the centre of the vegetation, and at 0.4 and 0.8m away from the centre of the vegetation in both directions (Fig. 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 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, both an adequate time of the year to start and complete the experiment.

Sediment Digital Elevation Models (DEMs)

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 0.5m 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 (SfM; Ullman, 1979). Ground control was achieved in the field with a Differential Global Positioning System (Leica dGPS GS08 GNSS) to an accuracy of ± 0.1cm. Ground control points (GCPs) were taken from the tops of the SEB posts, ensuring an even distribution of GCP's 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), the contour lines were superimposed onto the DEMs at 0.02m 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).

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 – August 2017, %). For high density plots, survival was determined using the Digital Elevation Models: vegetated areas were identified by pixel classification and outlined by polygons, and survival was quantified as percent change of vegetated areas (September 2016 – 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.

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, %).

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: exposed, moderate and sheltered), 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 et al. 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: exposed, moderate and sheltered) 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 et al. 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 Development Core Team 2017).

Results

Net changes in surface elevation

Wave forcing had a significant effect on the net change in sediment elevation within and around *Spartina anglica* patches (Fig. 3; Table S2). With increase in wave forcing, the cross-shore profile changed 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 (Fig. 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 (Figs 3-4; Table S3). While the seaward to landward lift in the landscape tended to steepen with increase in plant density (Fig. 3; Table S2), it was wave energy that determined plant density effects, highlighting the existence of a wave forcing x plant density interaction (Fig. 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 (Figs 3-4). Tussock formation was especially marked in high density patches at the moderate and exposed sites (Figs 3-4, S5; Table S3). Patch shape formation as a result of sediment depositioning and erosion gully formation was therefore most consistent around the densest patches at the most exposed sites (Figs 4 & 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) increased the predictive power of our model to 95% (Table S2).

Plant survival

Wave forcing, planting density and their interaction had a significant effect on plant survival (Fig. 5; Table S3). As with net sediment 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 survival rates, 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 (Fig. 5; Table S3, Table S4). The influence of wave forcing, vegetation density and their interaction explained 45 % of the variance in plant survival (Table S3).

Patch lateral expansion

Wave forcing, planting density and their interaction had significant effects on patch lateral expansion (Fig. 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 (Fig. 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 (Fig. 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).

Discussion

This study shows that wave forcing regulates the strength and direction of plant density-dependent feedbacks on sediment distribution (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 *et al.* 2009; Zong & Nepf, 2010; Duarte *et al.* 2013; van Maanen, Coco, & Bryan 2015). Whilst previous studies have demonstrated plant density effects on sediment feedbacks in flume settings (e.g. Bouma *et al*. 2009), the present 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. 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 *et al.* 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 the hummock (Ysebaert, Hart, & Herman 2009). In another example, 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, Bertness & Altieri, 2013). Species interactions may shift from facilitative to competitive with increasing environmental stress (Bertness & Callaway, 1994; He, Bertness & Altieri, 2013), as observed across a number of ecosystems (Bertness & Callaway, 1994; Bertness *et al.* 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, Michalet, & Callaway 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 (van Wesenbeeck *et al.* 2008; Wang & Temmerman, 2013). The formation of dome-shaped tussocks was thought purely the outcome of plant engineering, and to be particularly pronounced in high density vegetation (van Hulzen, van Soelen, & Bouma 2007; Bouma *et al.* 2009). Here, we show that tussocks arise from an interaction between vegetation density and hydrodynamics. Under lower wave forcing conditions, *Spartina* 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 (van Wesenbeeck *et al.* 2008; Bouma *et al.* 2009, 2013). Waves are shallow in marsh areas, typically <0.5m as in the present study; yet they create erosional shear stresses on the seabed that match or exceed those of currents (Shi *et al.* 2012, 2017). 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 (van Wesenbeeck *et al.* 2008; Bouma *et al.* 2009, 2013). Here, we had a natural situation with both waves and currents, where only wave forcing differed between the tree 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 (Shi *et al.* 2012, 2017; Maza *et al.* 2015; Yang & Irish, 2018). We propose a few simple principles that might explain the observed wave-current induced sediment patterns around the vegetation patches (Figure 6). We think flow deflection around the patch is key to gulley formation (Figure 6a). Having waves in addition to current flow will likely strengthening the flow deflection effect around the patch (Figure 6b) 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 6b). Wave reflection by (dense) vegetation is also likely to boost turbulence and erosion at the seaward-side of the tussock (Figure 6c), 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 present study.

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. Figure 7 summarises the outcomes of low, medium and high density transplanting of *Spartina* on sediment feedbacks (Fig. 7a) and patch survival and expansion (Fig. 7b). It illustrates, for instance, that planting low density vegetation at sheltered sites results in little or no sediment depositioning (signified by light coloured box in top-left corner of Fig 7a), with only moderate plant survival and patch lateral expansion (indicated by a medium shade of green in the top-left box of Fig 7b), despite lack of gully formation. Medium density planting might be a better option in sheltered conditions, as it should maximise survival and patch expansion. At exposed sites, planting low-density vegetation results in modest sediment deposition and mild erosion gully formation outside patches (Fig 7a, top-right box), offering only moderate scope for plant survival and patch expansion (Fig 7b, top-right box). Planting high density patches in wave exposed conditions will maximise plant survival (Fig 6b, bottom-right box) and sediment capture (Fig 7a, bottom-right box); however, patch expansion will be constrained by erosion gullies (Fig 7b). To overcome the latter issue, restoration success at high exposure might be boosted by planting dense vegetation in large patches (Gittman *et al.* 2018), because plant survival will be encouraged and negative edge effects (gullies) will represent a diminished proportion of the planted area (Angelini & Silliman, 2012; Silliman *et al.* 2015; Gittman *et al.* 2018). Interaction of patch size and planting density should also be considered at less exposed conditions. Thus, planting moderate-density vegetation in smaller patches at wave-sheltered sites will minimise competition between individual plants and encourage expansion over longer time scales. Here we have considered wave forcing as the main stressor for young patches of *Spartina*. 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 *Spartina* 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 (Van Hulzen *et al.* 2007; Balke *et al*. 2014). Here, the sediments were coarsest at our most exposed site. Arguably, gullies, and their restrictions on patch expansion, might not have emerged at the high-energy 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 (Silliman *et al.* 2015; Derksen-Hooijberg *et al.* 2017). However, the study here shows facilitation is not a pervasively positive force to capitalise 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; 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. Thus, most mangrove restoration in the Philippines met with little success, because plantations were done without due consideration for hydrological stresses at planting sites (Samson & Rollon, 2008). We call for wider integration of facilitation and stress-gradient principles into restoration design to safeguard restoration successes in a diversity of ecosystems.

Authors Contributions

M.DE, M.S and S.J conceived the ideas and designed the methodology; M.DE conducted the fieldwork and analysed the data. J.P provided statistical guidance; M.DE led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Tables and Figures

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

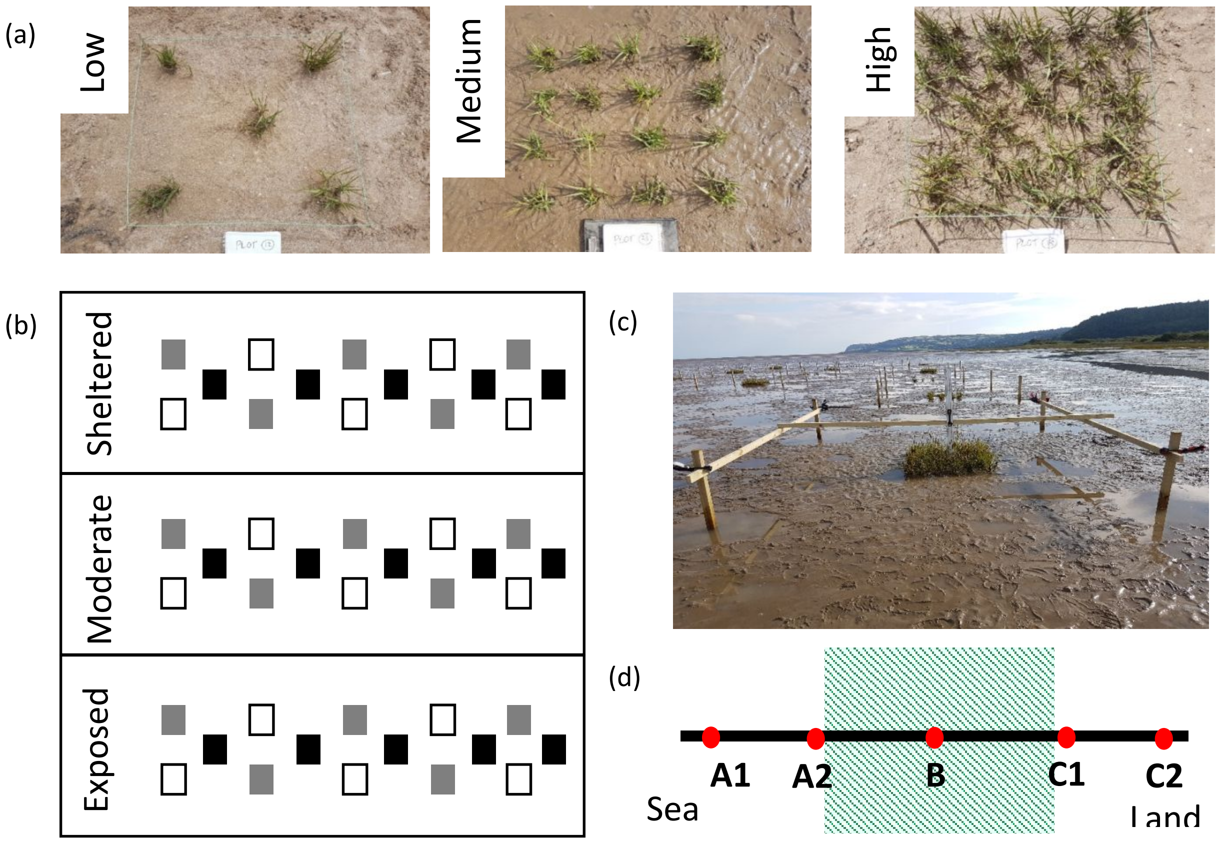


Fig 2. (a) Three vegetation density plots (0.8 x 0.8m) created from clumps of *Spartina* consisting of 15-20 shoots and associated roots, giving 80-100 shoots (Low density), 240-320 shoots (Medium) and 460-640 shoots (High). (b) Layout of plot distribution (5/treatment) at a Sheltered, Moderately exposed 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.

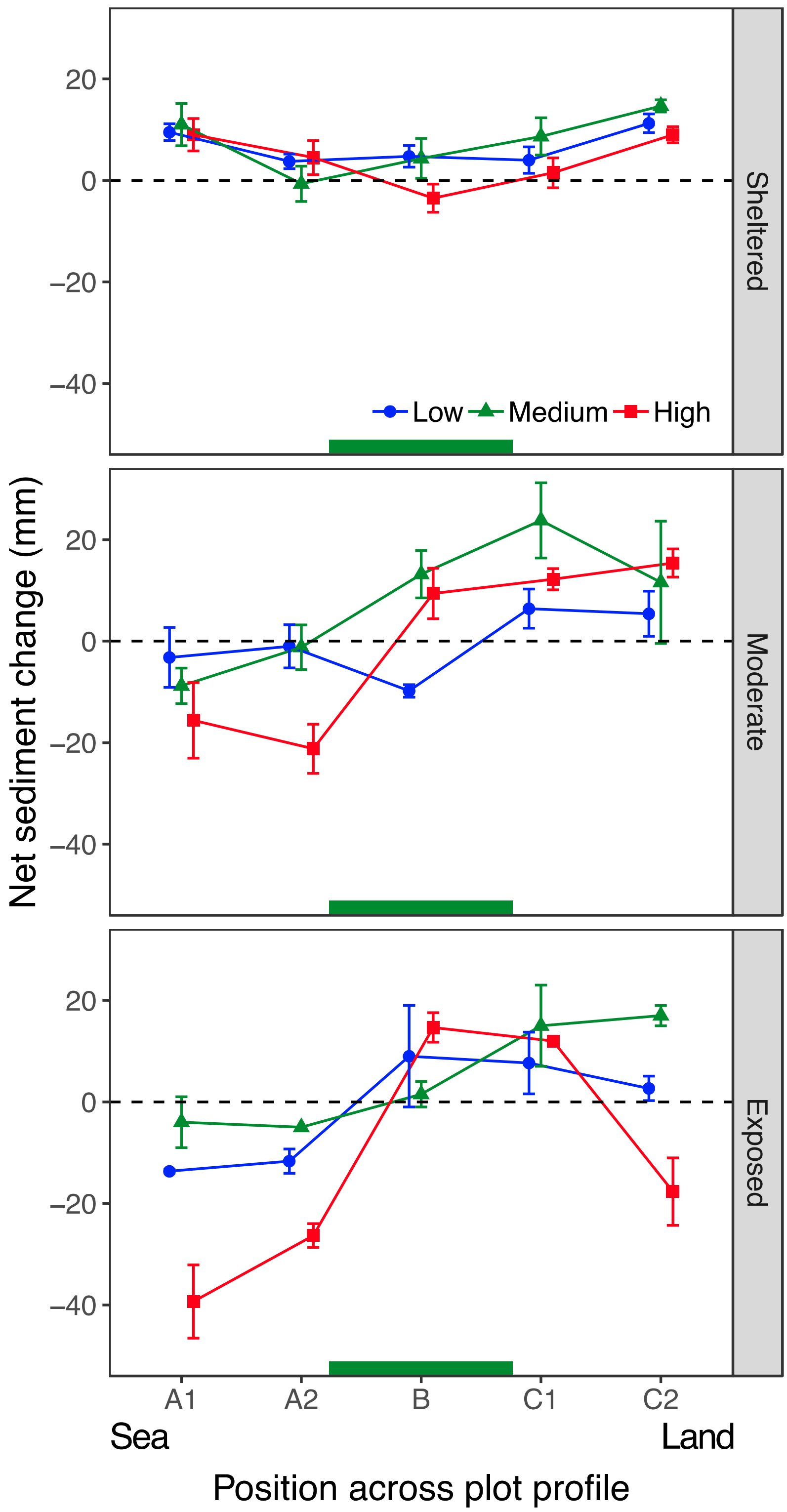


Fig 3. The mean ± std. error net change in sediment elevation, from the first (September 2016) to the last observation (August 2017) across cross-plot profiles with high, medium and low density vegetation at the exposed, moderate and sheltered sites (n = 225). X-axis codes: A1 and A2 represent measurements 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.

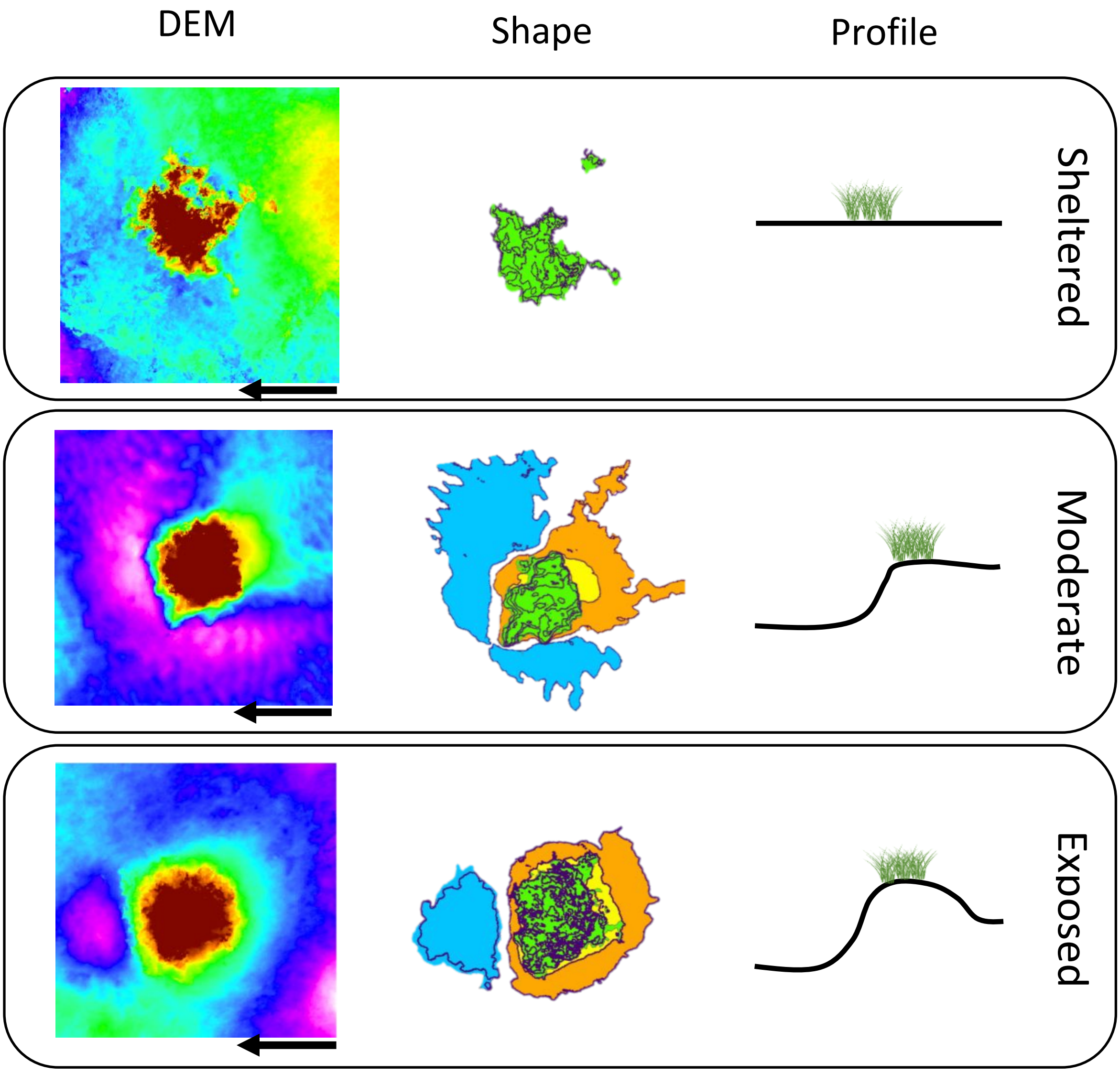


Fig 4. Schematic representation of the tussock shapes and profiles formed by high density vegetation at the sheltered, moderate and exposed sites (n = 15). The mean Digital Elevation Models (DEM) represent sediment bed elevations (blue to red colouring = low to high elevations) in the 2×2m DEM areas. The black arrow 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.

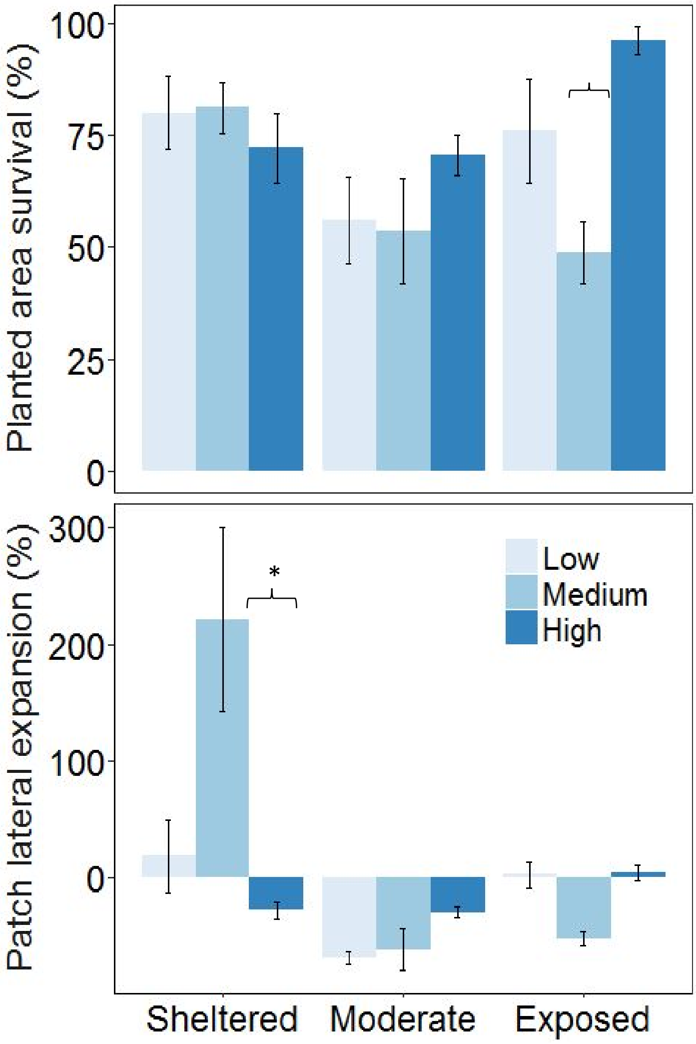


Fig 5. The mean ± std. error survival (of the originally planted area) and expansion (area cover of plants outside the planted areas) of low, medium and high density *Spartina* patches at the sheltered, moderate and exposed sites (n = 45). Significant differences between the sites are indicated as resulting from post-hoc tests (*, $p < 0.05$).

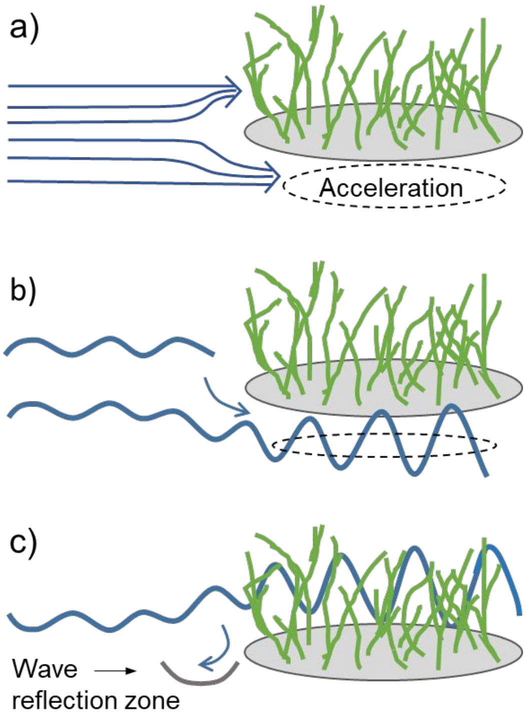


Fig 6. Interactions of current flow and waves on erosion around vegetation patches. (a) Diversion of the water current around the vegetation patch accelerates hydrological energy and associated erosion along the sides of the vegetation patch (van Wesenbeeck *et al.* 2008). (b) Incoming waves accentuate the deflection of current flow around the patch, to augment erosive forces along patch sides (dashed circle). (c) Turbulence associated with wave deflection at the seaward side of the patch erodes sediments in front of the patch.

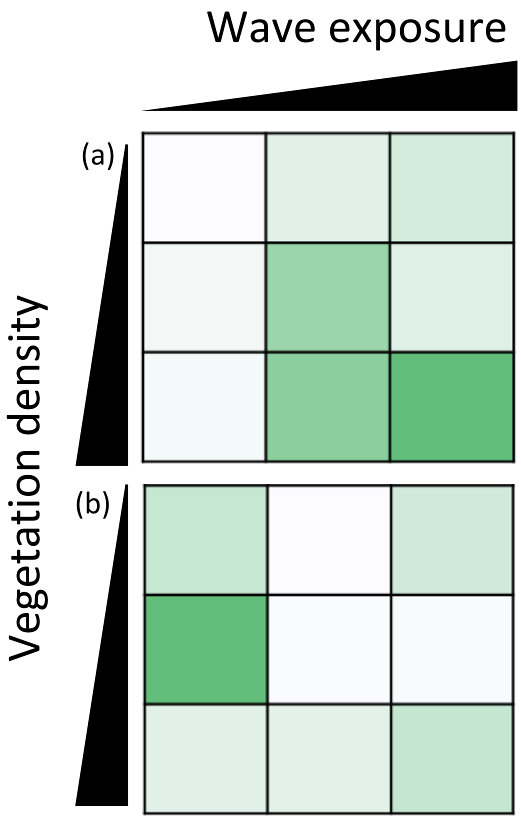


Fig 7. Conceptual representation of the effects of vegetation density and wave exposure on (a) sediment feedbacks (sediment depositioning/erosion, gully formation), and (b) the survival and expansion of planted areas. The colour gradient from dark green to white signifies a decrease in the strength of 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. .

Appendix S1.

Methods for measuring sediment grain size, waves and current velocities

Sediment grain size

Soil samples of ~10g (fresh mass) were extracted from the top layer (0-30cm) of the sediment at each site and then dried in an oven (105°C, 72 h). The dried samples were then ground and sub-sampled and any organic matter in ~3g of soil was digested using hydrogen peroxide prior to the grain size analysis. We quantified differences in sediment grain size by classifying the soil into 33 size fractions from 0.2-2000.0 um (Beckman Coulter LS 13 320 Laser diffraction particle size analyser) and grouped according to the Wentworth scale: clay (0.02-3.9 um), silt (3.9-63.0 um), fine sand (63-256 um), medium-coarse sand (256-2000 um).

Waves

We quantified differences in wave forcing by deploying pressure sensors (OSSI-010-003C-01; Ocean Sensor Systems, Inc.) simultaneously at the three sites over 1 month (September-October 2018). The pressure sensors were placed 0.05m above the seabed, and they measured at a frequency of 5Hz at 10-minute intervals. Thus, 3000 data points were generated at every 10-minute interval. The mean water level in an interval was determined by averaging all the data points. The wave analysis was based on pressure fluctuations. The attenuation of the pressure signals with water depth was corrected to derive bulk wave parameters, e.g. significant wave height (H_S) (Tucker & Pitt, 2001).

Current velocities

We quantified differences in current velocities by deploying Acoustic Doppler Velocity meters (ADVs, Nortek Vector) simultaneously at the three sites over a spring tide in April 2018. The ADVs were placed 0.25m above the seabed, and they measured at a frequency of 0.5Hz at 30-minute intervals.

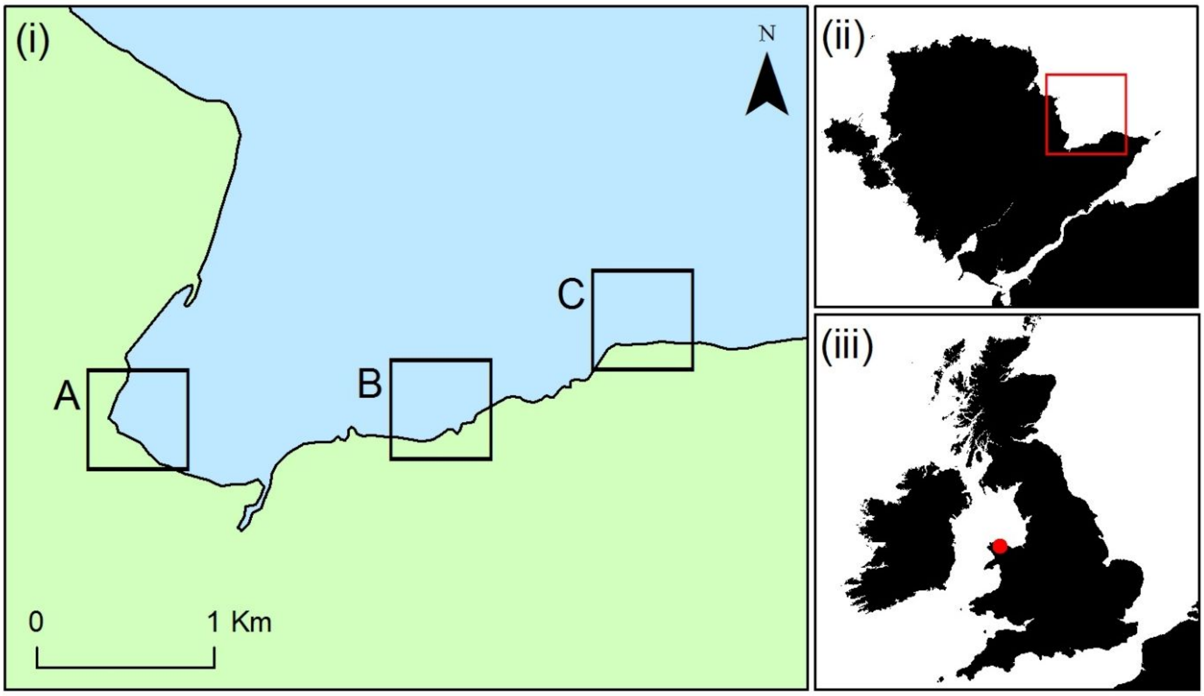


Fig S1. (i) Location of the experimental sites in Red Wharf Bay, with a gradient in wave exposure: (A) Sheltered, (B) Moderate and (C) wave Exposed. (ii) Location of Red Wharf Bay on the south-east coast of Anglesey, North Wales. (iii) Location of Anglesey in the United Kingdom.

Differences in maximum significant wave heights measured at the sheltered, moderate and exposed sites over the same observation period (September-October 2018). Significant differences in maximum wave heights were detected between the three sites, with the highest waves occurring at the exposed site, and the shortest waves at the sheltered site.

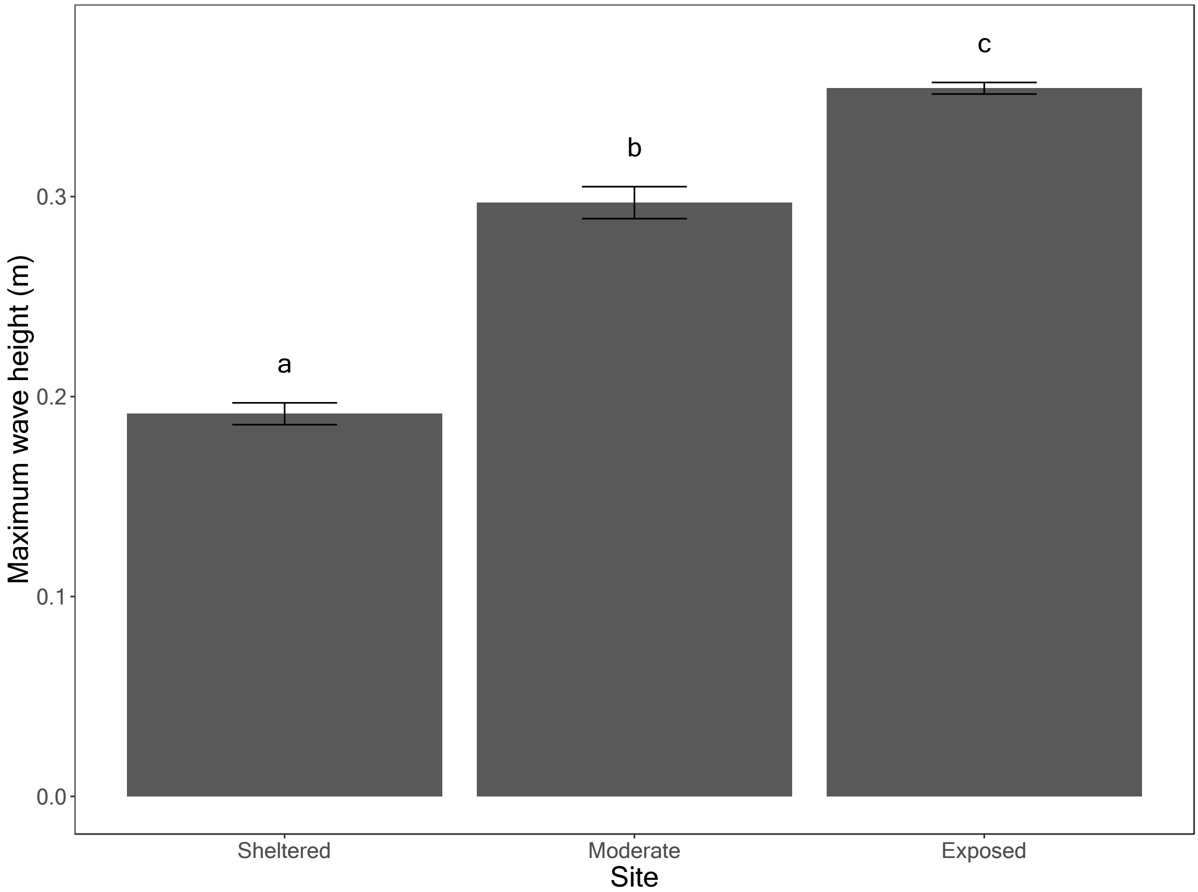
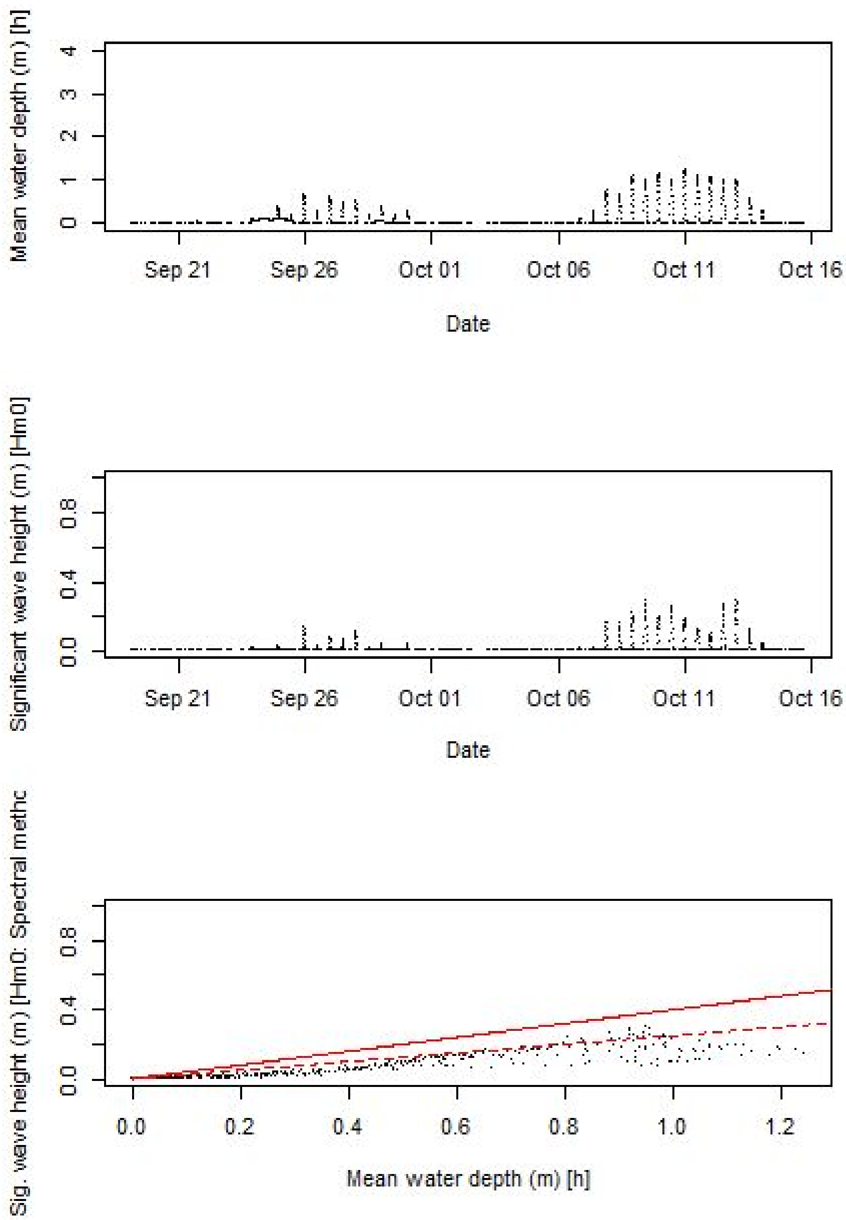


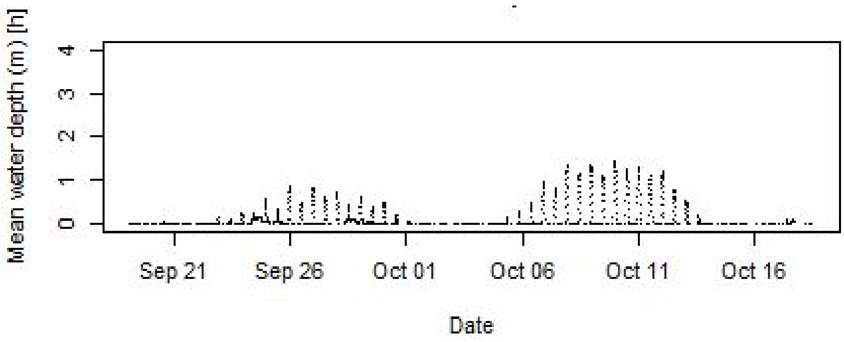
Fig S2. The mean ± std. error difference in maximum wave heights between the sheltered, moderate and exposed sites over a period of 1 month (September - October 2018).

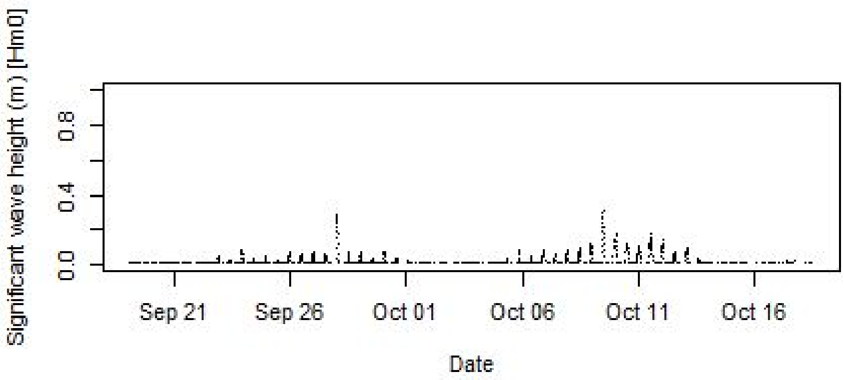
Differences in significant wave heights measured at the three sites over the same observation period (September-October 2018). Waves were highest at the exposed site, moderate at the moderate site and shortest at the sheltered site during both average and stormy days.

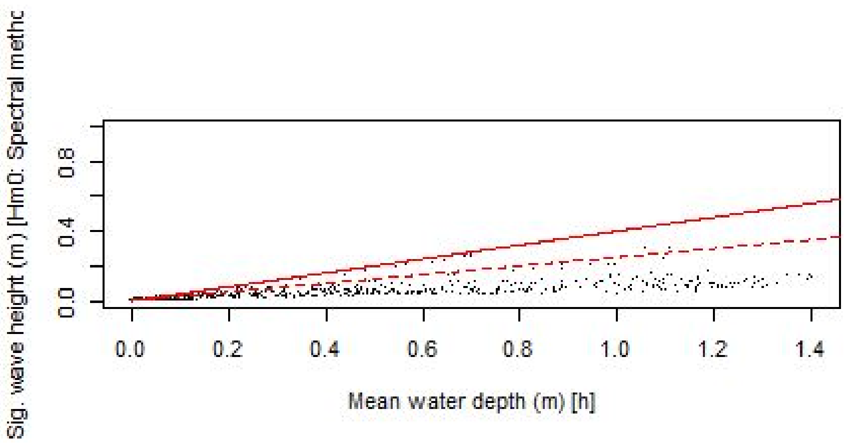
(a) Exposed Site



(b) Moderate Site







(c) Sheltered Site

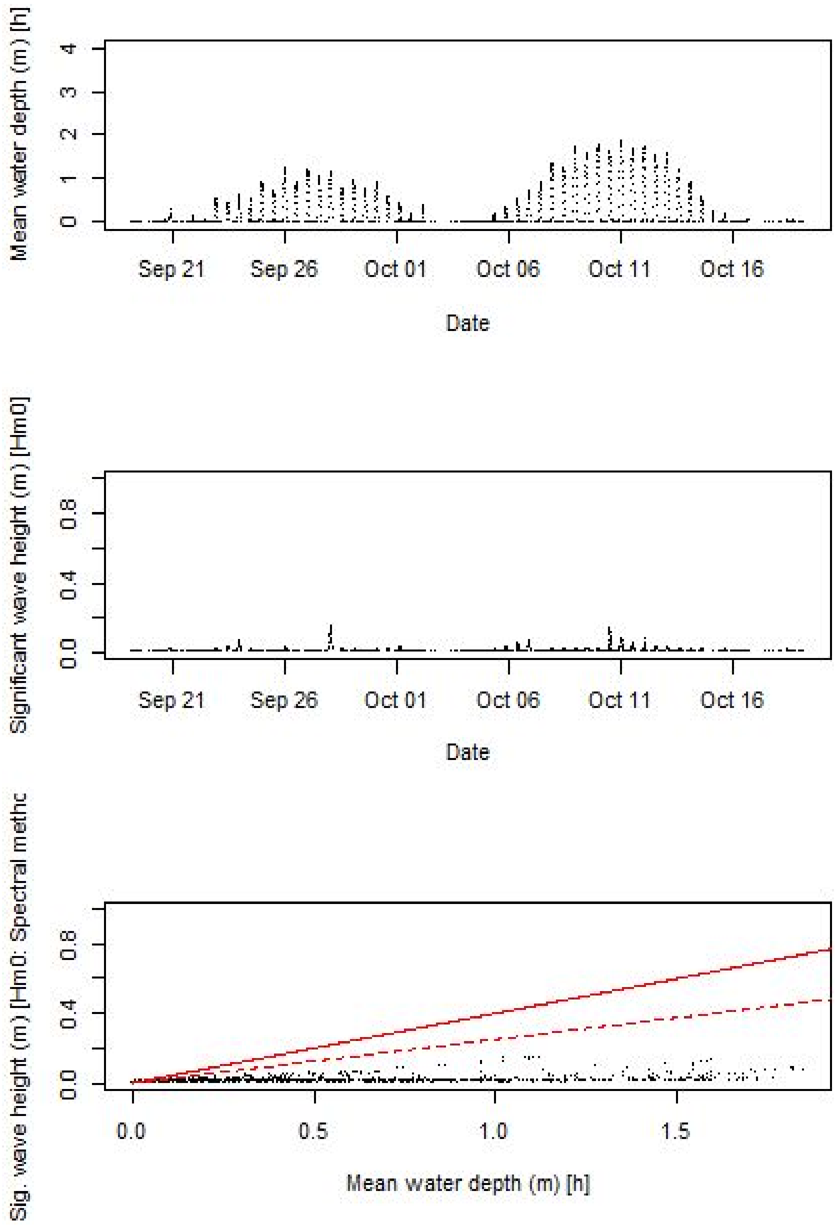


Fig S3. Mean water depths and significant wave heights measured at the three sites (a) Exposed, (b) Moderate and (c) Sheltered over the observation period (September-October 2018).

Differences in the current velocities measured at the sheltered, moderate and exposed sites over the same observation period (April 2018). No significant differences in current velocities were detected between the three sites.

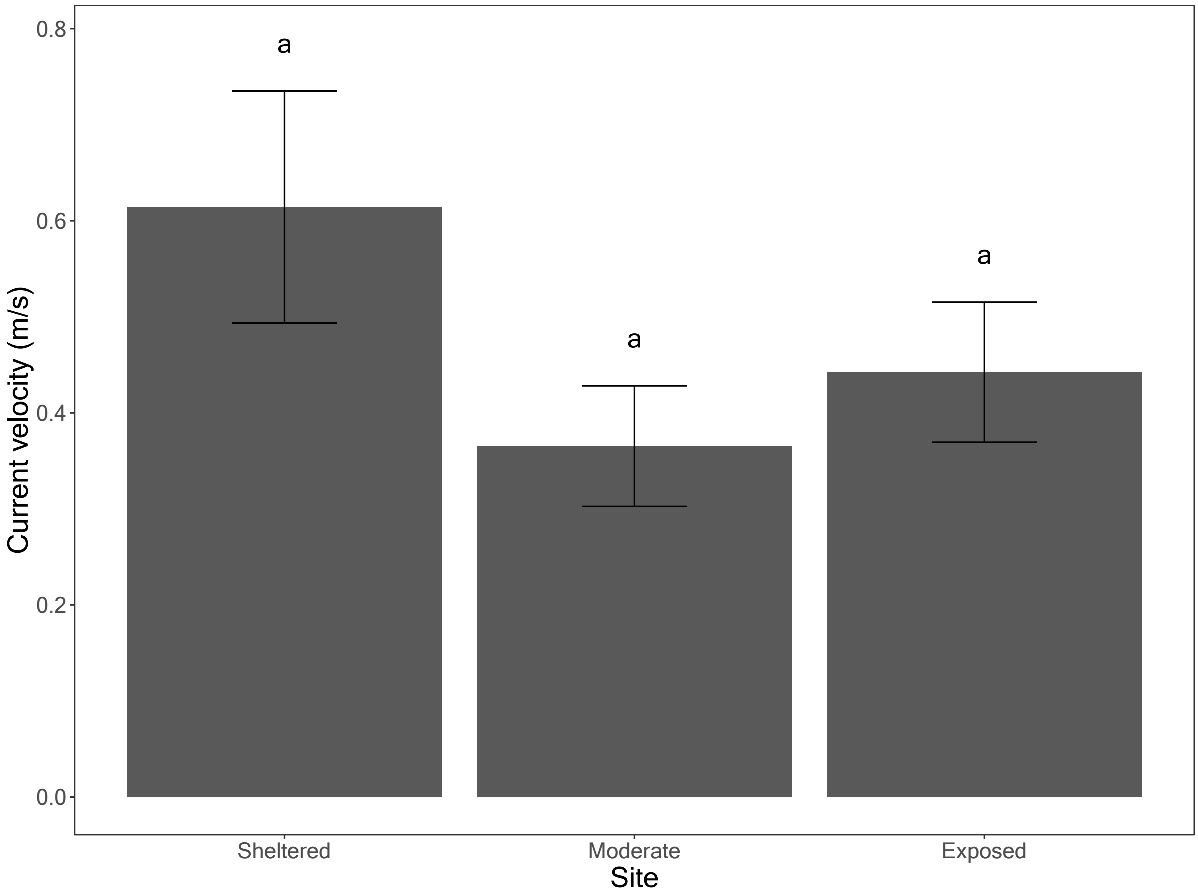


Fig S4. The mean ± std. error differences in the current velocities between the sheltered, moderate and exposed sites over a spring tide in April 2018.

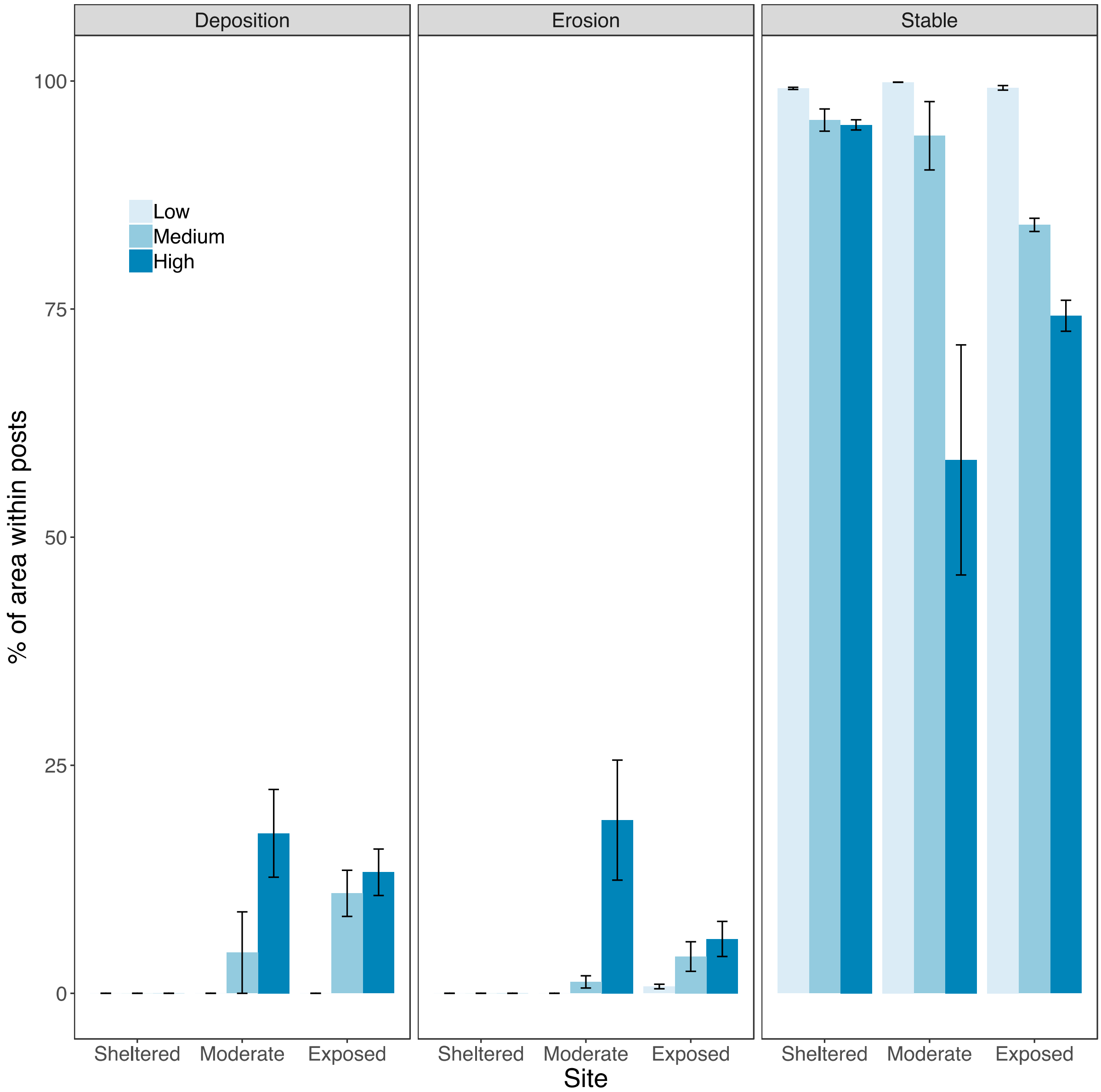


Fig S5. Percentage of the plot areas (i.e. within the posts) that had (a) a net increase in sediment elevation (i.e. sediment deposition), (b) a net decrease in sediment elevation (i.e. surface erosion) or (c) no change in sediment elevation (i.e. remained stable), in function of plant density (low, medium, high) and wave exposure (sheltered, moderate and exposed). Bars represent the means and error bars are the standard errors (total n = 45).

Sediment grain size analyses revealed that the sediment at all three sites was predominantly sandy, but that the sheltered site differed from the exposed and moderate sites by having a higher proportion of clay-silt particles in the sediment.

Table S1. Percentage of each sediment class at the sheltered, moderate and exposed sites in Red Wharf Bay.

Sediment type and size (um)	**Sheltered**	**Moderate**	**Exposed**
Silt-clay (0.02-63)	30	4	2
Fine sand (63-256)	68	82	78
Medium-coarse sand (256-2000)	2	14	20

Table S2. Output of the linear mixed effects model performed on the response variable ‘net change in sediment elevation’ across the cross-plot profiles. R^2 (marginal) = 0.51 (only fixed effects considered), R^2 (conditional) = 0.95 (taking the random effects into account).

Effect	**Df**	**Chi squared-statistic**	**p-Value**
Wave forcing	2	17.068	<0.001***
Vegetation density	2	24.808	<0.001***
Position across cross-plot profile	4	182.205	<0.001***
Forcing*Density	4	11.446	0.022*
Forcing*Position across profile	8	73.713	<0.001***
Density*Position across profile	8	28.627	<0.001***
Forcing *Density*Position across profile	16	57.491	<0.001***

Table S3. Outputs of the linear models and Tukey HSD post-hoc tests for effects of wave forcing and plant density on the mean percentage of plot areas (i.e. within the posts) that had a net increase in sediment elevation (i.e. sediment deposition), a net decrease in sediment elevation (i.e. surface erosion) and that had no change in sediment elevation (i.e. remained stable). In addition, the outputs for the mean percentage of plant survival (i.e. of the originally planted area) and patch lateral expansion (i.e. area cover of plants outside the planted areas) in experimental plots.

Response	**Effect**	**Df**	**F-statistic**	**p-Value**
Deposition	Wave forcing	2	11.56	<0.001
R^2 = 0.72	Vegetation density	2	7.56	<0.01
	Forcing*Density	4	3.36	<0.05
Erosion	Wave forcing	2	7.65	<0.01
R^2 = 0.73	Vegetation density	2	7.44	<0.01
	Forcing*Density	4	5.51	<0.01
Stable	Wave forcing	2	12.37	<0.001
R^2 = 0.82	Vegetation density	2	18.42	<0.001
	Forcing*Density	4	6.51	<0.01
% survival	Wave forcing	2	3.62	<0.05
R^2 = 0.45	Vegetation density	2	4.40	<0.05
	Forcing*Density	4	2.86	<0.05
% expansion	Wave forcing	2	38.12	<0.001
R^2 = 0.77	Vegetation density	2	53.88	<0.001
	Forcing*Density	4	29.16	<0.001

```
modelForSedimentChange <-
lme(sediment ~ energy*density*distance,
              random = ~1 + distance|plot,
              method = "REML",
              data = rwb_data)
```

TUKEY HSD FOR NET SEDIMENT CHANGE

```
$`simple contrasts for energy`
density = Low, distance = A1:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed     23.167  7.90 25   2.933  0.0187 *
Sheltered - Moderate    12.700  6.94 25   1.831  0.1803
Exposed - Moderate     -10.467  7.55 25  -1.386  0.3632

density = High, distance = A1:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed     48.333  7.90 25   6.120  <.0001 ***
Sheltered - Moderate    24.600  6.94 25   3.546  0.0043 **
Exposed - Moderate     -23.733  7.55 25  -3.143  0.0115 *

density = Med, distance = A1:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed     15.000  9.44 25   1.589  0.2688
Sheltered - Moderate    19.800  7.55 25   2.622  0.0377 *
Exposed - Moderate       4.800  8.65 25   0.555  0.8450

density = Low, distance = A2:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed     15.417  5.96 25   2.586  0.0408 *
Sheltered - Moderate     4.750  5.24 25   0.907  0.6409
Exposed - Moderate     -10.667  5.70 25  -1.871  0.1680

density = High, distance = A2:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed     30.833  5.96 25   5.172  0.0001 ***
Sheltered - Moderate    25.700  5.24 25   4.908  0.0001 ***
Exposed - Moderate      -5.133  5.70 25  -0.900  0.6450

density = Med, distance = A2:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed      4.333  7.13 25   0.608  0.8170
Sheltered - Moderate     0.533  5.70 25   0.094  0.9952
Exposed - Moderate      -3.800  6.53 25  -0.582  0.8310

density = Low, distance = B:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed     -4.250  6.60 25  -0.644  0.7976
Sheltered - Moderate    14.550  5.80 25   2.509  0.0481 *
Exposed - Moderate      18.800  6.31 25   2.978  0.0169 *

density = High, distance = B:
  contrast              estimate    SE df t.ratio p.value
Sheltered - Exposed    -18.167  6.60 25  -2.751  0.0283 *
Sheltered - Moderate   -12.900  5.80 25  -2.224  0.0865 .
```

```
Exposed - Moderate      5.267  6.31 25  0.834  0.6857

density = Med, distance = B:
  contrast             estimate    SE df t.ratio p.value
Sheltered - Exposed     2.833  7.89 25  0.359  0.9316
Sheltered - Moderate   -8.867  6.31 25 -1.404  0.3539
Exposed - Moderate    -11.700  7.23 25 -1.618  0.2570

density = Low, distance = C1:
  contrast             estimate    SE df t.ratio p.value
Sheltered - Exposed    -3.667  7.01 25 -0.523  0.8607
Sheltered - Moderate   -2.400  6.15 25 -0.390  0.9198
Exposed - Moderate      1.267  6.70 25  0.189  0.9805

density = High, distance = C1:
  contrast             estimate    SE df t.ratio p.value
Sheltered - Exposed   -10.500  7.01 25 -1.499  0.3085
Sheltered - Moderate  -10.700  6.15 25 -1.739  0.2109
Exposed - Moderate     -0.200  6.70 25 -0.030  0.9995

density = Med, distance = C1:
  contrast             estimate    SE df t.ratio p.value
Sheltered - Exposed    -6.333  8.37 25 -0.756  0.7326
Sheltered - Moderate  -15.133  6.70 25 -2.259  0.0807 .
Exposed - Moderate     -8.800  7.67 25 -1.147  0.4952

density = Low, distance = C2:
  contrast             estimate    SE df t.ratio p.value
Sheltered - Exposed     8.583  9.45 25  0.908  0.6403
Sheltered - Moderate    5.850  8.30 25  0.705  0.7630
Exposed - Moderate     -2.733  9.04 25 -0.302  0.9509

density = High, distance = C2:
  contrast             estimate    SE df t.ratio p.value
Sheltered - Exposed    26.667  9.45 25  2.821  0.0242 *
Sheltered - Moderate   -6.400  8.30 25 -0.771  0.7239
Exposed - Moderate    -33.067  9.04 25 -3.659  0.0033 **

density = Med, distance = C2:
  contrast             estimate    SE df t.ratio p.value
Sheltered - Exposed    -2.333 11.30 25 -0.207  0.9768
Sheltered - Moderate    3.067  9.04 25  0.339  0.9387
Exposed - Moderate      5.400 10.35 25  0.522  0.8616

P value adjustment: tukey method for comparing a family of 3
estimates

$`simple contrasts for density`
energy = Sheltered, distance = A1:
  contrast   estimate    SE df t.ratio p.value
Low - High    0.500  7.31 25  0.068  0.9974
Low - Med    -1.500  7.90 25 -0.190  0.9803
High - Med   -2.000  7.90 25 -0.253  0.9653

energy = Exposed, distance = A1:
  contrast   estimate    SE df t.ratio p.value
```

```
Low - High   25.667  8.44 25  3.040  0.0146 *
Low - Med    -9.667  9.44 25 -1.024  0.5689
High - Med  -35.333  9.44 25 -3.743  0.0027 **

energy = Moderate, distance = A1:
  contrast   estimate    SE df t.ratio p.value
Low - High   12.400  6.54 25  1.896  0.1607
Low - Med     5.600  6.54 25  0.856  0.6722
High - Med   -6.800  6.54 25 -1.040  0.5594

energy = Sheltered, distance = A2:
  contrast   estimate    SE df t.ratio p.value
Low - High   -0.750  5.52 25 -0.136  0.9899
Low - Med     4.417  5.96 25  0.741  0.7418
High - Med    5.167  5.96 25  0.867  0.6659

energy = Exposed, distance = A2:
  contrast   estimate    SE df t.ratio p.value
Low - High   14.667  6.37 25  2.301  0.0741 .
Low - Med    -6.667  7.13 25 -0.936  0.6234
High - Med  -21.333  7.13 25 -2.994  0.0163 *

energy = Moderate, distance = A2:
  contrast   estimate    SE df t.ratio p.value
Low - High   20.200  4.94 25  4.092  0.0011 **
Low - Med     0.200  4.94 25  0.041  0.9991
High - Med  -20.000  4.94 25 -4.051  0.0012 **

energy = Sheltered, distance = B:
  contrast   estimate    SE df t.ratio p.value
Low - High    8.250  6.11 25  1.350  0.3820
Low - Med     0.417  6.60 25  0.063  0.9978
High - Med   -7.833  6.60 25 -1.186  0.4720

energy = Exposed, distance = B:
  contrast   estimate    SE df t.ratio p.value
Low - High   -5.667  7.06 25 -0.803  0.7048
Low - Med     7.500  7.89 25  0.950  0.6143
High - Med   13.167  7.89 25  1.668  0.2369

energy = Moderate, distance = B:
  contrast   estimate    SE df t.ratio p.value
Low - High  -19.200  5.47 25 -3.512  0.0047 **
Low - Med   -23.000  5.47 25 -4.207  0.0008 ***
High - Med   -3.800  5.47 25 -0.695  0.7686

energy = Sheltered, distance = C1:
  contrast   estimate    SE df t.ratio p.value
Low - High    2.500  6.49 25  0.385  0.9216
Low - Med    -4.667  7.01 25 -0.666  0.7850
High - Med   -7.167  7.01 25 -1.023  0.5696

energy = Exposed, distance = C1:
  contrast   estimate    SE df t.ratio p.value
Low - High   -4.333  7.49 25 -0.579  0.8327
Low - Med    -7.333  8.37 25 -0.876  0.6602
```

```
High - Med   -3.000  8.37 25 -0.358  0.9319

energy = Moderate, distance = C1:
  contrast   estimate    SE df t.ratio p.value
Low - High   -5.800  5.80 25 -1.000  0.5838
Low - Med   -17.400  5.80 25 -3.000  0.0161 *
High - Med  -11.600  5.80 25 -2.000  0.1331

energy = Sheltered, distance = C2:
  contrast   estimate    SE df t.ratio p.value
Low - High    2.250  8.75 25  0.257  0.9643
Low - Med    -3.417  9.45 25 -0.362  0.9307
High - Med   -5.667  9.45 25 -0.600  0.8216

energy = Exposed, distance = C2:
  contrast   estimate    SE df t.ratio p.value
Low - High   20.333 10.10 25  2.012  0.1300
Low - Med   -14.333 11.30 25 -1.269  0.4254
High - Med  -34.667 11.30 25 -3.069  0.0137 *

energy = Moderate, distance = C2:
  contrast   estimate    SE df t.ratio p.value
Low - High  -10.000  7.83 25 -1.278  0.4205
Low - Med    -6.200  7.83 25 -0.792  0.7112
High - Med    3.800  7.83 25  0.486  0.8788

P value adjustment: tukey method for comparing a family of 3
estimates

$`simple contrasts for distance`
energy = Sheltered, density = Low:
  contrast estimate    SE  df t.ratio p.value
A1 - A2      5.75  6.38 100  0.901  0.8957
A1 - B       4.75  8.03 100  0.591  0.9761
A1 - C1      5.50  7.03 100  0.782  0.9351
A1 - C2     -1.75  8.10 100 -0.216  0.9995
A2 - B      -1.00  4.83 100 -0.207  0.9996
A2 - C1     -0.25  6.11 100 -0.041  1.0000
A2 - C2     -7.50  6.09 100 -1.231  0.7335
B - C1       0.75  5.12 100  0.147  0.9999
B - C2      -6.50  7.28 100 -0.892  0.8991
C1 - C2     -7.25  9.58 100 -0.757  0.9423

energy = Exposed, density = Low:
  contrast estimate    SE  df t.ratio p.value
A1 - A2     -2.00  7.37 100 -0.272  0.9988
A1 - B     -22.67  9.28 100 -2.444  0.1123
A1 - C1    -21.33  8.12 100 -2.628  0.0729
A1 - C2    -16.33  9.35 100 -1.746  0.4109
A2 - B     -20.67  5.58 100 -3.703  0.0032 **
A2 - C1    -19.33  7.06 100 -2.740  0.0551 .
A2 - C2    -14.33  7.04 100 -2.037  0.2562
B - C1       1.33  5.91 100  0.226  0.9994
B - C2       6.33  8.41 100  0.753  0.9432
C1 - C2      5.00 11.07 100  0.452  0.9913
```

energy = Moderate, density = Low:

contrast	estimate	SE	df	t.ratio	p.value	
A1 - A2	-2.20	5.71	100	-0.386	0.9952	
A1 - B	6.60	7.18	100	0.919	0.8891	
A1 - C1	-9.60	6.29	100	-1.527	0.5476	
A1 - C2	-8.60	7.25	100	-1.187	0.7589	
A2 - B	8.80	4.32	100	2.035	0.2569	
A2 - C1	-7.40	5.46	100	-1.354	0.6582	
A2 - C2	-6.40	5.45	100	-1.174	0.7660	
B - C1	**-16.20**	**4.58**	**100**	**-3.538**	**0.0054**	**
B - C2	-15.20	6.52	100	-2.333	0.1432	
C1 - C2	1.00	8.57	100	0.117	1.0000	

energy = Sheltered, density = High:

contrast	estimate	SE	df	t.ratio	p.value
A1 - A2	4.50	6.38	100	0.705	0.9548
A1 - B	12.50	8.03	100	1.556	0.5289
A1 - C1	7.50	7.03	100	1.067	0.8230
A1 - C2	0.00	8.10	100	0.000	1.0000
A2 - B	8.00	4.83	100	1.655	0.4663
A2 - C1	3.00	6.11	100	0.491	0.9880
A2 - C2	-4.50	6.09	100	-0.738	0.9469
B - C1	-5.00	5.12	100	-0.977	0.8651
B - C2	-12.50	7.28	100	-1.716	0.4290
C1 - C2	-7.50	9.58	100	-0.783	0.9351

energy = Exposed, density = High:

contrast	estimate	SE	df	t.ratio	p.value	
A1 - A2	-13.00	7.37	100	-1.765	0.3998	
A1 - B	**-54.00**	**9.28**	**100**	**-5.822**	**<.0001**	***
A1 - C1	**-51.33**	**8.12**	**100**	**-6.324**	**<.0001**	***
A1 - C2	-21.67	9.35	100	-2.316	0.1484	
A2 - B	**-41.00**	**5.58**	**100**	**-7.346**	**<.0001**	***
A2 - C1	**-38.33**	**7.06**	**100**	**-5.433**	**<.0001**	***
A2 - C2	-8.67	7.04	100	-1.232	0.7329	
B - C1	2.67	5.91	100	0.451	0.9913	
B - C2	**32.33**	**8.41**	**100**	**3.844**	**0.0020**	**
C1 - C2	29.67	11.07	100	2.681	0.0640	.

energy = Moderate, density = High:

contrast	estimate	SE	df	t.ratio	p.value	
A1 - A2	5.60	5.71	100	0.981	0.8630	
A1 - B	**-25.00**	**7.18**	**100**	**-3.480**	**0.0066**	**
A1 - C1	**-27.80**	**6.29**	**100**	**-4.422**	**0.0002**	***
A1 - C2	**-31.00**	**7.25**	**100**	**-4.278**	**0.0004**	***
A2 - B	**-30.60**	**4.32**	**100**	**-7.078**	**<.0001**	***
A2 - C1	**-33.40**	**5.46**	**100**	**-6.112**	**<.0001**	***
A2 - C2	**-36.60**	**5.45**	**100**	**-6.715**	**<.0001**	***
B - C1	-2.80	4.58	100	-0.612	0.9730	
B - C2	-6.00	6.52	100	-0.921	0.8882	
C1 - C2	-3.20	8.57	100	-0.373	0.9958	

energy = Sheltered, density = Med:

contrast	estimate	SE	df	t.ratio	p.value
A1 - A2	11.67	7.37	100	1.584	0.5112
A1 - B	6.67	9.28	100	0.719	0.9517

```
A1 - C1      2.33  8.12 100  0.287  0.9985
A1 - C2     -3.67  9.35 100 -0.392  0.9949
A2 - B      -5.00  5.58 100 -0.896  0.8978
A2 - C1     -9.33  7.06 100 -1.323  0.6777
A2 - C2    -15.33  7.04 100 -2.179  0.1961
B - C1      -4.33  5.91 100 -0.733  0.9483
B - C2     -10.33  8.41 100 -1.228  0.7348
C1 - C2     -6.00 11.07 100 -0.542  0.9827

energy = Exposed, density = Med:
  contrast estimate    SE  df t.ratio p.value
A1 - A2      1.00  9.02 100  0.111  1.0000
A1 - B      -5.50 11.36 100 -0.484  0.9887
A1 - C1    -19.00  9.94 100 -1.911  0.3182
A1 - C2    -21.00 11.46 100 -1.833  0.3607
A2 - B      -6.50  6.84 100 -0.951  0.8761
A2 - C1    -20.00  8.64 100 -2.315  0.1489
A2 - C2    -22.00  8.62 100 -2.553  0.0873 .
B - C1     -13.50  7.24 100 -1.865  0.3430
B - C2     -15.50 10.30 100 -1.505  0.5620
C1 - C2     -2.00 13.55 100 -0.148  0.9999

energy = Moderate, density = Med:
  contrast estimate    SE  df t.ratio p.value
A1 - A2     -7.60  5.71 100 -1.332  0.6720
A1 - B     -22.00  7.18 100 -3.062  0.0231 *
A1 - C1    -32.60  6.29 100 -5.185  <.0001 ***
A1 - C2    -20.40  7.25 100 -2.815  0.0454 *
A2 - B     -14.40  4.32 100 -3.331  0.0104 *
A2 - C1    -25.00  5.46 100 -4.575  0.0001 ***
A2 - C2    -12.80  5.45 100 -2.349  0.1385
B - C1     -10.60  4.58 100 -2.315  0.1486
B - C2       1.60  6.52 100  0.246  0.9992
C1 - C2     12.20  8.57 100  1.423  0.6142

P value adjustment: tukey method for comparing a family of 5
estimates
```

```
ModelSurvival <- lm(survival ~ energy*density,
              data = surv)
```

TUKEY HSD FOR PLANT SURVIVAL

```
`simple contrasts for energy`
density = Low:
  contrast             estimate   SE df t.ratio p.value
Sheltered - Exposed      4.00 12.2 33  0.328  0.9426
Sheltered - Moderate    24.00 12.2 33  1.966  0.1367
Exposed - Moderate      20.00 11.5 33  1.738  0.2066

density = High:
  contrast             estimate   SE df t.ratio p.value
Sheltered - Exposed    -23.95 12.2 33 -1.962  0.1377
Sheltered - Moderate     1.59 12.2 33  0.130  0.9907
Exposed - Moderate      25.54 11.5 33  2.219  0.0827 .

density = Medium:
  contrast             estimate   SE df t.ratio p.value
Sheltered - Exposed     32.50 12.2 33  2.662  0.0311 *
Sheltered - Moderate    27.50 12.2 33  2.253  0.0771 .
Exposed - Moderate      -5.00 11.5 33 -0.434  0.9015

P value adjustment: tukey method for comparing a family of 3
estimates

$`simple contrasts for density`
energy = Sheltered:
  contrast      estimate   SE df t.ratio p.value
Low - High        7.75 12.9 33  0.602  0.8199
Low - Medium     -1.25 12.9 33 -0.097  0.9948
High - Medium    -9.00 12.9 33 -0.699  0.7655

energy = Exposed:
  contrast      estimate   SE df t.ratio p.value
Low - High      -20.20 11.5 33 -1.755  0.2005
Low - Medium     27.25 11.5 33  2.367  0.0604 .
High - Medium    47.45 11.5 33  4.122  0.0007 *

energy = Moderate:
  contrast      estimate   SE df t.ratio p.value
Low - High      -14.66 11.5 33 -1.274  0.4197
Low - Medium      2.25 11.5 33  0.195  0.9792
High - Medium    16.91 11.5 33  1.469  0.3185

P value adjustment: tukey method for comparing a family of 3
estimates
```

```
modelExpansion <- gls(growth ~ energy*density,
              weights = varIdent(form = ~1|energy*density),
              method = "REML",
              data = expansion)
```

TUKEY HSD FOR PLANT EXPANSION

```
`simple contrasts for energy`
density = Low:
 contrast             estimate    SE   df t.ratio p.value
 Sheltered - Exposed     15.60 33.31 3.59  0.468  0.8896
 Sheltered - Moderate    87.30 31.88 3.20  2.738  0.1309
 Exposed - Moderate      71.70 12.57 1.21  5.705     NaN

density = High:
 contrast             estimate    SE   df t.ratio p.value
 Sheltered - Exposed    -32.38 10.51 5.95 -3.081  0.0496
 Sheltered - Moderate     1.51  9.09 4.14  0.167  0.9849
 Exposed - Moderate      33.90  8.37 7.30  4.051  0.0109 *

density = Medium:
 contrast             estimate    SE   df t.ratio p.value
 Sheltered - Exposed    273.20 79.52 2.02  3.435  0.1321
 Sheltered - Moderate   282.43 81.32 2.21  3.473  0.1168
 Exposed - Moderate       9.22 19.20 3.61  0.480  0.8844

P value adjustment: tukey method for comparing a family of 3
estimates

$`simple contrasts for density`
energy = Sheltered:
 contrast      estimate    SE   df t.ratio p.value
 Low - High       46.62 32.34 3.37  1.442  0.4182
 Low - Medium   -202.50 85.26 2.63 -2.375  0.2038
 High - Medium  -249.12 79.66 2.04 -3.127  0.1542

energy = Exposed:
 contrast      estimate    SE   df t.ratio p.value
 Low - High       -1.36 13.21 1.39 -0.103     NaN
 Low - Medium     55.10 12.85 1.24  4.288     NaN
 High - Medium    56.46  9.41 3.70  5.997  0.0107 *

energy = Moderate:
 contrast      estimate    SE   df t.ratio p.value
 Low - High      -39.16  7.32 4.49 -5.349  0.0095 **
 Low - Medium     -7.38 19.01 3.57 -0.388  0.9222
 High - Medium    31.79 18.71 3.39  1.699  0.3270

P value adjustment: tukey method for comparing a family of 3
estimates
```