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DOCTOR OF PHILOSOPHY

Erosional resilience of salt marshes:

Bio-physical processes from patch to national scales

Duggan Edwards, Mollie

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**Erosional resilience of salt marshes:
Bio-physical processes from patch to
national scales**



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BANGOR
UNIVERSITY

Mollie F. Duggan-Edwards

PhD Thesis, June 2019

Summary

Coastal salt marshes are at 50% of their historical cover and threatened by sea-level rise. Salt marsh resilience is key to their future survival, but the mechanisms of resilience are poorly understood. This thesis explored patterns and drivers of marsh erosion and expansion from patch scale (a few meters) to geographical scales across the United Kingdom, focusing on changes at the seaward edges of marshes where marsh erosion or expansion is known to take place. Resilience of salt marshes is a product of environmental context and marsh bio-physical properties that collectively govern feedback mechanisms between vegetation, sediments and hydrological forcing. The relative importance of these factors to marsh change is likely to vary depending on the spatial scale of the study, although this principle has not been addressed to date. This thesis (1) investigated the intrinsic marsh bio-physical traits that underpin salt marsh resilience, (2) quantified resilience of marshes across different environmental contexts, and (3) explored whether spatial variation in resilience is explained by local to large-scale differences in external forcing and internal resilience traits. Three experimental chapters combined observational and experimental approaches at the patch to geographical scale across 1 to 20 salt marshes in the UK.

Chapter 2 investigated how bio-physical feedbacks between vegetation density, sediment vertical accretion and wave forcing interact to affect plant survival and patch lateral expansion. Vegetation density has feedback effects on sediment accretion and thus patch growth, but it is not known how feedbacks are affected by variation in wave forcing. This study planted out 3 levels of vegetation density across 3 levels of wave forcing, to test how bio-physical feedbacks depended on density-force interactions. The results showed vegetation density interacted with wave forcing to impact on plant survival, growth and lateral expansion. At the wave-exposed site, plant survival was highest inside dense patches, as plant density ameliorated erosive forcing; yet the diversion of water generated erosion gullies at the patch perimeter that prevented lateral patch expansion. The wave-sheltered site had no gully formation around dense patches, but plant competition had a negative effect on patch survival. This study shows that plant interactions can switch from positive to negative across stress gradients, according to the stress-gradient hypothesis. Furthermore, the study demonstrates that bio-physical processes occurring at the small, patch-scale have the potential to influence larger, landscape-scale patterns of marsh resilience. Plant interactions across erosive gradients should be considered in future restoration planting designs to increase marsh growth success. For example, salt marsh locations with higher levels of erosive forcing might require moderate vegetation density to permit resilience and growth at the patch scale.

Chapter 3 investigated the drivers and bio-physical properties of salt marsh resilience at a geographical, cross-UK scale. There is indication that marsh down-shore extent varies geographically, from north-west to south-east regions of the UK, potentially indicating that marsh resilience to erosion varies systematically over the same scales. Yet, there is limited empirical evidence to support this, and thus the causes for these large-scale geographical patterns are unclear. Marsh down-shore extent is the degree to which the lower marsh edge protrudes into the intertidal and is a product of the strength of external hydrological forcing balanced against the intrinsic properties of the marsh that enable it to withstand erosion. By observing patterns of down-shore extents of marshes across six UK regions, Chapter 3 aimed to identify which environmental contexts and resilience traits best explained the observed patterns in resilience. The results showed that wave forcing explained the variation in down-shore extents across the UK as marshes in the south-east extended further down-shore than marshes

in the north-west, where forcing was greatest. At more local scales (i.e. within the same region), intrinsic marsh properties such as sediment and vegetation characteristics became more important in promoting marsh resilience by acting to increase erosion resistance. The study confirmed that marsh resilience can vary over large- geographical scales as a product of large-scale external drivers such as wave forcing, which increases from south-east to north-west regions of the UK. Despite large-scale drivers regulating patterns of marsh resilience across the UK, intrinsic sediment and vegetation properties mediated cliff erosion to increase marsh resilience at more local, regional scales. The study highlights the importance of considering the scale at which resilience is observed before making assessments of salt marsh resilience.

Chapter 4 tested marsh resilience directly by observing how vegetation recovery to experimental disturbance depended on large-scale variation in environmental context and marsh-intrinsic properties across the UK, as large-scale variation in marsh resilience and their underlying mechanistic causes are imperative to marsh conservation and restoration, but are poorly understood. Chapter 4 aimed to determine which environmental gradients and bio-physical properties, which varied systematically across the UK, best explained variation in vegetation recovery after disturbance. The study experimentally disturbed above- and below-ground patches of salt marsh vegetation in twelve salt marsh locations of six regions in the UK, to test how vegetation recovery was affected by environmental contexts. In general, marshes in the south-east recovered better than marshes in the north-west. Variation in marsh recovery was explained by a combination of temperature and intrinsic marsh properties, including sediment characteristics and above-ground vegetation biomass. These variables varied systematically with a latitudinal gradient from the north-west to the south-east, which shows that marshes have geographical resilience contexts that are driven by large-scale variation in climate and geology. Large-scale variation in resilience is likely to be a common trend across other ecosystems, and although the intrinsic bio-physical properties behind resilience contexts will be system specific, climate is likely to be a common driver.

Overall, the thesis demonstrates how system inherent properties are key to understanding small to large-scale variation in salt marsh resilience to erosive forcing. It showed that resilience varied systematically across latitudinal gradients in the UK, and that smaller-scale patterns at patch (tussock) and local (regional) scales should not be overlooked because they can affect larger scale patterns of marsh change. This thesis emphasises that marsh resilience is specific to the temporal and spatial scales at which we observe it, and in a time of climatic uncertainty, it addresses a pressing need to understand what increases the vulnerability of salt marshes to disturbance. This thesis suggests that by observing the drivers and properties of resilience across different scales and contexts, we might be able to gain useful insights into understanding the mechanisms of resilience in salt marshes and other ecosystems.

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Thesis Stucture

Each of the three experimental chapters (Chapters 2-4) have been written as scientific research papers. Chapter 2 has already been submitted for publication in the Journal of Applied Ecology, whilst Chapters 3 and 4 are prepared for submisssion in peer reviewed journals. The names of co-authors are listed on the title pages of each chapter, and the contributions of each of the authors to the papers have been described in sections titled 'Author Contributions' which feature on the title pages. At the end of each experimental chapter I have inserted a Supplementary Materials section to support the text, and the content is referred to in chronological order. For example, Table S4.1 refers to the first table in the Supplementary Materials section of Chapter 4. Figures and tables are referred to in chronological order from Chapters 1-5.

CHAPTER 1

General Introduction

Mollie F. Duggan-Edwards

1.1 Resilience in a coastal context

Resilience is a theme that is understood by many people across a number of disciplines spanning social, economic and ecological fields. It encompasses the ability of an object (e.g. a person, a community or an ecosystem) to resist, recover or adapt to stress (Boin et al., 2010). For example, in sports, resilience might be defined as the capacity for a team to overcome a late game deficit (Boin et al., 2010). To psychologists, resilience might be the capacity for a human to overcome trauma or tragedy (Comas-Diaz, 2016), whilst financial institutions might perceive resilience as the stability of stock markets in the wake of a geo-political event (Kose & Prasad, 2011). Resilience has become a topical concept in recent years, resulting from a rising need for resilience, as advances in technology, terrorism and climate change are creating new and previously unimaginable threats to modern society and the natural world (Boin et al., 2010). Our inability to foresee these new threats makes preparation and reconciliation a challenge (Boin et al., 2010). Understanding the mechanisms and processes of resilience holds the promise of an answer (Boin et al., 2010).

Over the last 50 years, the number of climate-driven flooding and extreme weather events have increased by 250% (International Disasters Database, 2018). Over 40% of the human population live within 100 kilometres of the coast making them extremely vulnerable to future climate events (Agardy et al., 2012). In 2005, the city of New Orleans on the south-east coast of the USA was struck by hurricane Katrina, which devastated the entire city and killed thousands of people. This event questioned the resilience of the people, the city and the world (Boin et al., 2010). Extreme weather events such as these are becoming increasingly common, raising questions about the resilience of our global coastlines (International Disasters Database, 2018). For example, in 2018, the UK was hit by 25 storms, and extreme weather caused temperatures to plummet to -15°C for the first time in 30 years (Met Office, 2018). This emphasises a serious need to act on these extreme events along global coastlines.

Our coastlines are buffered with 1.6 million kilometres of natural systems that protect our livelihoods from such extreme weather events (UNEP, 2006). Coral reefs and mangrove forests in tropical regions, and seagrass meadows and salt marshes in temperate regions absorb wave energy, acting as important natural flood protectors along coastlines (Spalding et al., 2014). The problem is that these habitats are degrading on a global scale, with implications for their persistence and the delivery of natural coastal protection and other valuable ecosystem services. Over the past 50 years, as extreme weather events have significantly increased, 67% of coastal wetlands around the globe have disappeared (Lotze et al., 2006). There is, therefore, substantial interest in understanding the dynamics and potential resilience of these valuable coastal ecosystems, and furthermore in predicting how they are going to respond to a changing climate. In this thesis, I use salt marshes as a model system to address these questions, although my findings have great relevance to other sedimentary coastal systems in general.

1.2 Defining ecosystem resilience

Ecological resilience encompasses three major elements; (1) Resistance, (2) Recovery and (3) Adaptation (Fig. 1.1) (Holling, 1973). Resistance is the capacity of an ecosystem to maintain a healthy functioning state in the face of disturbance and environmental change (Fig. 1.1a). Ecosystems with low resistance to disturbance may transition into an 'alternative state' (Fig. 1.1a) (Beisner, Haydon, & Cuddington, 2003) relatively easily, even after a small disturbance event. In contrast it may take a significantly larger disturbance, or multiple disturbance events, to cause ecosystems with high resistance to shift into alternative states (Fig. 1.1). If an ecosystem transitions into an alternative state following disturbance, recovery is the capacity of that ecosystem to return to its pre-disturbed state (Fig. 1.1b). Ecosystem recovery is a measure of the time it takes for the system to return to its pre-disturbed state (Dakos, van Nes, Donangelo, Fort, & Scheffer, 2010; Scheffer et al., 2009). Therefore, ecosystems that recover quickly have a high recovery potential, whilst ecosystems that recover slower

have a low recovery potential (Dakos et al., 2010; Scheffer et al., 2009). Finally, adaptation is the capacity of an ecosystem to adapt and adjust its responses to a new set of environmental conditions within its current state (Walker et al., 2004). Thus, adaptive capacity maintains certain processes despite changing internal demands and external forces on the system (Carpenter & Brock, 2008). Salt marshes exist at the interface between land and sea and represent an abrupt spatial change between a landward-vegetated ecotone, the salt marsh, and a seaward un-vegetated ecotone, the tidal flat. As marshes regularly switch between visibly distinct, easily detected vegetated and bare states, they represent an ideal model system to investigate mechanisms of resistance, recovery and adaptation.

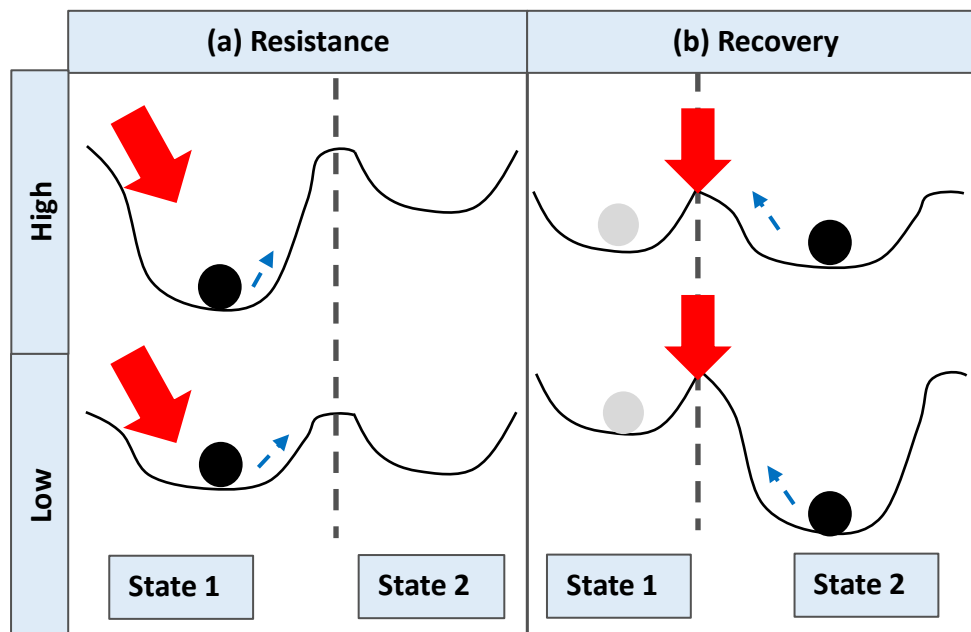


Fig 1.1. Schematic representation of ecosystems with high and low resilience (resistance and recovery) using the cup and ball theory (Holling, 1973). Cups represent ecosystem states (e.g. vegetated state), whilst the black balls represent the ecosystems within those states. In the recovery example, the grey balls represent the prior state of the ecosystem. The dashed blue arrows represent the movement of the ecosystem within or between states. The dashed grey line represents a threshold beyond which the ecosystem enters an alternative state (e.g. mudflat state). The red arrow represents a disturbance. (a) Ecosystems with high resistance are less likely to transition into an alternative state following a disturbance than those with low resistance. (b) Ecosystems with high recovery potential recover quicker from disturbance than ecosystems with low recovery potential.

1.3 The salt marsh ecosystem

Salt marshes are coastal wetlands that develop in sheltered intertidal environments including estuaries and bays, occupying approximately 5.5 million hectares of the global coastline (Mcowen et al., 2017). They occur from the arctic to the tropics, although they are most dominant in temperate climates (Adam, 1990). Salt marshes are dominated by halophytic (salt-tolerant) plants such as grasses, shrubs and herbs, which form distinct zones of vegetation communities across an elevation gradient from the sea to the land (Fig. 1.2) (Allen & Pye, 1992). Plant zonation along the elevation gradient is due to variable tolerances of the different plant species to a number of physio-chemical stressors including tidal inundation, waves, soil waterlogging and soil salinity (Allen, 2000; Boorman, 2003). Occupying a stressful interface between marine and terrestrial habitats, marsh persistence and expansion on intertidal mudflats across the globe depends on important interactions between plants, sediment and hydrodynamic conditions, so called 'bio-physical feedbacks' (Bouma et al., 2009; van Wesenbeeck, van de Koppel, Herman, & Bouma, 2008b) (refer to '1.6. Bio-physical Feedbacks' section).

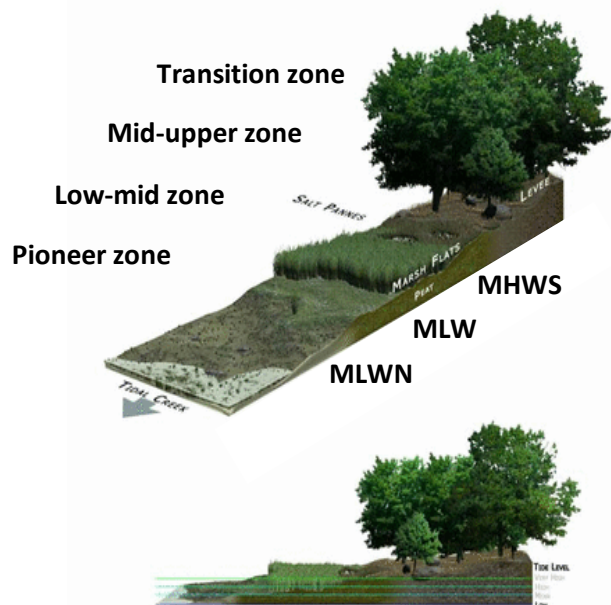


Fig 1.2. Zonation of a western European salt marsh with four recognisable zones of vegetation along an elevation gradient from land to sea: the transition zone, mid-upper zone, low-mid zone and the pioneer zone. MHWS = Mean High Water Spring tide level, MLW = Mean Low Water tide level, MLWN = Mean Low Water Neap tide level (NOAA, 2018).

In general, four distinct zones of salt marsh plants occupy an elevation gradient from land to sea in most western European salt marshes, which are the focus of the present thesis (Fig. 1.2) (Allen, 2000). These are defined by the transition zone (i.e. the boundary between terrestrial and marine plants), the mid-upper zone, the low-mid zone and the pioneer zone (i.e. the boundary between marine plants and the commencement of the bare mudflat) (Fig. 1.2) (Allen, 2000; Boorman, 2003). Salt marsh zonation patterns are defined by the tolerances of different plant species to a number of bio-physical factors including tidal inundation, soil salinity and waterlogging (Allen, 2000; Boorman, 2003). Plant species that are most tolerant of soil physio-chemical stressors occupy the lowest zones, closest to the sea, whilst the least tolerant species occupy the highest zones, closest to the land (Allen, 2000; Boorman, 2003). Zonation by species tolerances to environmental conditions is common across ecosystems that span uni-directional environmental gradients, such as intertidal rocky shores (Southward, 1958) and alpine forests along mountain slopes (Salter et al., 2005). On a rocky shore, organisms that are least tolerant to tidal emersion occupy the lowest shore zones, whilst species that are more tolerant to emersion and less competitively strong occupy the highest zones (Southward, 1958). Similarly, in alpine forests that occupy a steep elevation gradient, tree species that are most tolerant of low temperatures occupy the highest zones, whilst the least tolerant species occupy the lowest zones (Salter et al., 2005).

Within these four zones, salt marsh plants are restricted between mean low water and mean high water spring tide levels (Allen, 2000; Boorman, 2003). Salt marsh pioneer plants occupy zones between mean low water levels and mean high water of neap tide levels, which means that these plants endure the highest inundation (Fig. 1.2) (Emery, Ewanchuk, & Bertness, 2001). Conversely, transition plants occupy areas that may only be flooded during the highest astronomical tides or during severe storm events, and these zones resemble more of a terrestrial habitat (Fig. 1.2) (Emery et al., 2001). Despite these general patterns, there is much variation across the globe, and this is most obvious when comparing UK versus USA marshes (Adam, 1990). On the south-east coast of the USA, marshes tend to be flatter (i.e. they occupy less of an elevation gradient), but they occupy much lower

elevations than western European marshes because they tend to be dominated by pioneer plant species of the genus *Spartina* that can tolerate high inundation and soil salinities (Fig. 1.3) (Adam, 1990; Thompson, McNeilly, & Gray, 1991).

1.4 Salt marsh values and threats

The salt marsh ecosystem is recognised globally for its importance in delivering a diverse range of ecosystem services, which are valued in excess of \$10,000 per hectare (Costanza et al., 2014). Salt marshes are well known for their ability to offer important natural flood protection along the coast by dissipating waves before they propagate onto the land, with potential savings on constructing artificial coastal defences (Möller et al., 2014). Marshes are also important for sequestering and storing ‘blue carbon’, with an estimated accumulation of 162 Mg of carbon within the upper 1m of soil per hectare (Duarte, Losada, Hendriks, Mazarrasa, & Marbà, 2013). Salt marshes are also used agriculturally for livestock grazing (Nolte et al., 2013; Davidson et al., 2017), they provide important refuges and feeding grounds for birds (Sharps, Smart, Skov, Garbutt, & Hiddink, 2015) and commercially important fish species (Kneib et al., 1997) as well as marine and terrestrial invertebrates (Ford, Garbutt, Jones, & Jones, 2013) (Fig. 1.4). In recent years, salt marshes have also been recognised for their cultural services, as they provide aesthetically pleasing landscapes for human recreation (McKinley, Ballinger, & Beaumont, 2018).

The range and extent of ecosystem services delivered by salt marshes are at risk since these valuable coastal habitats are in a severe state of decline, with approximately half of the global marsh coverage lost in the last century alone (Moreno-Mateos, Power, Comín, & Yockteng, 2012). Direct human impacts have threatened salt marsh existence for centuries (Gedan, Bromberg, Silliman, & Bertness, 2009); vast tracts of salt marsh have been embanked and drained for conversion to agricultural and urban land since human habitation of the coast began (Hatvany, Cayer, & Parent, 2015; Jongepier, Wang, Missiaen, Soens, & Temmerman, 2015). Extensive urbanisation along coastlines has

also indirectly contributed to salt marsh decline by restricting the marsh plants from retreating landward in response to stresses, a phenomenon known as coastal squeeze (Nicholls et al., 2007). Salt marshes have been extensively exploited for commercial salt extraction, hay harvesting and turf stripping (Gedan et al., 2009). Coastal eutrophication through nutrient loading (Deegan et al., 2012), trophic cascades (Silliman & Bertness, 2012), and reductions in sediment flux to the coastline through land change (Syvitski, Vo, Kettner, & Green, 2005) and dredging (Cox, Wadsworth, & Thomson, 2003) are also implicated in the degradation of salt marshes.

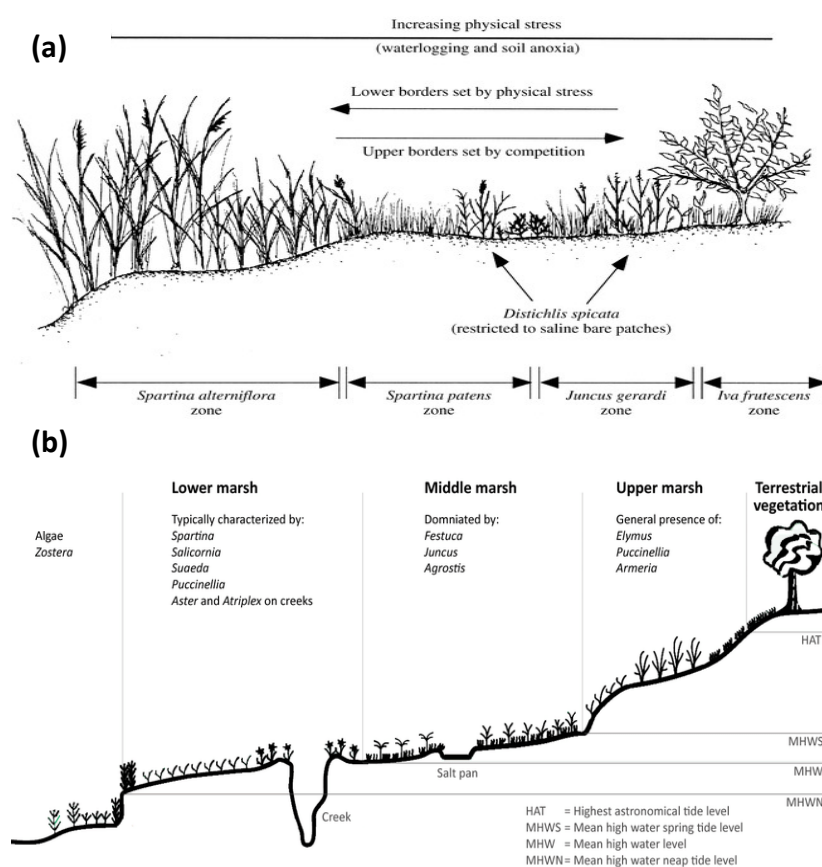


Fig 1.3. Zonation in a typical (a) East coast USA salt marsh (note domination by *Spartina* species), and (b) Western European salt marsh (note distinct zonation patterns) (Bertness, Ewanchuk, & Silliman, 2002; Boorman, 2003).

In addition to a large range of localised anthropogenic pressures, salt marshes now face the threat of climate change, which is contributing towards rising temperatures (Gabler et al., 2017;

Kirwan, Temmerman, Skeeahan, Guntenspergen, & Fagherazzi, 2016) and sea levels, as well as increasing the frequency and severity of extreme storm events (Kirwan & Megonigal, 2013; Giulio Mariotti & Fagherazzi, 2010). Sea level rise threatens marsh vegetation by increasing the risk of drowning (Spencer et al., 2015), with some forecasters predicting that it will be responsible for the loss of 60-90% of remaining salt marsh habitat by 2100 (Giuliani & Bellucci, 2019). However, the vulnerability of salt marshes to sea level rise is contentious, with some studies predicting global losses (e.g. Spencer et al., 2015), and others predicting resilience via sediment supply and accretion that enable marshes to keep pace with rising sea levels (e.g. Kirwan et al., 2016).

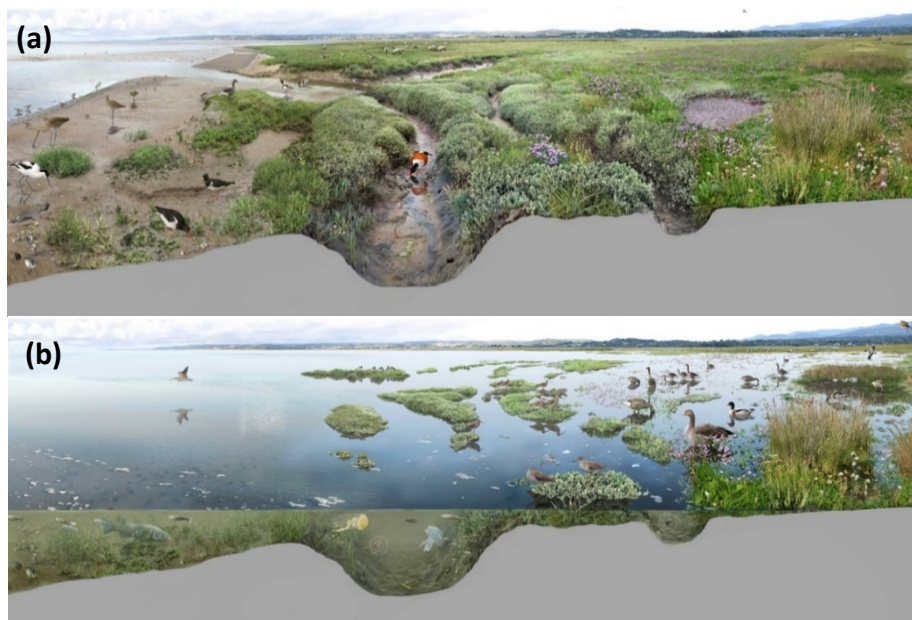


Fig 1.4. Salt marsh provisioning of important ecosystem services during (a) low and (b) high tides. The marsh offers important feeding grounds for birds, grazing grounds for livestock and recreational space for humans during low tide. At high tide, the marsh offers important refuge for commercially important fish species (artwork by Toni Llobert, www.tonillobert.com).

1.5 Salt marsh mechanisms

Part of the challenge to predicting future change in salt marshes is of the need to consider not only the vertical dynamics of sea level rise (Fig. 1.5), but also the potential for sea level rise to contribute towards marsh decline in the lateral direction (Fig. 1.5). Rising sea levels increase water depths and

thus the size of waves propagating over the marsh (Leonardi, Ganju, & Fagherazzi, 2015). Together, rising sea levels and storminess are implicated as the greatest threats to salt marshes, and they may be most vulnerable to erosion in the lateral, up-down shore direction (Fig. 1.5) (Marani, D'Alpaos, Lanzoni, & Santalucia, 2011; Mariotti & Fagherazzi, 2013; Kirwan et al., 2016; Wang et al., 2017).

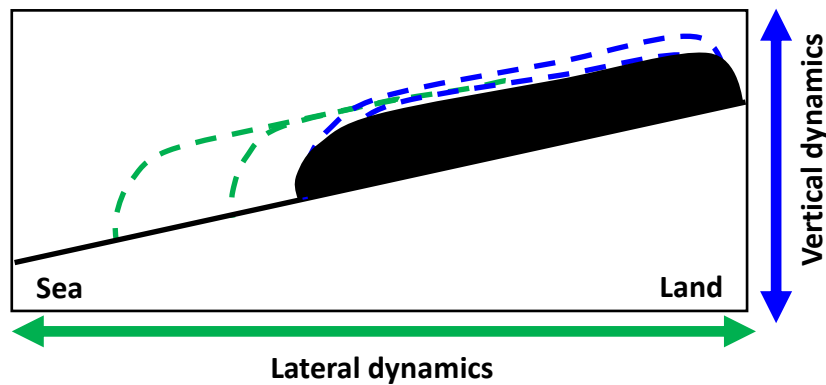


Fig 1.5. Cross-shore profile of vertical and lateral salt marsh dynamics. Blue dashed lines indicate the capacity for the marsh platform to move up and down (vertical marsh dynamics), whilst the green dashed lines indicate the capacity for the marsh to move landwards and seawards (lateral marsh dynamics).

Erosion at the lower marsh edge (lateral erosion) (Fig. 1.5) occurs in two main ways (Francalanci, Bendoni, Rinaldi, & Solari, 2013; Wang et al., 2017). Firstly, large amounts of sediment may be removed during a severe storm event, similar to the process that occurs during cliff erosion (Fig. 1.10) (Francalanci, Bendoni, Rinaldi, & Solari, 2013). Secondly, sediment erosion can occur via the gradual removal of small amounts of particles, which is the process that occurs as a result of a continuous physical force at the marsh edge (Wang et al., 2017). The drivers of erosion at the lower marsh edge are well understood (Balke et al., 2016; Bouma et al., 2009; Callaghan et al., 2010; Mariotti & Carr, 2014; Giulio Mariotti & Fagherazzi, 2010; Silinski, Fransen, Bouma, Meire, & Temmerman, 2016). They include tidal inundation frequency and duration (Balke et al., 2016; Willemsen et al., 2018), wave forcing (Callaghan et al., 2010; Silinski et al., 2016) and tidal currents (Bouma et al., 2009). For estuarine marshes protected from severe wind-wave action, tidal channels are the main source of sediment

erosion at the lower marsh edge (Pringle, 1995; Cox et al., 2003). The drivers discussed so far largely operate continuously, over long time periods, but there are some drivers of sediment erosion that operate suddenly, over scales of hours to days, such as severe storms events (van der Wal & Pye, 2004). Similarly, a switch of a tidal channel from one side of an estuary to the other can cause significant erosion at the lower edge of the marsh within only a few months (Pringle, 1995; Cox et al., 2003).

In addition to the direct drivers of sediment erosion discussed above (waves, tidal channels etc.), there are also some indirect drivers of sediment erosion at the lower marsh edge. For example, sediment supply from marine or fluvial sources can diminish erosion risks when the replenishment of sediment is sufficiently large to cause tidal flats and the marsh to elevate through accretion (Hoitink, 2003; Ganju et al., 2017). However, when sediment supply is insufficient, it contributes to the erosional impact at the lower marsh edge (Fagherazzi, 2013; Mariotti & Fagherazzi, 2013). Building on this, Bouma et al., (2016) and Willemsen et al., (2018) emphasised the importance of sediment dynamics (i.e. sediment erosion versus accretion) in influencing periods of sediment erosion at the lower marsh edge. These studies suggested that ‘dynamic sediments’ where substrate elevation regularly changes from alternating periods of erosion and accretion, are indicative of erosional settings (Bouma et al., 2016; Willemsen et al., 2018).

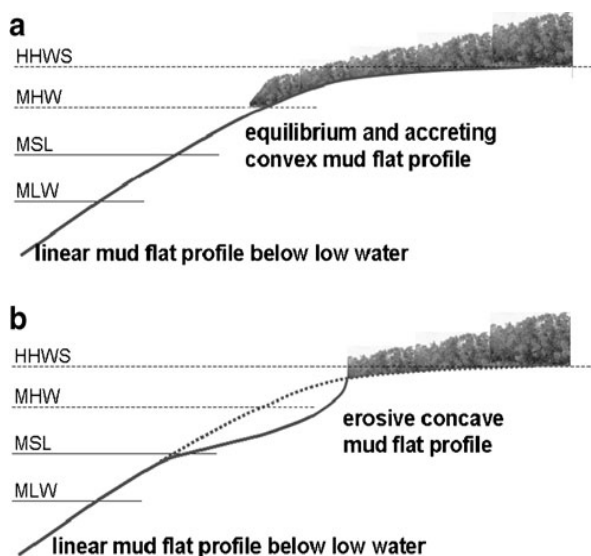


Fig 1.6. Shapes of intertidal mudflats fronting salt marshes. (a) Accreting convex mudflat profile. (b) Eroding concave mudflat shape (Winterwerp et al., 2013).

Studies have also suggested that the shape and width of the intertidal mudflat in front of the marsh can drive sediment erosion at the lower marsh edge (Fig. 1.6) (Winterwerp et al., 2013; Hu et al., 2015; Wang et al., 2017). Tidal flats typically have either concave or convex shapes, with concave shapes typically encouraging more erosion than convex shapes (Fig. 1.6) (Bearman, Friedrichs, Jaffe, & Foxgrover, 2010; Winterwerp et al., 2013; Hu et al., 2015). Studies have also shown that the width of the tidal flat in front of the marsh can affect sediment erosion, as wider mudflats may benefit the marsh by dissipating waves over longer distances before they reach the lower marsh edge (Bearman, Friedrichs, Jaffe, & Foxgrover, 2010). In addition, Wang et al., (2017) suggested that the presence of pioneer vegetation could attenuate hydrodynamic energy before it reaches the marsh edge, thus acting to reduce sediment erosion.

Despite a comprehensive understanding of the main drivers of sediment erosion at the lower marsh edge, we still lack a fundamental understanding of the mechanisms of resilience. This is a key knowledge gap to address if we are going to be able to predict marsh persistence along global coastlines in the face of climate change

1.6 Bio-physical feedbacks

The establishment and persistence of coastal wetlands including salt marshes, seagrasses and mangroves on tidal flats around the globe depends on important interactions between the plants and their physical environments (van de Koppel et al., 2005; van Wesenbeeck et al., 2008a). Salt marsh vegetation traps sediments by reducing hydrodynamic energy, which causes the vegetation to grow better and hence to become more effective in trapping sediment (Bouma et al., 2016). These so-called bio-physical interactions begin during marsh establishment, and remain equally important throughout the evolution of the marsh landscape. At the settlement stage on an intertidal mudflat, it is important that the seedlings of pioneer plants (*Spartina anglica*, *Zostera marina* and *Avicennia marina* in salt

marshes, seagrasses and mangroves, respectively) are exposed to a series of prolonged disturbance-free periods, known as 'Windows of Opportunity (WoO)', to avoid dislodgement from waves and currents (Wiehe, 1935; Balke, Herman, & Bouma, 2014; Hu et al., 2015). The stages of the Windows of Opportunity are as follows, (1) seedling establishment and rapid development of a rootlet before tidal inundation to avoid dislodgement, (2) development of sufficiently long roots over ~3 days to avoid dislodgement from waves and currents during tidal inundation, and (3) periods of low storm activity over 2-4 weeks, allowing the shoots to develop sufficient root growth to tolerate storm-induced sediment elevation changes on the tidal flat (see Fig. 1.7) (Wiehe, 1935; Balke, Herman, & Bouma, 2014; Hu et al., 2015). Therefore, over a period of hours to months (stages 1-3), the seedlings and juvenile plants need a number of episodes of low physical disturbance to establish and anchor into the mudflat (Balke, Herman, & Bouma, 2014). If the physical disturbances are too great, the plants will fail to establish on the mudflat and over time the landscape will remain in a bare, un-vegetated state (Balke, Herman, & Bouma, 2014).

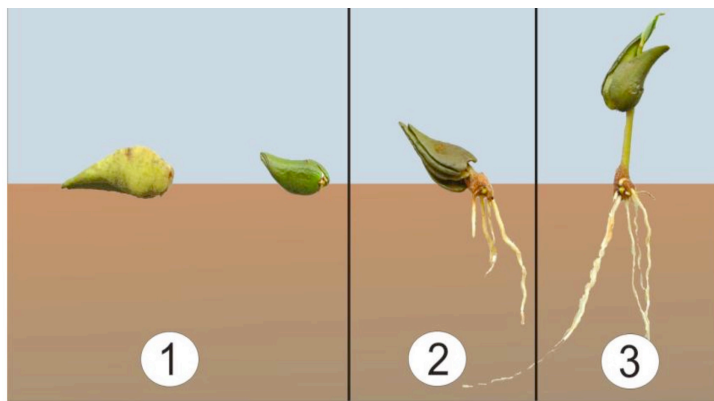


Fig 1.7. The establishment of a pioneer seedling on a tidal flat depends on (1) inundation (e.g. ~3 days), (2) hydrodynamics and (3) sediment dynamics (e.g. 2-4 weeks) (Balke, 2013).

Disturbance-free periods from physical stress alone are not enough to ensure the successful establishment of the seedlings on the intertidal mudflat (Hu et al., 2015; Cao et al., 2018). Others have suggested that periods without hydrological disturbances must coincide with periods without

disturbance from sediment mobility (i.e. erosion and accretion), because sediment dynamics also affects seedling capacity to establish (Hu et al., 2015; Cao et al., 2018). Hu et al., (2015) refers to this as a second Window of Opportunity, in which bed shear stress induced by waves and currents (a proxy for sediment resuspension) (Callaghan et al., 2010) must remain below a critical level for 2-4 weeks following the anchorage of the seedling (in the first WoO) to avoid uprooting and dislodgement. Additionally, the seedlings must avoid significant sediment accretion, which threatens them with burial and suffocation (Balke, 2013). These studies demonstrate the importance of incorporating physical forcing and sediment dynamics in the prediction of salt marsh establishment (Hu et al., 2015; Cao et al., 2018). At this critical establishment phase, physical forces (i.e. inundation stress, waves and currents) and sediment dynamics (i.e. erosion or accretion) have a dominant control over the establishment of the new seedlings on bare mudflats (Balke, Herman, & Bouma, 2014). Sediment and hydrological controls of plant establishment persist until the newly colonised vegetation reaches a suitable density where it can exert some control over its physical environment, in a process known as 'ecosystem engineering' (Jones, Lawton, & Shachak, 1994). Once established, pioneer plants such as *Spartina anglica* act as important ecosystem engineers (Jones, Lawton, & Shachak, 1994). These are defined as organisms that modify their environment to create optimal conditions for themselves and associated organisms (Jones et al., 1994; Bos, Bouma, de Kort, & van Katwijk, 2007). *Spartina* plants engineer the tidal flat environment by dissipating wave energy, which stimulates sediment 'accretion' inside the vegetation canopy as a result of dampened hydrodynamic conditions (Fig. 1.8) (van Hulzen, van Soelen, & Bouma, 2007; van Wesenbeeck et al., 2008b). This positive feedback leads to enhanced survival and growth of the engineering organism, because sediment trapping leads to elevated bed levels inside the canopy, which further reduces inundation stress and the impact of waves (Fig. 1.8) (van Wesenbeeck et al., 2008a; Bouma et al., 2009). These positive feedbacks (defined as a process that enhances or amplifies an effect by having an influence on the processes that gave rise to it) act to re-enforce marsh resilience at the tussock scale, but also at the larger landscape scale (van Hulzen, van Soelen, & Bouma, 2007). Bio-physical feedbacks have landscape-scale consequences by promoting the

expansion and growth of other individuals; more vegetation leads to a greater degree of sediment trapping which ultimately can lead to the formation of a dense, homogenous vegetated state (Figs. 1.8, 1.9) (van Wesenbeeck et al., 2008b; Bouma et al., 2009).

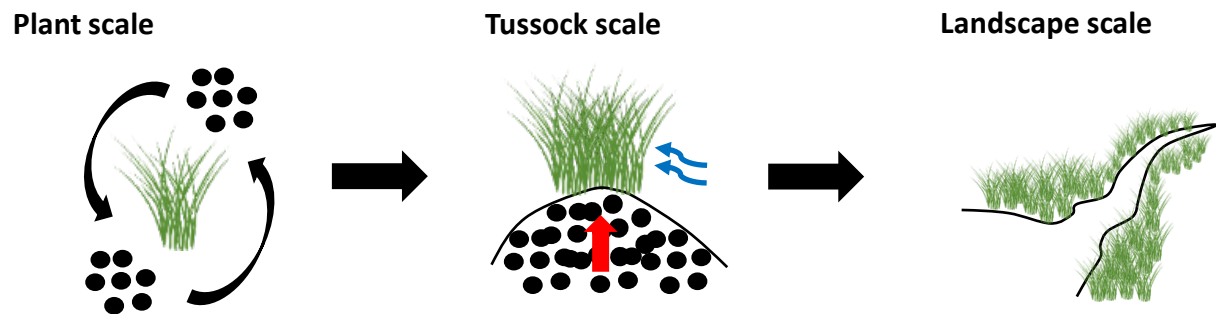


Fig 1.8. Bio-physical feedbacks between plants, sediment and hydrodynamics at the plant and tussock scales lead to landscape scale dynamics (based on van Wesenbeeck et al., 2008b). Blue arrows represent wave forcing which is dampened inside the vegetated tussock, and the red arrow represents sediment build-up inside the canopy.

An alternative scenario to the one described above (Fig. 1.8) is that pioneer patches of vegetation fail to develop into homogeneous states, resulting in the formation of patchy zones of vegetation at the marsh edge (Fig. 1.9) (van Wesenbeeck et al., 2008a). Patchy zones often exist because the positive feedbacks of wave dampening and sediment build-up that lead to plant growth and vegetation expansion inside the vegetated tussocks can lead to negative feedbacks, such as erosion gully formation and sediment erosion immediately outside the vegetated tussocks (Bouma et al., 2009). This negative feedback is caused by the diverted flow of the water from within the canopy to around the edges of the tussock (Bouma et al., 2009). The diversion of the energetic water causes scouring and hence leads to the formation of significant depressions around the tussock, known as erosion gullies (Fig. 1.10) (Bouma et al., 2009). The negative feedback of gully formation restricts the plants from expanding laterally, making the tussocks vulnerable to wave attack and erosion (Fig. 1.10) (van Hulzen, van Soelen, & Bouma, 2007). This leads to a patchy, unstable marsh landscape with less

resilience to physical disturbance (Fig. 1.9) (van Wesenbeeck et al., 2008a). The above illustrates the principle of ‘scale-dependent feedbacks’: what appears to be a positive effect at the tussock scale does not carry through to a positive effect at the landscape scale (Fig. 1.9). Similar scale-dependent feedbacks have been described in other ecosystems, including mussel beds (van de Koppel et al., 2005) and diatom-aggregated biofilms on intertidal mudflats (Ysebaert, Hart, & Herman, 2009).

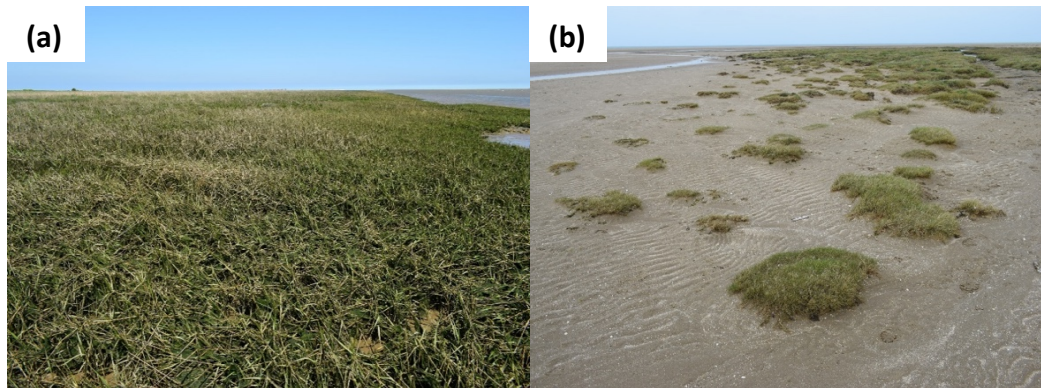


Fig 1.9. Differences in landscape scale patterns as a result of bio-physical feedbacks; (a) Dense marsh pioneer zone, and (b) Patchy marsh pioneer zone.

Switches between positive and negative feedbacks described here are largely determined by vegetation density (Fig. 1.10) (Bouma et al., 2005, 2007). In a study investigating pioneer zone dynamics, van Wesenbeeck et al., (2008b) noted that *Spartina* plants were only capable of sustaining themselves on mudflats provided the patches were large enough. High density *Spartina* vegetation encourages greater sediment deposition by reducing wave energy inside the canopy, leading to higher plant survival (Fig. 1.10) (Bouma et al., 2005, 2009; van Hulzen et al., 2007). At the same time, deeper erosion gullies form immediately outside dense vegetation as the energy is deflected and concentrated, which limits the opportunity for patch lateral expansion (Fig. 1.10) (van Hulzen et al., 2007; van Wesenbeeck et al., 2008b; 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 et al., 2007; van Wesenbeeck et al., 2008b; Bouma et al., 2009). Yet, low density patches have less gully formation at the vegetated boundary, thus retaining

the potential for lateral expansion (Van Hulzen et al., 2007; van Wesenbeeck et al., 2008b; Bouma et al., 2009).

Despite an acknowledgement that these bio-physical feedbacks are density- dependent, few studies have investigated the likelihood that they are also highly dependent on external forcing conditions. Bouma et al., (2009) demonstrated in a flume experiment that density-dependent feedbacks changed at different current speeds and suggested that bio-physical feedbacks must also change in field conditions across natural gradients of hydrological forcing. However, no study has tested the interaction between plant density and external forcing conditions under field conditions, which is vital for understanding future landscape dynamics and marsh resilience under new climate regimes.

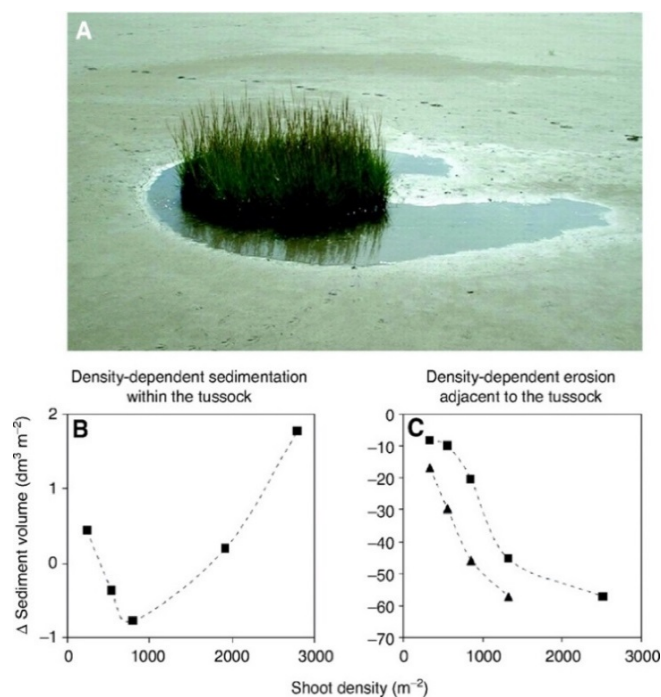


Fig 1.10. (A) *Spartina* tussock demonstrates that bio-physical interactions are both scale- and density-dependent. (B) Density-dependent sedimentation within the tussock. The relationship between tussock density and net sedimentation within a tussock of *Spartina* shows a clear density dependence. (C) Density-dependent erosion adjacent to the tussock: the relationship between the density of shoots inside the tussock and erosion immediately outside the tussock (modified from Bouma et al., 2009).

The outcomes of bio-physical feedbacks in marsh pioneer zones can therefore have significant implications for salt marsh dynamics over larger spatial and temporal scales (van de Koppel et al., 2005; van Wesenbeeck et al., 2008b). Despite their importance, we still lack information about how interactions between plants and their environments change across physical stress gradients, which ultimately drives variations in landscape dynamics and marsh resilience. In Chapter 2, the present thesis investigates how bio-physical interactions change across environmental stress gradients to ultimately affect long-term dynamics.

1.7 Dynamics at the lower marsh edge

As highly dynamic ecosystems, salt marshes regularly switch between periods of seaward expansion and landward retreat, with switching thought to be driven by changes in the external conditions (Fig. 1.11) (Yapp, Johns, & Jones, 1917; Gray, 1972; Pringle, 1995; Allen, 2000; Cox et al., 2003; van de Koppel et al., 2005; Fagherazzi, 2013). Cycles of marsh expansion, which are characterised by lateral vegetation growth onto the fronting mudflat, typically starts with seedling establishment. Conversely, marsh retreat, which is characterised by lateral erosion, occurs when retreating cliffs remove both the vegetation and sediment layers. Both periods of marsh expansion and retreat characterise these cyclical marsh patterns (Fig. 1.11) (Pye, 1995; Allen, 2000; van der Wal, Wielemaker-Van den Dool, & Herman, 2008; Singh Chauhan, 2009). Cycles of expansion and retreat can be short-term over seasons (van Proosdij, Davidson-Arnott, & Ollerhead, 2006), or they can last over much longer time periods of decades (Allen & Haslett, 2002) or even centuries (Singh Chauhan, 2009).

Cyclic marsh dynamics are not always apparent, as sites can appear to be static (for decades to centuries before the next shift to erosion or expansion occurs). Although these cyclic dynamics have been recognised for over 100 years (Allen, 2000; Gray, 1972; Yapp et al., 1917), our understanding of the actual processes driving salt marsh dynamics remains poor (Bouma et al., 2016). At the landscape scale the initiation of lateral marsh erosion has generally been attributed to sudden changes in external

forcing, such as increased shipping that increases local wave-state, shifted positions of estuarine channels, wind-wave activity or sea level rise (Allen, 2000; Cox et al., 2003; van der Wal & Pye, 2004; van der Wal et al., 2008). Alternatively, the initiation of marsh erosion may be an autonomous process that will inevitably occur, as faster long-term vertical sediment accretion of the marsh than the tidal flat leaves an unstable and erosion-prone cliff at the marsh-mudflat boundary (van de Koppel et al., 2005; Singh Chauhan, 2009). Recent empirical evidence has shown that seasonal sediment flux on the tidal flat fronting the marsh edge can trigger long-term periods of expansion or erosion (Bouma et al., 2016). During rough winter weather, wave erosion lowers the surface of the tidal flat, forming a marsh cliff vulnerable to wave attack (Callaghan et al., 2010; Mariotti & Fagherazzi, 2010; Bouma et al., 2016). In calmer spring/summer weather, sediment deposition onto the tidal flat increases the chance of seedling establishment and clonal expansion onto the foreshore (Bouma et al., 2016; Silinski et al., 2016; Cao et al., 2018). However, the further the marsh extends seaward and into increasing hydrological forcing conditions, the greater is the risk of marsh lateral erosion (Bouma et al., 2016). Thus, periods of marsh lateral expansion may eventually turn into periods of lateral erosion (Fig. 1.11).



Fig 1.11. Outcomes of lateral marsh dynamics; (a) a marsh in the process of erosion (note the erosion cliff), (b) a marsh in the process of expansion with the lowest zone dominated by pioneer plants (*Spartina anglica*) and, (c) a recovered marsh with recolonised vegetation in front of the remnants of an old erosional cliff.

In the past, salt marshes have recovered from long periods of retreat (Gedan et al., 2009), but in the last century over 50% of the global salt marsh habitat has disappeared (Moreno-Mateos et al., 2012). Some of this large-scale global loss could be due to historical disturbances including land reclamation and channel dredging (Gedan et al., 2009), but this may have reduced the inherent resilience of the marsh to disturbances. Recent studies investigating marsh lateral dynamics focus on the processes driving erosion at the marsh edge, rather than the interaction between drivers of erosion and mechanisms of resilience (Bouma et al., 2016). Hence, there is a lack of understanding of the exact mechanism that enable marshes to resist erosional forces at the marsh edge, and to recover from extended periods of erosion (Bouma et al., 2016). The present thesis focusses on the drivers and mechanisms of resilience at the lower marsh edge, to understand in which contexts marshes might be most vulnerable to dramatic switches between marsh expansion and retreat.

Salt marshes may respond in different ways to environmental forces operating at their lower edges due to inherent differences in their exposure to those forces (Raposa et al., 2016), but also because they might differ in their internal characteristics which enable them to resist erosion (Feagin et al., 2009; Ford, Garbutt, Ladd, Malarkey, & Skov, 2016). Marsh exposure to environmental forces could be defined by the frequency of tidal inundation (Balke et al., 2016; Willemsen et al., 2018), the degree of wave forcing (Callaghan et al., 2010), or the proximity of the lower marsh edge to the nearest tidal channel in an estuary (Pringle, 1995; Cox et al., 2003). For example, Balke et al., (2016) and Willemsen et al., (2018) both demonstrated that the risk of sediment erosion at the lower marsh edge increased with higher inundation stress. Callaghan et al., (2010) demonstrated that cliff edge erosion increased with the amount of wave forcing in the system. Pringle (1995) and Cox et al., (2003) demonstrated a positive relationship between cliff edge erosion and the proximity of the marsh to the nearest tidal channel in an estuary. However, fewer studies have investigated important interactions between both the drivers of sediment erosion and the internal mechanisms of marshes, which might enable them to resist erosion. Most studies have investigated either the extrinsic drivers of sediment erosion, or the marsh-intrinsic traits of erosion resistance. Yet, the bio-physical feedbacks (refer to the

'1.6. Bio-physical feedbacks' section) that are fundamental to marsh vertical and lateral growth are a product of that interaction of external drivers of erosion with internal resilience mechanisms. In recent years, a few studies have started to investigate interactions to determine marsh vulnerability and resilience against erosional forces (Lo et al., 2017; Wang et al., 2017) and it is the aim of this thesis to add to this important knowledge gap.

Several studies have identified important resilience traits in salt marshes, including sediment and vegetation properties (Angelini & Silliman, 2012; Feagin et al., 2009; Ford et al., 2016; Wang et al., 2017). Sediment type has long been acknowledged as an important property in salt marshes, and one that affects both plant growth (Tansley, 1939; Chapman, 1941; Huckle, Potter, & Marrs, 2000) and marsh stability against erosional forces (Feagin et al., 2009; Ford et al., 2016). Under laboratory conditions, Huckle et al., (2000) investigated the effect of sediment grain size on the growth of salt marsh plants. Huckle et al., (2000) found that coarse-grained sandy sediments mostly inhibited plant growth, whilst fine-grained muddy sediments encouraged plant growth. Feagin et al., (2009) and Ford et al., (2016) both demonstrated the importance of sediment type in provisioning important erosion resistance in salt marshes. Marshes with muddier, more cohesive sediments resisted erosion better than marshes with sandier sediments, which were more vulnerable to erosion (Feagin et al., 2009; Ford et al., 2016). Another important parameter for marsh stability is the compressibility of the sediment (Bradley & Morris, 1990), which is positively correlated to the silt-clay fraction in the sediment. Therefore, muddier marshes with more compressed soils resist erosion better than sandier marshes with less compressed soils (Bradley & Morris, 1990; Pagès, Jenkins, Bouma, Sharps, & Skov, 2018). Other studies have linked marsh erosion resistance to biological properties, including vegetation type, vegetation composition, plant species richness (Fig. 1.12), below-ground root biomass and organic matter content (Feagin et al., 2009; Ford et al., 2016). Lo et al., (2017) demonstrated that marshes with *Spartina anglica* at their edges were more resistant to erosion than marshes without *Spartina*, whilst Ford et al., (2016) demonstrated a positive relationship between erosion resistance and plant species richness. This study suggested that a likely reason was that a higher diversity of plant

species increased the variety of root structures and depths in the sediment, which in turn boosted the binding of the sediment (Ford et al., 2016). The fact that marshes with *Spartina* resisted erosion better than those without was linked to the morphological traits of the plant, as *Spartina* is rhizomatous and robust, enabling it to resist erosion better than a high shore species such as *Puccinellia maritima*, which is stoloniferous and fragile (Huckle et al., 2000; Ford et al., 2016; Lo et al., 2017).

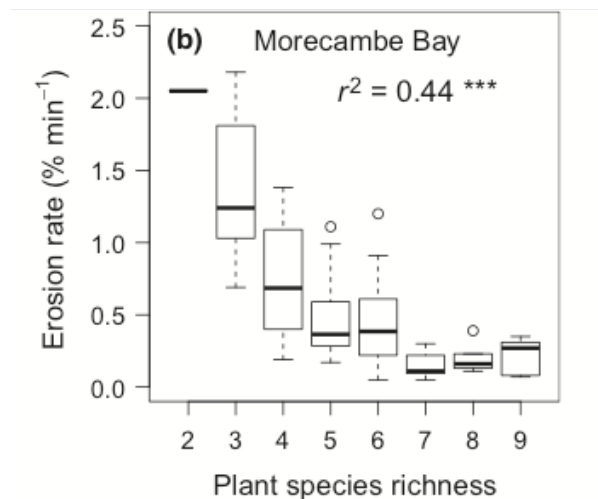


Fig 1.12. Salt marsh erosion reduces with plant species richness, as demonstrated using vegetation soil cores extracted from marshes in Morecambe Bay, UK (Ford et al., 2016). Thick horizontal bars = median, box = interquartile range, vertical whiskers = full range, open circles = outliers.

1.8 Aims and Hypotheses

Investigating the mechanisms by which salt marshes can be resilient to erosional forces is fundamental if we are going to be able to predict their persistence along global coastlines and continue benefitting from their valuable ecosystem services in the face of climate change. This thesis addresses a vital need to investigate the mechanisms by which marshes can be more or less resistant to erosion, focusing particularly on resilience processes at the lower marsh edge where dramatic switches from expansion to retreat are most likely to occur. The preceding literature review has outlined the plausible importance of bio-physical feedbacks to salt marsh resilience. It has illustrated that such feedbacks could be scale dependent, or at least that the underpinning processes might operate at a number of spatial scales. Heeding these scale perspectives, I will investigate interactions between the drivers and

traits of resilience at multiple scales, from local marsh patches and individual marshes, to national scales, in which I contrast marsh sites and regions across the UK. Through a series of observational and manipulative field experiments, the aims of the present thesis are (1) to gain a better understanding of the specific levels and underpinning mechanisms of salt marsh resilience at the lower marsh edge. (2) To explore how the variation in resilience is explained by local to large-scale gradients in external forcing and internal marsh resilience traits. Three chapters combining observational and experimental approaches, meet the aims of this thesis (Fig. 1.13). Chapter 2 investigates mechanisms of resilience at the small, patch scale (Fig. 1.13) to try to explain how plant density affects patch resilience and expansion across gradients in external wave forcing. Chapters 3 and 4 investigate mechanisms of resilience at larger scales but differ in that one (Chapter 3) is observational and the other is experimental (Chapter 4) (Fig. 1.13), as detailed below.

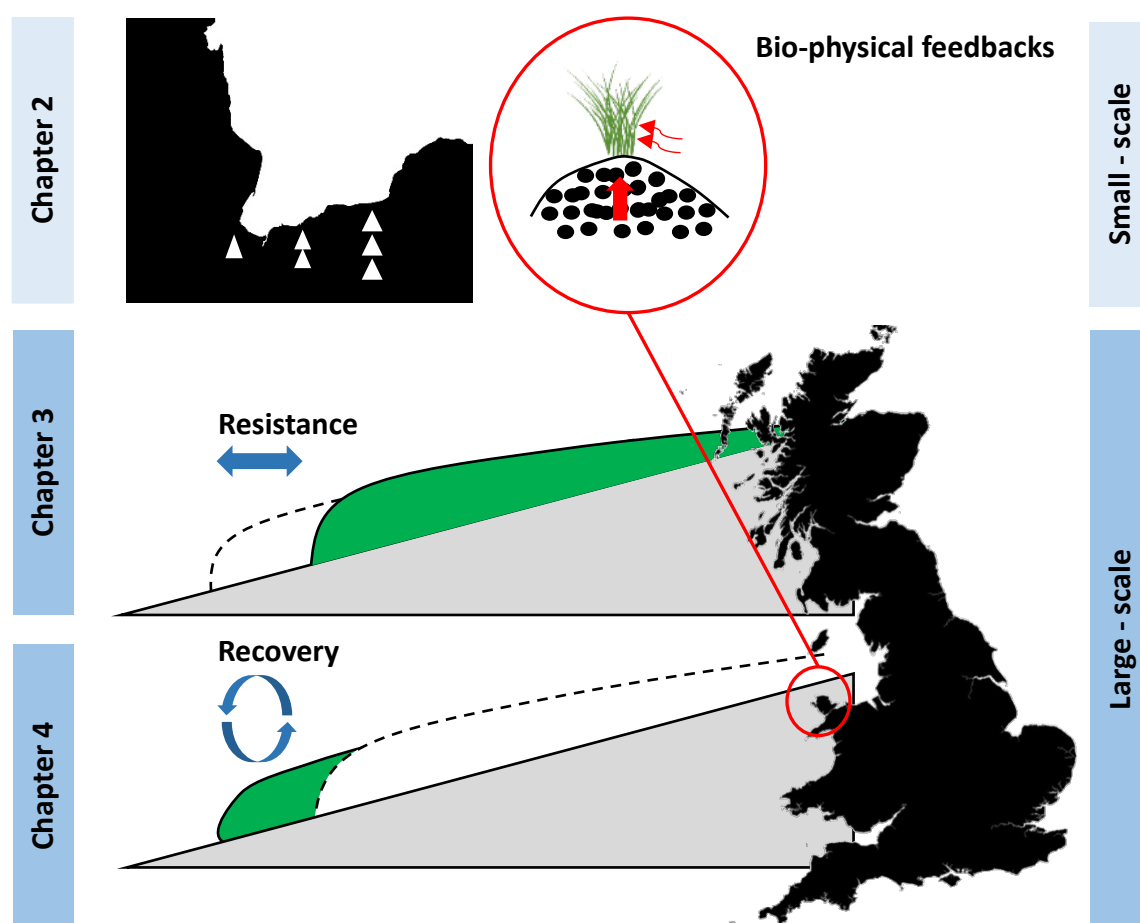


Fig 1.13. Themes and scales of the three experimental chapters of the thesis.

Chapter 2

Chapter 2 investigates the mechanisms of salt marsh resilience at the tussock-scale to explain how plant density affects patch establishment and growth, and how this might change across a gradient in wave forcing. Here I ask whether plant density-dependent feedbacks with sediment, plant survival and the lateral expansion of the vegetation changes with wave forcing to influence the success of replanted patches of *Spartina anglica*. I 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*, and (3) *patch lateral expansion will be lowest under exposed wave forcing conditions, and in the densest patches, due to accentuated scouring around the patch perimeters*.

Chapter 3

Chapter 3 investigates the mechanisms of salt marsh resilience at larger scales, by observing and comparing the positions of seaward marsh edges, as a proxy for long-term resilience, across five geographical regions of the United Kingdom. The study examines the degree to which UK-wide variations in the down-shore extent of salt marshes, and hence resilience patterns, are explained by geographical changes in environmental conditions and/or intrinsic marsh bio-physical properties. The study considers large-scale changes in the forces that erode marshes, and the bio-physical properties of the marsh itself. I hypothesise that (1) *marshes on the south-east coast of the UK will extend further down-shore than marshes on the north-west coast* and (2) *patterns of resilience across the UK will be principally explained by geographical variation in wave forcing and second, by sediment properties, in particular geographical variation in sediment grain size*.

Chapter 4

Chapter 4 investigates the mechanisms of salt marsh resilience at larger scales, by directly testing the recovery of marsh vegetation after experimental disturbances in the same five geographical regions as in Chapter 2. It explores the extent to which large-scale, geographical variation in salt marsh recovery is governed by differences in external disturbance and bio-chemical drivers and internal marsh properties that affect sediment stability, plant establishment and growth. I hypothesise that *large-scale variation in salt marsh recovery will be principally explained by regional differences in intrinsic marsh properties including soil characteristics, and secondarily by a latitudinal gradient in temperature, which affects marsh re-growth after disturbance.*

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CHAPTER 2

Plant regulation of salt marsh growth: density-dependent feedbacks vary with wave exposure

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Author Contributions:

MDE conceived the research ideas and designed the methodology with assistance from MS and SJ.

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Abstract

Coastal salt marshes are threatened by erosion from storminess and sea level rise. Although more than \$1billion has been spent to reconcile losses, restoration has had varying success, partly because of poor survival of planted patches. Marsh patch expansion after colonisation or re-plantation is regulated by positive and negative feedbacks between vegetation density and sediment capture. Dense vegetation positively stimulates sediment capture and plant survival, but negatively constrains patch expansion by concentrating wave energy along patch edges, causing erosion gullies. Conversely, low-density vegetation may not stimulate enough sediment capture, which increases the risk of plant mortality via dislodgement. The strength of positive and negative feedbacks are likely to vary with wave forcing, but this has never been tested before in a natural setting. We combined observations of (1) density-dependent sediment feedbacks, (2) plant survival and (3) lateral expansion in planted patches of *Spartina anglica* across a natural gradient of wave forcing. Patches (0.8 x 0.8m) were planted at three levels of vegetation density at each of three levels of wave forcing (three sites). We found an interactive effect of plant density and forcing on the strength of positive and negative feedbacks within and around vegetated patches. Density-dependent feedbacks only emerged at moderate and exposed forcing 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. Plant survival was enhanced in high density patches under exposed conditions, as dense canopies dissipated waves and diverted energy away from the vegetation. Expansion was significantly higher in medium density patches at the sheltered site, while at the sheltered site there was high mortality and overall size reduction in high density patches, indicating a switch from facilitative to competitive interactions across the stress-gradient. *Policy implications.* The study confirms that density- dependent feedbacks can switch from positive to negative along external stress gradients, although this principle is rarely demonstrated for erosional processes. Our findings emphasise the need to consider external conditions when making decisions on planting configurations,

as interactions between forcing and density can determine the success or failure of marsh establishment.

Introduction

Fifty percent of global salt marsh habitat was lost in the last century (Silliman et al., 2015). This loss is a concern since salt marshes offer important ecosystem services, including 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), potentially a consequence of poor restoration designs. There is thus a 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 the fact that species interactions, both 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. Current discussions about planting configurations in wetland habitats 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 (Kirwan et al., 2016). *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; which can have both positive and negative feedbacks on marsh development. While energy dissipation stimulates vertical sediment build-up ('accretion') inside the vegetation canopy (Fig. 2.1), 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 expansion (Fig. 2.1) (van Hulzen, van Soelen, & Bouma 2007; van Wesenbeeck et al., 2008; Bouma et al., 2009).



Fig 2.1. 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.

Plant density determines switches between positive and negative sediment feedbacks, which ultimately affects the potential for marsh development (Bouma et al., 2005, 2007). High density *Spartina* vegetation encourages greater sediment deposition by reducing wave 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 conditions might encourage sediment deposition without generating erosion gullies, because the 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 between positive and negative feedbacks, to affect plant survival and vegetation 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 re-planted 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.

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 east coast of the isle of Anglesey, North Wales (United Kingdom) (Fig. 2.2). Red Wharf Bay is characterised by broad sand flats and low-lying sandy beaches and has a spring tidal amplitude of up to 7.6m (relative to Chart Datum). Waves are generally wind generated. Experiments were performed on the mudflats (approximately 50m in front of the lower marsh pioneer zone) 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 moderate site in the middle (Fig. 2.2). The three sites were located 5.25 to 5.85m above Chart Datum. Wave observations (September - October 2018) confirmed significant differences in wave heights between the three sites (Supplementary Materials Section A). 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. Tidal current speeds did not vary significantly between the three sites with average peak flows of around 1.09, 1.08 and 1.69 cm/s at the exposed, moderate and sheltered sites respectively (Supplementary Materials Section B). The sediment was predominantly fine sand at all three sites, with some differences in silt-clay and medium-coarse sand percentages (Supplementary Materials Section C).

Between June and August 2016 *Spartina* was transplanted to create plots of three density treatments (low, medium and high) at each of the three wave exposure sites (Fig. 2.3c). Each density treatment was replicated five times at each of the three sites, giving a total of 45 plots (*3 sites *3 densities *5 replicates). Clumps of *Spartina* consisting of 15-20 shoots and associated roots covering approximately 0.1 x 0.1m were dug up from the pioneer zone of the established salt 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. 2.3c).

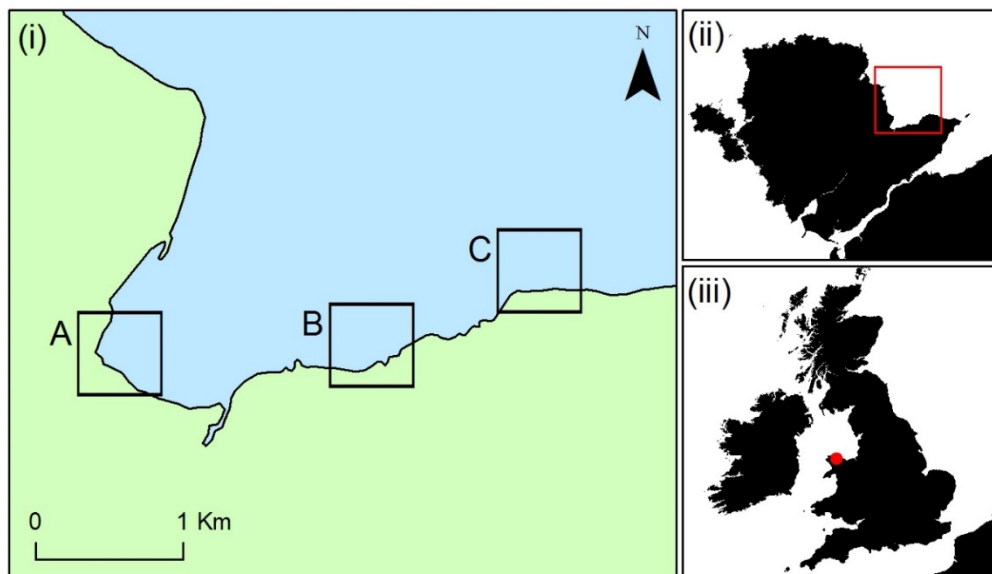


Fig 2.2. (i) Location of the experimental sites in Red Wharf Bay, with a gradient in wave exposure: (A) Sheltered, (B) Moderate and (C) wave Exposed. (ii) Red square indicates the location of Red Wharf Bay on the south-east coast of Anglesey, North Wales. (iii) Red circle indicates the location of Anglesey in the United Kingdom.

Cross-plot sediment elevation profiles

Sedimentary changes were measured inside and immediately outside experimental plots using Sedimentation-Erosion-Bars (SEB's) (Nolte et al., 2013) (Fig. 2.3a). 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. Posts were placed 1m away from the vegetation to avoid scouring effects. These posts marked the boundaries of the measured areas and will be referred to as the 'SEB areas' from now on (Fig. 2.3a). During observations of sediment elevation, a horizontal beam was temporarily clamped onto the seaward and the landward posts to make two trestles (Fig. 2.3a); a straight-edge beam was then placed from the landward to the seaward trestle, and sediment elevation was quantified as the vertical distance from the straight-edge beam to the sediment surface. Sediment elevation was measured at five points to create a cross-shore profile of the SEB area (Fig. 2.3a): in the centre of the vegetation, and at 0.4 and 0.8m away from the centre of the vegetation in both directions (Fig. 2.3b). 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.

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 (dGPS) to an accuracy of $\pm 0.1\text{cm}$. 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 mean 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).

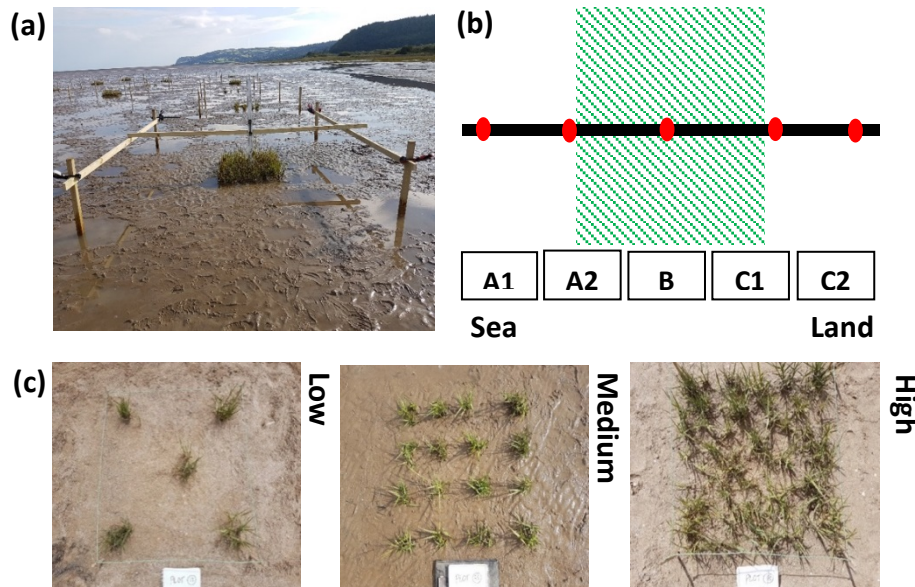


Fig 2.3. (a) Sedimentation-Erosion-Bar (SEBs) set-up around an experimental plot, creating the boundaries of the SEB area. The three horizontal bars were only in place whilst taking sediment elevation measurements. (b) Measurement profile across a plot (cross-plot sediment elevation profile). Green area represents the vegetation. Red dots represent measurement points along the horizontal beam (A1 – C2: seaward to landward direction). (c) Three vegetation density plots (0.8 x 0.8m) created from clumps of *Spartina* consisting of 15-20 shoots and associated roots; Low (~80-100 shoots), Medium (~240-320 shoots) and High (~460-640 shoots).

Plant survival

Plant survival was quantified in the field by counting the number of clumps remaining in medium and low density plots. It was difficult to define individual clumps in high density plots because the vegetation appeared as a dense sward. Thus, in order to get an accurate measure, the Digital Elevation Models were used to quantify plant survival in high density plots. Pixel classification was used to define vegetated areas in the DEMs, and polygons were drawn around them to calculate the area (in m²). Vegetated areas in the August 2017 DEMs were subtracted from the September 2016 DEMs to calculate percentage survival of planted areas in the high density plots. For the medium and low density plots, the number of clumps remaining at the end of the experiment (August 2017) was

subtracted from the initial total number of clumps (September 2016) to calculate the percentage survival of the plants.

Lateral patch expansion

Lateral patch expansion was quantified in ArcGIS (10.4) using the DEMs. Polygons were drawn around the vegetation to establish 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. The DEMs were also used to quantify patch lateral expansion, by using pixel classification to measure the total area of vegetation in high, medium and low density plots in the August 2017 DEMs, and subtracting them from the September 2016 DEMs.

Statistical Analyses

Linear models were used to test for the effects of the fixed factors 'wave forcing' (three levels: exposed, moderate and sheltered), 'vegetation density' (three levels: low, medium and high) and 'position across the cross-plot elevation profile' (five levels: A1, A2, B, C1, C2), in influencing the response variables 'net change in sediment elevation', 'percentage of plot areas that accreted, eroded and remained stable', 'percentage of plant survival', and 'percentage of lateral patch expansion'. Data followed normality and homoscedasticity assumptions without need for data transformation. 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. 2.4; Table 2.1). As wave forcing increased, the total amount of sediment distribution around the vegetated patches also increased, whilst sediment elevation remained stable at the sheltered site (Fig. 2.4). Vegetation density significantly affected sediment elevation, not only within, but also around *Spartina* patches (Fig. 2.4; Table 2.1). As plant density increased, sediment distribution within and around patches was enhanced (Fig. 2.4; Table 2.1). However, the main effects reported above were moderated by several interactions. As physical forcing increased, the effect of vegetation density on sediment dynamics was exacerbated, highlighting the existence of a wave forcing x plant density interaction (Fig. 2.4; Table 2.1). Specifically, tussock shapes (indicated by the cross-plot elevation profiles) remained relatively flat and stable 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. 2.4- 5). This was especially consistent around high density patches at the moderate and exposed sites (Figs. 2.4- 6; Table 2.2). We also showed that the position across the cross-plot elevation profile was important in influencing sediment distribution, as greatest 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. 2.4- 6; Table 2.2).

Table 2.1. Output of the linear model performed on the response variable 'net change in sediment elevation' across the cross-plot profiles.

Effect	Df	F-statistic	p-Value
Wave forcing	2	47.35	<0.001
Vegetation density	2	30.10	<0.001
Position across cross-plot profile	4	90.61	<0.001
Forcing*Density	4	24.21	<0.001
Forcing*Position across profile	8	155.50	<0.001
Density*Position across profile	8	14.16	ns
Forcing *Density*Position across profile	16	79.79	<0.001

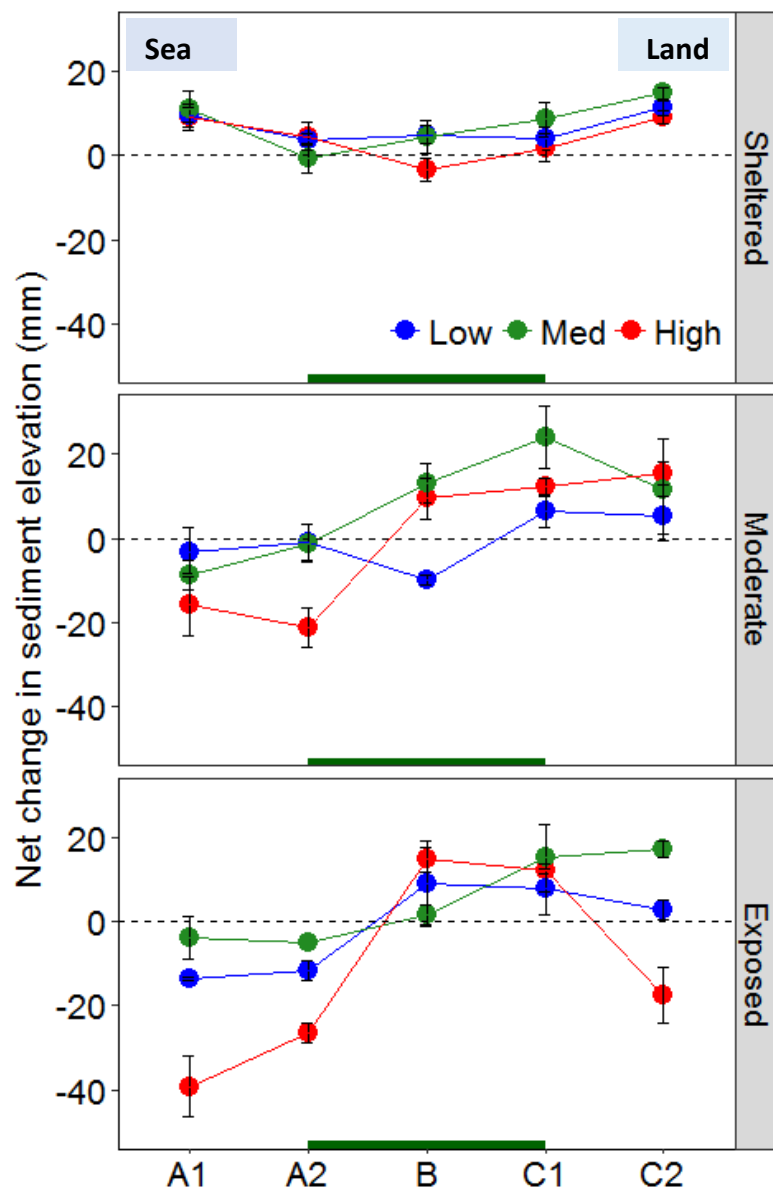


Fig 2.4. The mean \pm std. error net change in sediment elevation, from the first (September 2016) to the last observation (August 2017) across cross-plot profiles with high, medium and low density vegetation at the sheltered, moderate and exposed sites. X-axis codes as in Figure 2.3b: A1 and A2 represent 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 line on x-axis represents the vegetated area of the plot. $n = 45$ plots.

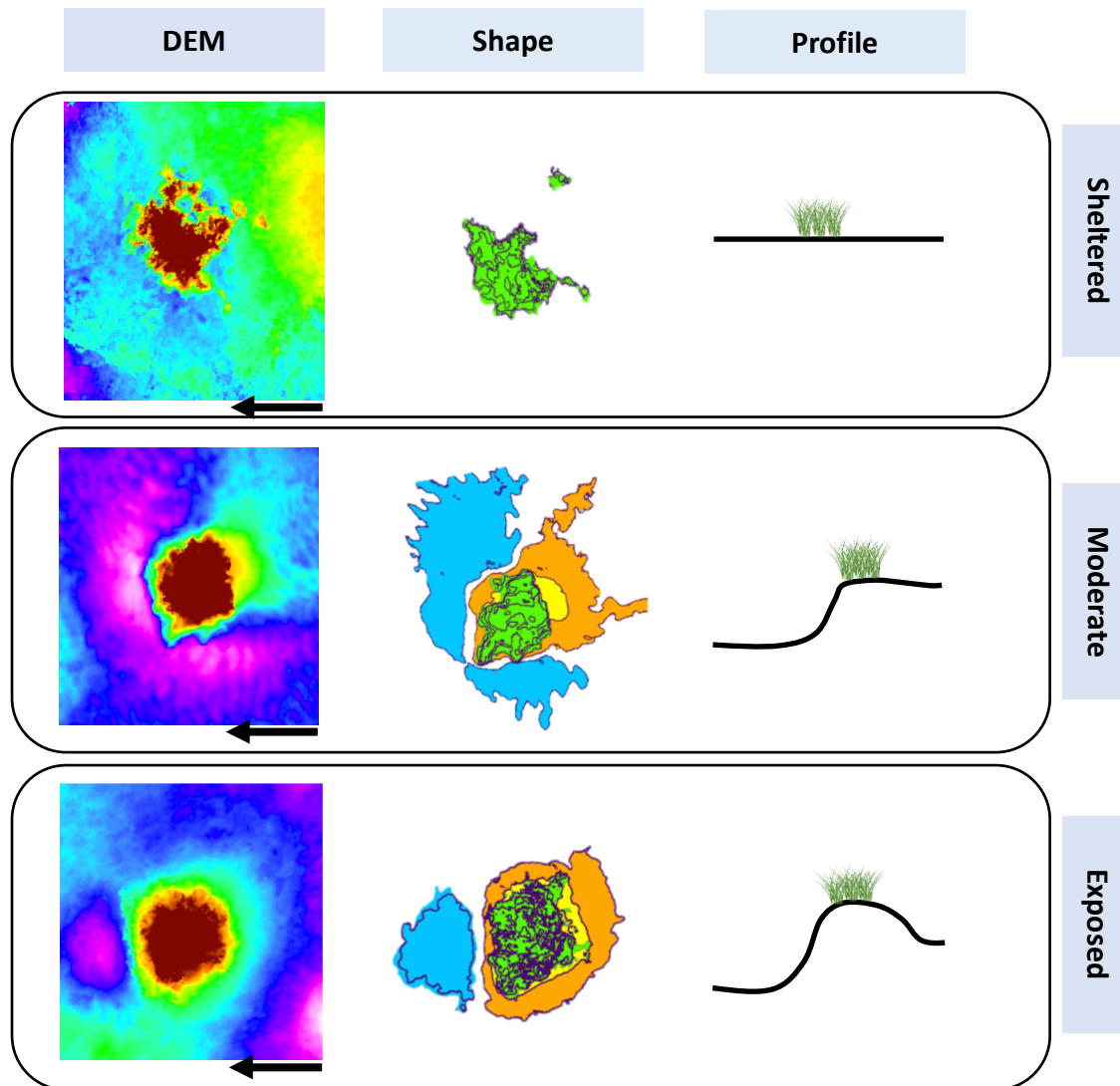


Fig 2.5. Schematic representation of the tussock shapes and profiles formed by high density vegetation at the sheltered, moderate and exposed sites. The mean Digital Elevation Models (DEM's) represent sediment bed elevations (blue to red colouring = low to high elevations). Black arrow points towards 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.

Table 2.2. 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).

Response	Effect	Df	F-statistic	p-Value	Post-hoc contrasts (Tukey HSD)	p-Value
Deposition	Wave forcing	2	11.56	<0.001	Exposed – Moderate	ns
					Exposed – Sheltered	<0.01
					Moderate – Sheltered	<0.01
	Vegetation density	2	7.56	<0.01	High-Low	<0.001
					High-Medium	ns
					Medium-Low	ns
	Forcing*Density	4	3.36	<0.05	Exposed	ns
					Moderate	<0.05
					Sheltered	ns
Erosion	Wave forcing	2	7.65	<0.01	Exposed – Moderate	ns
					Exposed – Sheltered	ns
					Moderate – Sheltered	<0.01
	Vegetation density	2	7.44	<0.01	High-Low	<0.05
					High-Medium	<0.05
					Medium-Low	ns
	Forcing*Density	4	5.51	<0.01	Exposed	ns
					Moderate	<0.01
					Sheltered	ns
Stable	Wave forcing	2	12.37	<0.001	Exposed – Moderate	ns
					Exposed – Sheltered	<0.01
					Moderate – Sheltered	<0.01
	Vegetation density	2	18.42	<0.001	High-Low	<0.001
					High-Medium	<0.01
					Medium-Low	ns
	Forcing*Density	4	6.51	<0.01	Exposed	<0.05
					Moderate	<0.001
					Sheltered	ns

Table 2.3. Outputs of the linear models and Tukey HSD post-hoc tests for effects of wave forcing and plant density on 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	Post-hoc contrasts (Tukey HSD)	p-Value
% survival	Wave forcing	2	3.62	<0.05	Exposed – Moderate	ns
					Exposed – Sheltered	ns
					Moderate – Sheltered	<0.05
	Vegetation density	2	4.40	<0.05	High – Medium	<0.05
					High – Low	ns
					Medium – Low	ns
	Forcing*Density	4	2.86	<0.05	Exposed	<0.05
					Moderate	ns
					Sheltered	ns
% expansion	Wave forcing	2	13.54	<0.001	Exposed – Moderate	ns
					Exposed – Sheltered	<0.05
					Moderate – Sheltered	<0.001
	Vegetation density	2	4.22	<0.05	High – Medium	<0.05
					Medium – Low	<0.05
					High – Low	ns
	Forcing*Density	4	10.61	<0.001	Exposed	ns
					Moderate	ns
					Sheltered	<0.05

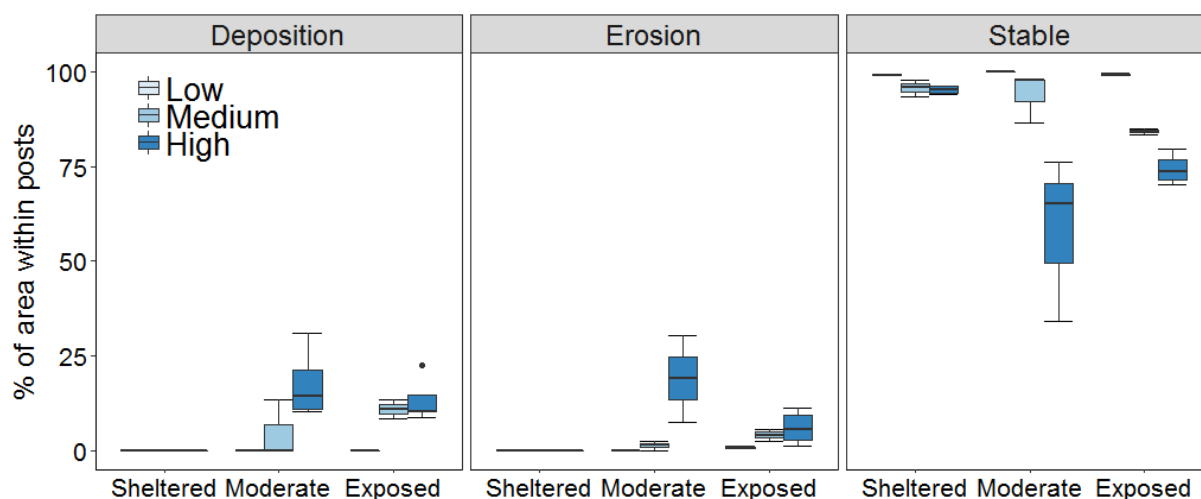


Fig 2.6. The percentage of the SEB areas (i.e. within the posts) that had (a) a net increase in sediment elevation (i.e. sediment deposition), (b) a net decrease in sediment elevation (i.e. surface erosion) or (c) no change in sediment elevation (i.e. remained stable), in function of plant density (low, medium, high) and wave exposure (sheltered, moderate and exposed). Thick horizontal lines = median, box = interquartile range, vertical whiskers = full range, black circles = outliers. n = 45 plots.

Lateral patch expansion

Wave forcing had a significant effect on lateral patch expansion (Fig. 2.7; Table 2.3). Overall, expansion was higher at the sheltered site, in contrast to the moderate and exposed sites. Expansion was also significantly higher in medium density patches, compared to high and low density patches (Fig. 2.7; Table 2.3). Vegetation density had a significant effect at the sheltered site, with medium density patches expanding by 221%, but there was no effect of density on patch expansion at the moderate and exposed sites (Fig. 2.7; Table 2.3).

Plant survival

Wave forcing had a significant effect on plant survival within vegetated patches (Fig. 2.7; Table 2.3). Irrespective of vegetation density, survival was highest at the sheltered site, and lowest at the moderately exposed site. Vegetation density also had an effect on plant survival, with plants in high density patches surviving better than in lower densities (Fig. 2.7; Table 2.3). There was also an

interaction between wave forcing and plant density, as high density patches significantly boosted plant survival at the exposed site, but there was no effect of plant density at the moderate and sheltered sites (Fig. 2.7; Table 2.3).

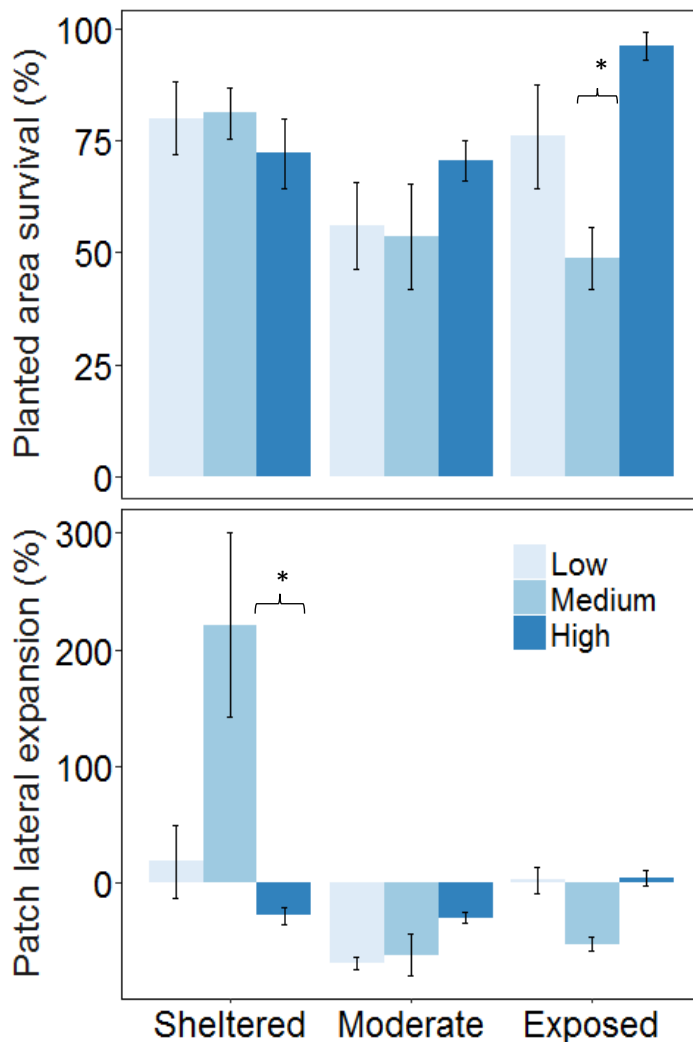


Fig 2.7. The mean \pm std. error survival (of the originally planted area) and expansion (area cover of plants outside the planted areas) of low, medium and high density *Spartina* patches at the sheltered, moderate and exposed sites. $n=5$ plots. Significant differences between the sites are indicated as resulting from post-hoc tests ($p < 0.001$ '***', $p < 0.01$ '**', $p < 0.05$ '*'). $n = 45$ plots.

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. It shows, 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 wave 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. While the deflection of wave energy boosted plant survival, it also generated erosion gullies around the vegetation which discouraged lateral patch expansion. High density patches in sheltered wave conditions had no major sediment accretion and no gully formation but had high mortality and smaller patch sizes at the end of the experiment 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 organism 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 mussel 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, the plants benefit from the additional protection provided by neighbouring individuals within high-density patches, thus promoting a positive (facilitative) interaction between individual plants (Bertness & Shumway, 1993; Callaway & Walker, 1997). 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). Studies have previously shown that species interactions shift from facilitative to competitive with increasing environmental stress (Bertness & Callaway, 1994) and, furthermore, that these patterns can be seen across a number of ecosystem types (Bertness & Callaway, 1994; Bertness et al., 1999; Choler, Michalet, & Callaway 2001). For example, in alpine forests along mountainous slopes, growth facilitation between individual trees increases at higher altitudes, whilst competition is the dominant interaction at lower altitudes where stress is significantly reduced (Choler, Michalet, & Callaway 2001). Similarly, on rocky intertidal shores, species interactions switch from positive to negative with decreasing elevation (i.e. nearer to the sea), as the intensity of competition increases in more benign conditions on the low shore (Bertness et al., 1999).

The patchiness of vegetation that might ensue from the processes described here is frequently seen in salt marsh pioneer zones (van Wesenbeeck et al., 2008; Wang & Temmerman, 2013). The formation of dome-shaped tussocks was thought to be 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* may be able to exist at higher densities without causing the associated negative effects, as observed here, and hence is more likely to develop into a homogenous vegetated state (Bouma et al., 2009). The absence of sediment feedbacks by dense vegetation at the sheltered site could eventually facilitate the expansion of such

tussocks into a continuous sward, as is frequently observed under hydrologically calm conditions (Bouma et al., 2009).

Implications for management: restoration

The findings of this study provide useful insights for the development of planting configurations in salt marsh restoration designs. We highlight the need to consider the wave forcing conditions at a proposed site before making decisions about planting designs. We have come up with two conceptual diagrams (Fig. 2.8) that predict outcomes on (1) sediment feedbacks and (2) vegetation survival and expansion, associated with *Spartina* vegetation. Using the conceptual diagrams, we can suggest, as an example, that planting medium density patches under sheltered wave conditions could maximise plant survival and lateral patch expansion, in the absence of plant feedbacks on sediment distribution. Planting high density patches under exposed wave conditions will maximise plant survival, but also minimise lateral expansion outside the patch due to restriction from the presence of erosion gullies.

Although we make useful suggestions for restoration planting designs, we only tested plant-sediment feedbacks in one patch size (0.8 x 0.8m), despite looking at different plant densities. Previous studies have suggested that an interaction between patch size and environmental stress plays an important role in the outcome of positive and negative feedbacks, and hence on marsh growth and/or recovery potential (Bouma et al., 2007; Suding & Hobbs, 2009; Angelini & Silliman, 2012; Gittman et al., 2018). Thus, at wave-exposed sites, restoration success might be boosted by dense planting in large patches (Gittman et al., 2018) because plant survival will be encouraged, while the negative effect of erosion gully formation will be reduced by a diminished patch circumference to interior ratio (Angelini & Silliman, 2012; Silliman et al., 2015; Gittman et al., 2018). In contrast, planting moderate-density vegetation in smaller patches at wave-sheltered sites will minimise competition between individual plants, and thus 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. More work is needed to investigate the effect of patch-size and its interaction with other environmental stressors on restoration planting success, especially since there is a growing need to learn how to restore salt marshes under new climate regimes (Gittman et al., 2018).

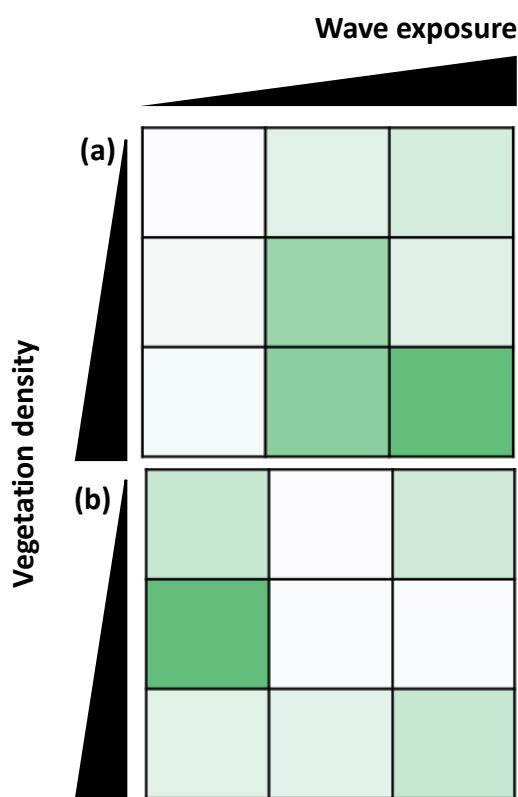


Fig 2.8. Conceptual models showing the effect of vegetation density and wave exposure on (a) sediment feedbacks (depositioning, erosion), and (b) plant survival and patch lateral expansion (i.e. area cover of plants outside the planted areas). In the sediment feedbacks model, a gradient from dark green to white represents a decrease in the strength of the sediment feedbacks (i.e. positive sediment deposition and negative surface erosion). In the plant survival and patch lateral expansion model, dark green to white indicates a switch from high to low plant survival and patch lateral expansion.

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SUPPLEMENTARY MATERIALS FOR CHAPTER 2

Supplementary Materials Section A

Wave forcing measurements

We quantified differences in wave forcing by deploying pressure sensors (OSSI-010-003C-01; Ocean Sensor Systems, Inc.) (Fig. S2.1) 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 burst frequency of 5Hz for 1-minute at 10-minute intervals, following methods by Willemsen et al., (2018). The mean water level in an interval was determined by averaging all of the data points. The wave analysis was based on pressure fluctuations. The attenuation of the pressure signals with water depths was corrected to derive bulk density wave parameters, e.g. significant wave height (H_s) (Figs. S2.3- 5) (Tucker & Pitt, 2001). The results of the wave observations are shown in Table S2.2 and Figure S2.2.



Fig S2.1. Pressure sensor deployed at one of the study sites.

Table S2.1. Output of the one-way ANOVA analysis performed on the wave data. Df: degrees of freedom.

Effect	Df	F-statistic	p-Value
Wave forcing	2	200.2	<0.001

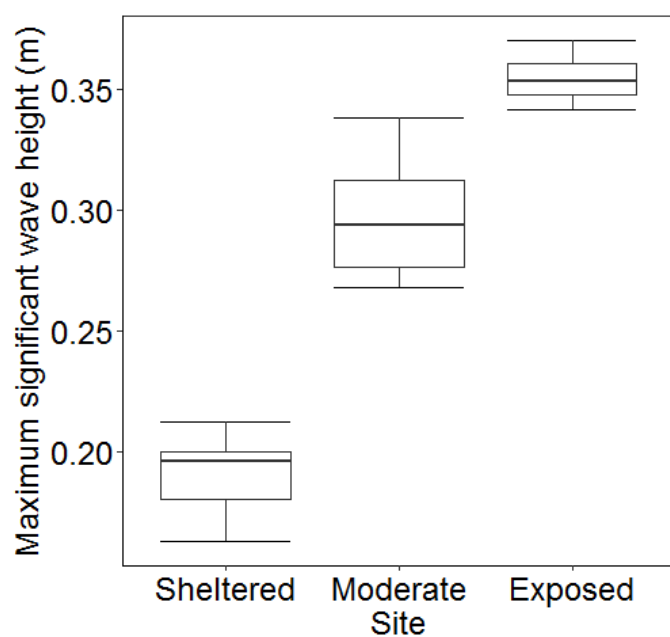


Fig S2.2. Differences in maximum significant wave heights between the sheltered, moderate and exposed sites over a period of 1 month (September - October 2018). Thick horizontal lines = median, box = interquartile range, vertical whiskers = full range, black circles = outliers.

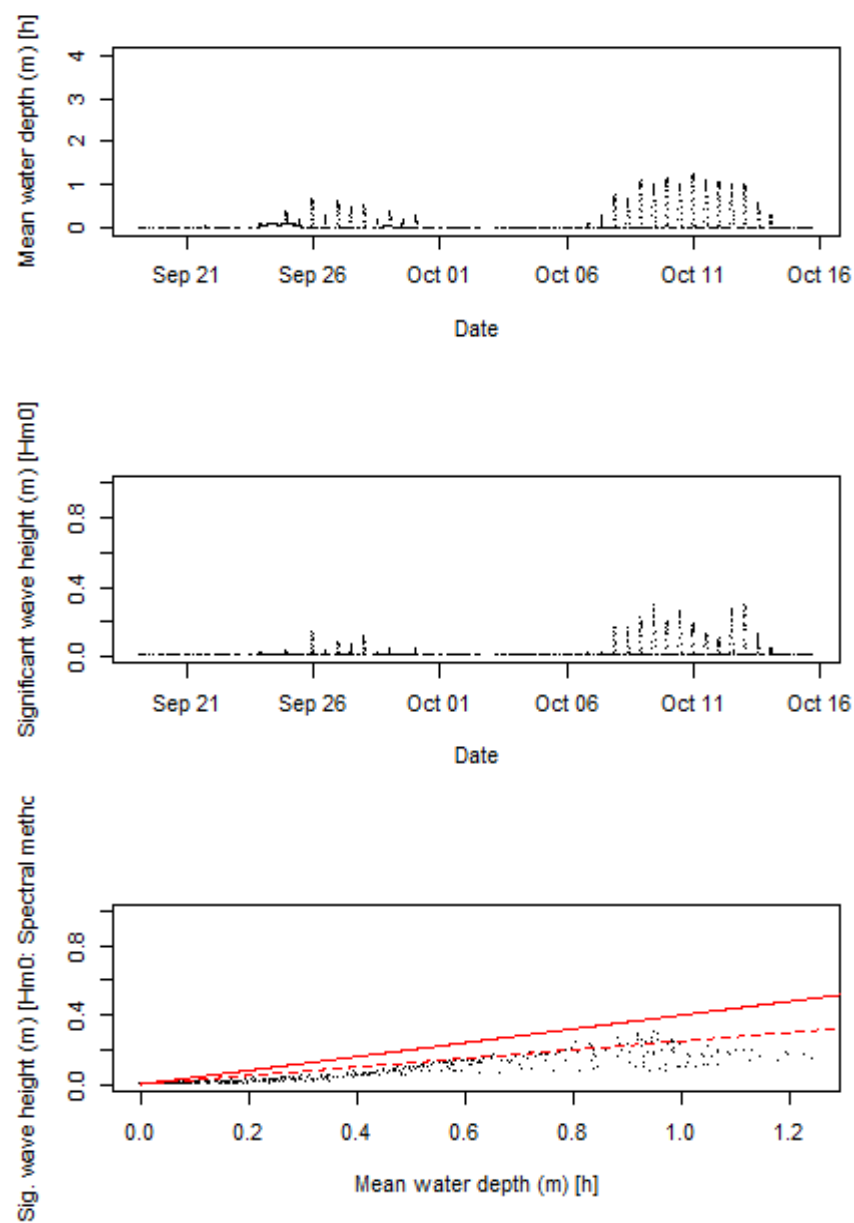


Fig S2.3. Mean water depths and significant wave heights measured at the Exposed site over the observation period (September-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

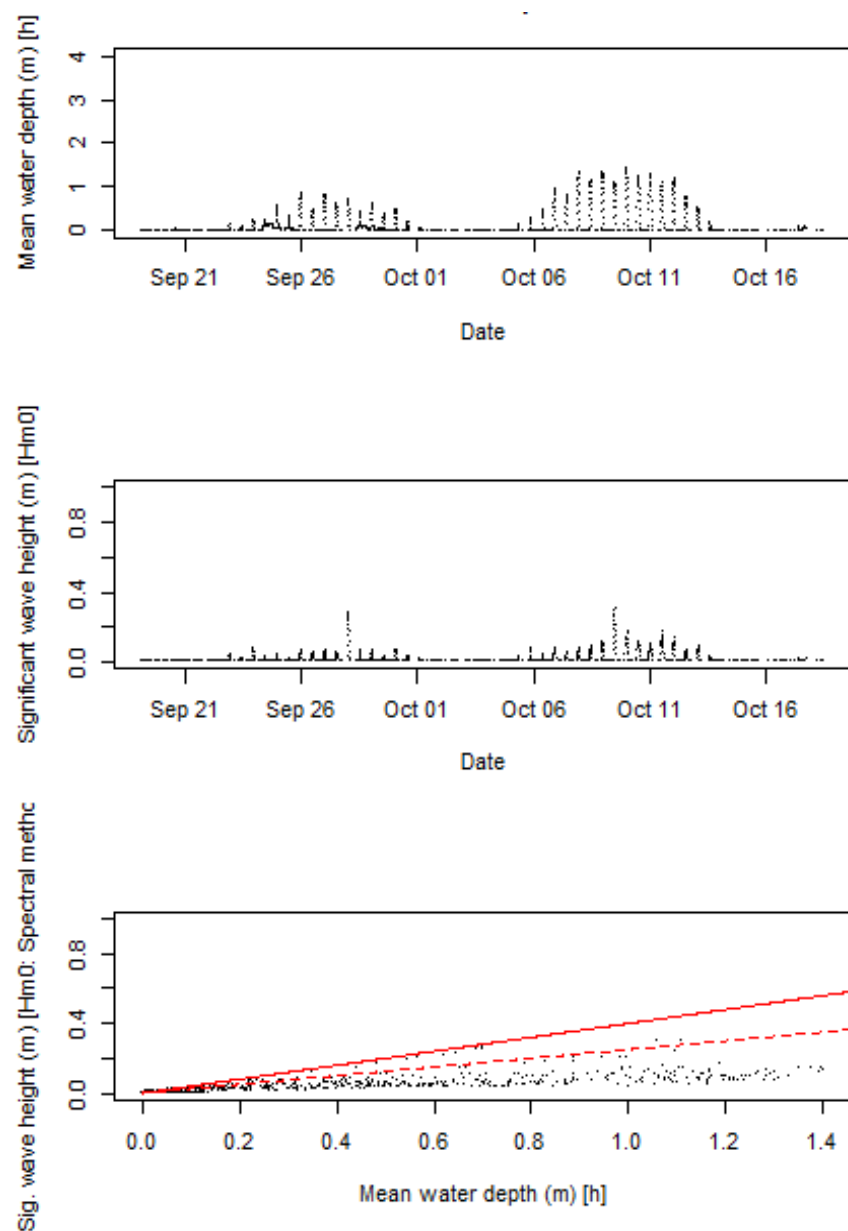


Fig S2.4. Mean water depths and significant wave heights measured at the Moderate site over the observation period (September-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

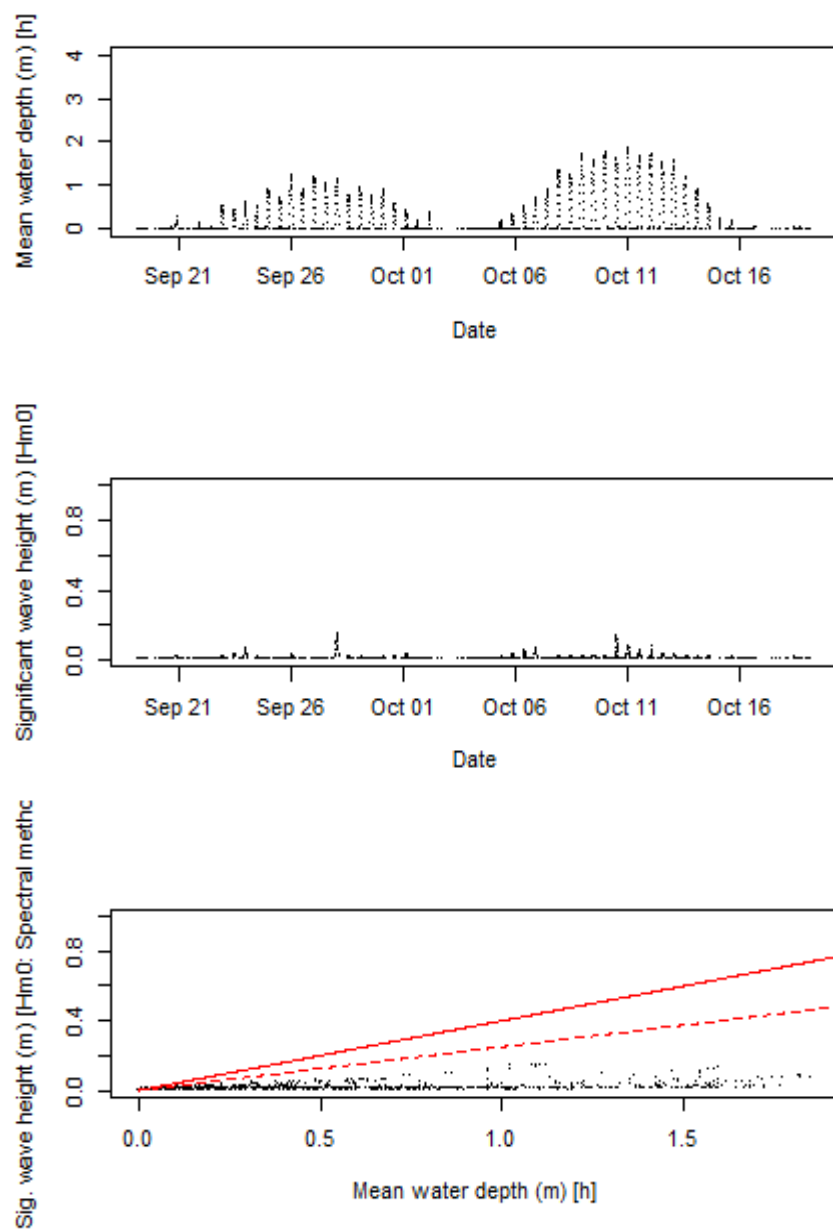


Fig S2.5. Mean water depths and significant wave heights measured at the Sheltered site over the observation period (September-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

Supplementary Materials Section B

Current speed measurements

We quantified differences in current velocities by deploying Acoustic Doppler Velocity meters (ADVs, Nortel Vector) (Fig. S2.6) 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 every 30 minutes. The results of the current speed measurements are shown in Table S2.3 and Figure S2.7.



Fig S2.6. ADV sensor deployed at one of the study sites.

Table S2.2. Output of the one-way ANOVA analysis performed on the current velocity data. Df: degrees of freedom.

Effect	Df	F-statistic	p-Value
Current velocity	2	2.05	ns

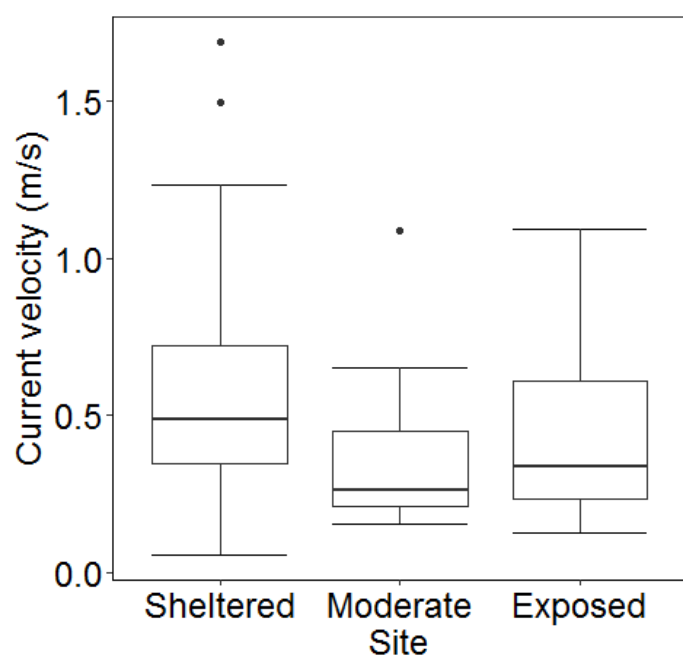


Fig S2.7. Differences in current velocities between the sheltered, moderate and exposed sites over a spring tide in April 2018. Thick horizontal lines = median, box = interquartile range, vertical whiskers = full range, black circles = outliers.

Supplementary Materials Section C

Sediment grain size data

Table S2.3. Percentage of each sediment class at the sheltered, moderate and exposed sites in Red Wharf Bay.

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

CHAPTER 3

Small- and large-scale drivers of variation in salt marsh down-shore extent

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Martin W. Skov

Status: Prepared for Submission

Author Contributions:

MDE conceived the research ideas and designed the methodology with assistance from MS and AG. MDE conducted the fieldwork with assistance from MS and various undergraduate and postgraduate students. MDE performed the statistical analyses with guidance from JFP. MDE led the writing of the paper and all of the co-authors contributed critically to the drafts.

Abstract

Coastal salt marshes provide valuable ecosystem services, but they are threatened by erosion. The positions of the lower edges of marshes relative to the tidal range (down-shore extent, DSE) varies geographically, implying large-scale variation in erosive forcing and/or internal marsh resilience. The drivers of marsh down-shore extent are poorly understood, yet relevant to large-scale management of marsh resilience. We sampled 20 marshes in six regions of the United Kingdom for down-shore extent and erosion resistance, and three potential explanatory variables: vegetation properties, sediment properties and wave forcing. Down-shore extent increased from the north-west (5% of the tidal range) to the south-east (39% of the tidal range) coast. Differences in down-shore extent were explained primarily by wave forcing; marshes exposed to lower forcing extended further than those exposed to higher wave forcing regimes. Sediment properties and vegetation type were also important, as marshes with higher fractions of fine-grained sediments and with *Spartina anglica* at their edges extended further down-shore. Soil erodibility in the flume was also principally dependent on sediment type. Erosion rates dropped with increasing silt-clay fractions, and biological variables added vital erosion resistance in sandy settings. This study showed that at a large-scale (UK-wide) variation in down-shore extent was driven by differences in wave forcing, whilst, at the regional-scale, important sediment and vegetation properties enhanced marsh resilience. This study shows that resilience to erosion is dependent on a complex interaction between large-scale drivers and marsh-scale resilience mechanisms/traits. It emphasises the need to consider scale when predicting marsh resilience, with important implications for management and policy makers.

Introduction

Coastal salt marshes provide valuable ecosystem services, including sequestering and storing 'blue carbon' (Himes-Cornell et al., 2018), providing nursery habitats for fisheries species (Kneib, 1997), regulating coastal nutrient cycles (Mitsch & Gosselink, 2000) and delivering natural coastal protection (Nicholls et al., 2007; Barbier et al., 2008; Möller et al., 2014). Centuries of human modification of the coast through land reclamation, channel dredging and waste pollution have caused a 50% decline in the historical cover of salt marshes (Gedan et al., 2009; Moreno-Mateos et al., 2012), which are now further compounded by stressors associated with sea level rise (Kirwan & Megonigal, 2013) and storminess (Leonardi et al., 2016). Considerable efforts to prevent any further losses of marshes by conserving and restoring them (Gedan et al., 2009; Silliman et al., 2015) require a good level of understanding of the processes that regulate marsh resilience to lateral erosion under natural conditions (Bouma et al., 2016; Wang et al., 2017); yet the empirical evidence is often lacking.

Salt marshes naturally erode or expand from their seaward margin (Fig. 3.1), and the degree to which their seaward edge protrudes into the intertidal (their 'down-shore extent (DSE)') is a product of the strength of external hydrological forcing balanced against the intrinsic characteristics of the marsh that enable it to withstand erosion and tolerate tidal inundation (Fig. 3.2). Knowledge of what mediates variation in marsh DSE could therefore contribute towards an understanding of what regulates marsh resilience to erosion. There are indications that marsh DSE varies systematically over large geographical scales (Gray, 1972; Adam, 1990; Balke et al., 2016), but the cause for this is not always clear. Some of the large-scale variability in DSE is thought to be due to geographical differences in hydrodynamic conditions associated with waves and tides. Thus, marshes in regions exposed to higher wave forcing and marsh cliff-edge erosion (Fig. 3.1) are restricted to higher positions on the shore (Adam, 1990; Callaghan et al., 2010; Silinski et al., 2016; Wang et al., 2017). This is not surprising, given that hydrology is a key source of stress on salt marshes. Wave forcing (Callaghan et al., 2010; Mariotti & Carr, 2014; Wang et al., 2017), tidal currents (Friedrichs & Perry, 2001) and shifting channels in estuaries (see Fig. 3.1a) (Pringle, 1995; Cox et al., 2003) can all induce lateral erosion at the marsh

edge. Sea level rise is expected to contribute to lateral erosion by increasing the probability of wave propagation (Mariotti & Fagherazzi, 2010). The frequency and duration of tidal inundation influences the average duration of marsh exposure to hydrological forces. This sets the maximal possible down-shore limit of plant colonisation, given that salt marsh plants have a reduced tolerance of tidal inundation lower down the shore (Balke et al., 2016).

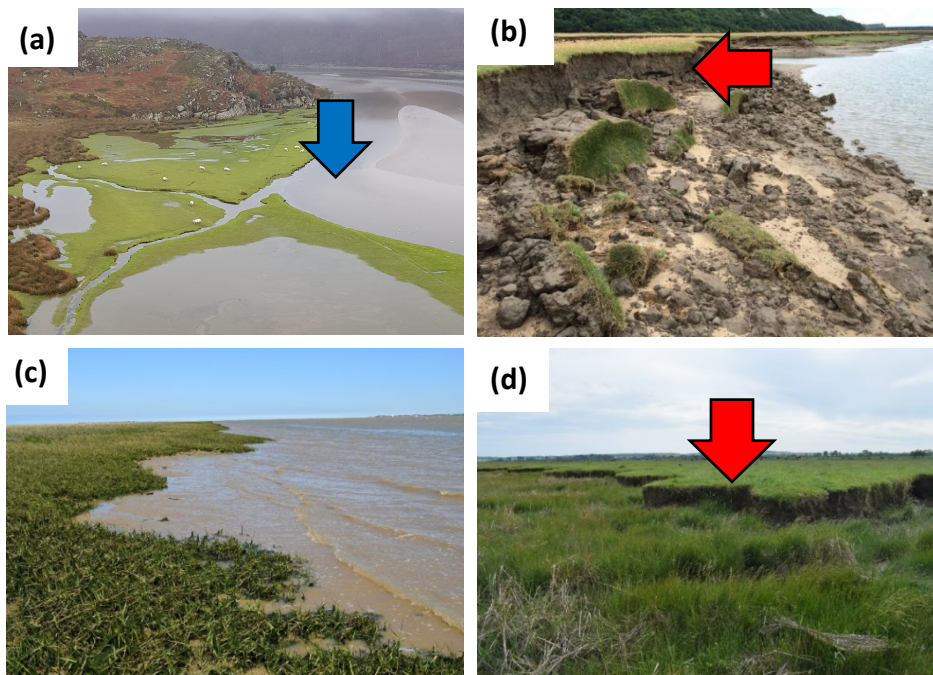


Fig 3.1. (a) Aerial view of an estuarine salt marsh; note the tidal channel (blue arrow). (b-d) Three different states of lateral change in salt marshes. (b) A marsh in the process of erosion, note the erosion cliff (red arrow). Cliffs form at the edges of marshes that are eroding, or when the marsh reaches an intertidal level where erosional forces inhibit further down-shore expansion. (c) A marsh in the process of expansion. Expanding marshes have no erosional cliff, and they may be dominated by pioneer species at their lower edges; here, the pioneer species is *Spartina anglica*. (d) A marsh that historically eroded back to a cliff (red arrow), but which has since re-colonised in front of the cliff to expand seaward.

Yet, there are also indications that salt marsh down-shore extent can be mediated by a number of intrinsic bio-physical and chemical properties of the marsh, some of which might also vary systematically over larger scales to explain geographical variation in marsh DSE (Gray, 1972; Adam, 1990; Balke et al., 2016) (Fig. 3.2). For example, differences in marsh DSE between the USA and Europe

have been linked to species composition, with US east coast marshes extending to much lower positions on the shore (mean tidal level) than most European marshes (mean height of neap high tides) (Adam, 1990). This is because the dominant pioneer plant species in USA marshes (*Spartina alterniflora*) is more tolerant of hydrological forcing including frequent tidal inundation, and high soil salinities, than the European equivalent species (*Spartina anglica*) (Raposa et al., 2016).

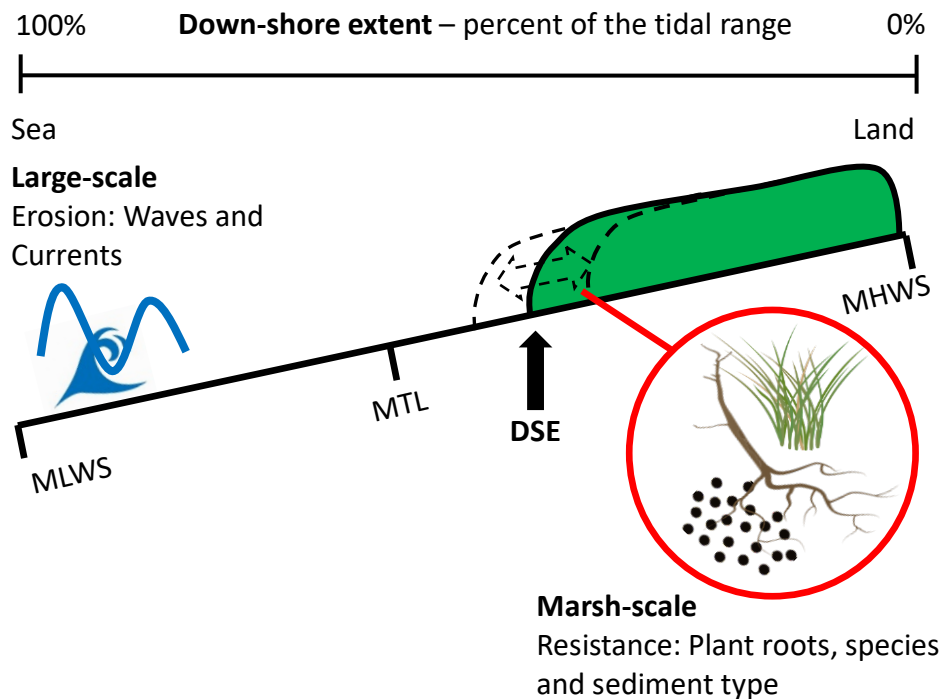


Fig 3.2. Schematic illustration of the down-shore extent (DSE) of a salt marsh. DSE is the percentage of the tidal range reached by the seaward marsh edge. DSE is an outcome of the balance between erosional forces including waves and currents, shown in blue, and the inherent resistance of the marsh to erosion, shown in the red circle. Marsh resistance is hypothesised to be boosted by bio-physical properties, including root biomass, plant species diversity and fine grained sediments (Ford et al., 2016; Wang et al., 2017). If marsh resistance to erosion is greater than the strength of the erosional forces, the marsh has the potential to protrude lower into the tidal range (dashed line in front of the marsh edge). If marsh vulnerability to erosion is greater than the strength of the erosional forces, the marsh will be restricted to higher elevations in the tidal range (dashed line above the marsh edge). The dashed arrow represents the lateral movement of the lower marsh edge as an outcome of greater resistance or vulnerability to erosional forces. MLWS, MTL and MHWS refer to tide mark levels; MLWS = Mean Low Water during Spring tides, MTL = Mean Tide Level, MHWS = Mean High Water during Spring tides.

Other important intrinsic biological properties that have been shown to increase marsh resistance to erosion include the below-ground root density and organic matter content in the sediment. Plant roots help to bind the sediment together, which increases marsh resistance to erosion (Chen et al., 2012; Ford et al., 2016), whilst soil organic material such as root exudates glue the sediment together, which further increases marsh capacity to resist erosional forces operating at the lower edge (Fig. 3.2) (Reid & Goss, 1981). Marsh erosion resistance has also been shown to increase with plant species diversity, as a higher diversity of plants increases the diversity of root structures (i.e. different depths and widths) to boost sediment stability (Mullarney & Henderson, 2010; Ford et al., 2016; Bilkovic et al., 2016). Abiotic properties including sediment type (i.e. grain size and organic content) and soil bulk density increase marsh resistance to erosion (Trimble & Mendel, 1995; Ford et al., 2016). Feagin et al., (2009) suggested that sediment type might be the most important property regulating marsh resistance to erosion, as marshes with fine-grained, muddier sediments resist erosion better than coarse-grained sandy marshes (Ford et al., 2016; Wang et al., 2017). Increased soil bulk density, which is typical of finer-grained sediments, implies greater soil compaction (Stavi et al., 2008; Schrama et al., 2013) which again diminishes sediment erosion rates (Feagin et al., 2009; Pagès et al., 2018). Biotic and abiotic properties of the marsh may have interactive effects on erosion resistance. Thus, plant root biomass and diversity are more important to marsh resistance in erosion-prone sandy soils than in the more erosion-resistant clay marshes (Ford et al., 2016; Lo et al., 2017).

Here, we examine the causes of variation in the down-shore extent of salt marshes across the United Kingdom, where marshes are known to reach further down the shore on the south-east than on the north-west coast (Gray, 1972; Adam, 1990). The study examined the degree to which UK-wide variations in the DSE of salt marshes are explained by geographical changes in environmental conditions and/or intrinsic marsh bio-physical properties. The study considered large-scale changes in the forces that erode marshes, such as wave exposure, as potential drivers for marsh DSE (Fig. 3.2). It also examined the influences of bio-physical properties of the marsh itself, such as soil properties and species composition, which influences marsh resistance to erosion (Fig. 3.2). We expected marshes on

the south-east coasts to extend further down-shore than marshes in the north-west, as previously suggested by Gray (1972) and Adam (1990), and for this pattern to be principally explained by geographical variation in wave forcing and secondary to that, by sediment properties, in particular geographical variation in sediment grain size.

Methods

Study sites

We sampled six regions around the United Kingdom covering areas with known differences in salt marsh elevation (Adam, 1990) (Fig. 3.3): the Solway (north-west Scotland); Morecambe (north-west England); Anglesey (Red Wharf Bay) and Sarnau (west Wales) regions on the north-west coast in the Irish Sea, as well as Southampton (south England) and Kent (south-east England) regions on the south-east coast in the English Channel and the North Sea. These regions were selected to represent the widest possible range of expected drivers and properties of salt marsh resilience in the UK (Fig. 3.3). Previous work indicated that wave forcing and sediment characteristics, both of which are likely to affect marsh resilience, vary systematically from the north-west to the south-east coasts of the UK (Ladd et al., in review). Energetic mineral-rich sandy sediments dominate north-western regions, whilst organic-rich muddy sediments dominate the calmer south-eastern regions (Adam, 1990). All regions are exposed to macrotidal regimes with tidal range highest in the north-west (Ladd et al., in review).

Wave forcing was expected to be an important driver of marsh resilience because it is the main cause of lateral erosion and retreat at the lower marsh edge (Callaghan et al., 2010; Wang et al., 2017). Six well-spread study regions offered the opportunity to detect the effect of large-scale variation in wind-wave forcing on salt marsh resilience. Yet, wave forcing can also vary on a local scale, for example between marshes within the same regions, depending on their relative fetch distances, the distance of open water in front of a site over which wind can build up wave energy (Denny et al., 2004), and the orientation of the marsh towards prevailing wind conditions (Burrows et al., 2008). To unravel the

large-scale (UK-wide) versus local-scale (within regions) effects of wind-wave forcing, the study incorporated one wave-exposed and one wave-sheltered site per region (Fig. 3.3) (full details in Supplementary Materials Table S3.1). Categorisation of site exposure was based on wind-fetch following methods by Silinski et al., (2016): sheltered sites had restricted fetch and open water windows, whilst exposed sites had long fetch distances and open water windows (Silinski et al., 2016).

Experimental design

Each region was represented by a minimum of one wave-exposed and one wave-sheltered site. Some additional sheltered and exposed sites were sampled within the Sarnau and Morecambe regions (regions nearest to our research institute) (see Supplementary Materials Table S3.1 for full details). This generated 20 sites overall (Supplementary Materials Table S3.1) which were sampled between January 2016 and May 2017. Each marsh was sampled along a 50m stretch of the vegetated marsh platform, 1 -4m landward of the seaward edge of the marsh (defined as the boundary between marsh plants and the commencement of the bare mudflat). Normally, the boundary between marsh plants and the commencement of the bare mudflat is defined by having > 10% (marsh) or < 10% (mudflat) plant cover, but in this study much sharper transitions defined the boundary between the marsh and the commencement of the bare mudflat, with switches from > 80% (marsh) and 0% (mudflat) plant cover. Each marsh was sampled inside five 1 x 1m quadrats, randomly placed a minimum of 5m apart. Areas near creek edges or depressions were avoided because these were unrepresentative of the entire marsh platform. The following section outlines the observations and samples taken inside each quadrat.

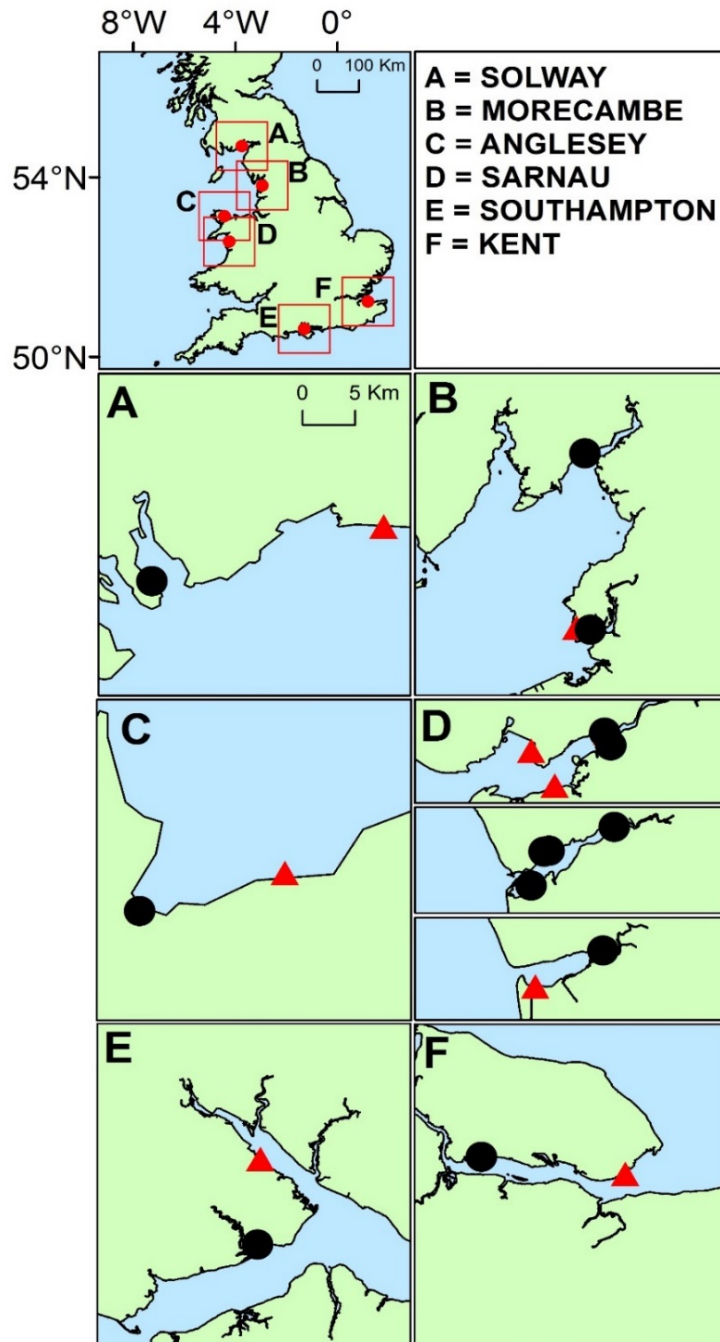


Fig 3.3. Six sampled geographical regions in the United Kingdom. (A) Solway, (B) Morecambe, (C) Anglesey (Red Wharf Bay), (D) Sarnau, (E) Southampton and (F) Kent. Red triangles represent wave-exposed sites, and black circles represent wave-sheltered sites.

Soil characteristics

The following variables were measured due to their known influence on lateral vegetation growth and marsh- resistance against erosion. Soil salinity is a stressor of plant growth and it has the capacity to restrict seaward marsh expansion (Huckle et al., 2000; Raposa et al., 2016). Soil samples of ~10g were extracted from the top 10cm of the soil per quadrat and measured for electrical conductivity (EC) (as a proxy for salinity) after diluting with distilled water according to methods by Ford et al., (2016). Soil bulk density, which is a measure of soil density and a proxy for soil compaction, plays an important role in erosion resistance (Schrama et al., 2013). Bulk density was measured by removing soil samples centrally from the top 10cm per quadrat using a stainless-steel ring (3.1cm height, 7.5 cm diameter) and then drying (105°C, 72 h) to remove all moisture following methods by Emmet et al., (2008). Organic material in the salt marsh soil acts as a cohesive to bind the sediment together (Reid & Goss, 1981) which might increase resistance against erosion. The percentage of organic matter was estimated by loss-on-ignition (375°C, 16 h) (Ball, 1964; Schumacher, 2002) using the dried sediment from the bulk density analyses. Previous studies have suggested that sediment grain size is the most important variable for regulating marsh erodibility (Feagin et al., 2009; Ford et al., 2016). Sediment grain size was measured from sub-samples (~1g) of the soil from the organic content analyses, after removal of any remaining organic material by hydrogen peroxide (Blott et al., 2004). Grain size was measured using a Beckman Coulter LS 13 320 Laser diffraction particle size analyser, in which the sediment samples were classified into 33 size fractions ranging from 0.2- 2000.0 µm. Grain size classes were then expressed as the percentage within each sample (e.g. the % of the sand class, >63 µm, and the % of the clay-silt class, 0.02-63 µm). The percentage of the clay-silt class in the sediment samples was used in all of the statistical analyses.

Plant variables

Above-ground vegetation percentage cover per species was observed in quadrats. Root dry biomass (60°C, 72 h) was obtained using 16cm diameter 'erosion cores' inserted 30cm into the soil as the majority of plant roots in UK salt marshes are in the top 30cm of the soil (Ford et al., 2016). Cores were collected from three out of the five 1 x 1m quadrats, making a total of three cores per marsh. Roots were extracted after washing away the remaining sediment following erosion (see 'Soil erosion cores' section).

Wave measurements

Observations of wave height and wave periods were done in eight out of the twenty sites (Supplementary Materials Table S3.1 for details) over a two-month period during July – September 2018, by use of water pressure sensors (OSSI-010-003C-01; Ocean Sensor Systems, Inc.). Following methods by Willemsen et al., (2018), sensors were placed on the fronting mudflats 0.05m above the seabed and set to record pressure fluctuations at 5Hz with 1-minute bursts every 10 minutes. Pressure readings were converted to water level fluctuations and used to derive bulk wave parameters, including significant wave height (H_s) and peak wave period (T_p) (Tucker & Pitt, 2001). Refer to Section B in the Supplementary Materials for more detail on the extraction of bulk wave parameters. Mean maximum wave height per site was then derived from the pressure readings, as a standard indicator of potential erosional forcing from wind-generated waves (Tonelli et al., 2010). Mean maximum wave heights were used as an indicator of the wind-wave forcing at the study sites and it was used as a predictor variable in the statistical analyses.

The presence or absence of a cliff at the lower edge of a salt marsh may be indicative of the erosional state of the site (Fig. 3.1). Given that the erosional condition of a marsh might influence its position in the tidal frame, it was important to account for its effect here. We noted whether the marsh edge was cliffed or un-cliffed and entered this information into the subsequent analyses. It was not possible to simplify the overall study design by focusing only on cliffed or un-cliffed marshes, as in

some regions cliffed or un-cliffed marshes were rare or absent. Cliffling was not confounded by wave exposure: it occurred in both wave-exposed and wave-sheltered sites.

Response variables (Soil erosion rates and Down-shore extent)

Two response variables were used in the present study to determine marsh resilience. *Down-shore extent* was an observed variable; used as an indicator for the resistance of the marsh against erosional forces and the tolerance of the plants against harsh environmental conditions. *Soil erosion rates* were also used to directly compare the vulnerability of marsh edges to erosion. Details of the methods used to obtain the two response variables are given in the next sections.

Soil erosion rates

To evaluate marsh resistance to erosion, we measured sediment erosion rates. From three quadrats per marsh, a 16cm diameter PVC pipe ('erosion core') was inserted 30cm into the marsh and then the core, containing soil, roots and protruding vegetation, was extracted. Observations of soil erosion rates followed methods by Ford et al., (2016), whereby cores were eroded in a re-circulating flume in the lab (Fig. 3.4). A 10cm wide opening was cut through the entire length of one side of the core to expose the sediment surface. The core was then placed horizontally, with the exposed opening facing up, under the nappe of a recirculating overshoot-weir flume at the Hydrolab facility in the School of Ocean Sciences (Bangor University, United Kingdom) (Fig. 3.4) (Ford et al., 2016). The set-up simulated side impact on the margin of a vegetated bank by waves and currents. Cores were eroded for 1hr, and core weights were measured at 0 (initial weight), 15, 30, 45 and 60 minutes. Erosion rates were expressed as the percentage mass loss of soil per minute.

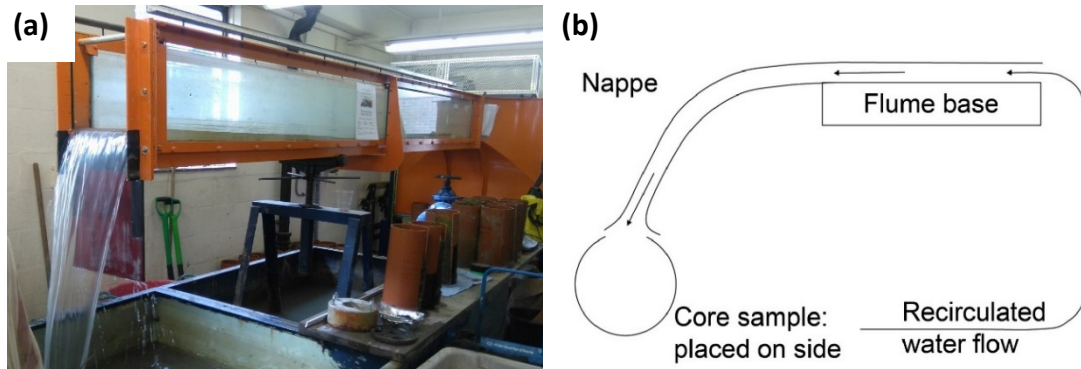


Fig 3.4. (a) Photograph and (b) schematic representation of the re-circulating flume set-up (schematic by Ford et al., (2016)).

Down-shore extent (DSE)

The degree to which the marsh edge protrudes into the intertidal is indicative of the marsh's inherent resistance to erosional forces, and the tolerance of the plants to harsh environmental conditions (Balke et al., 2016; Raposa et al., 2016). To measure marsh down-shore extent, the elevation of each quadrat was recorded to within $\pm 0.1\text{m}$ with a differential GPS (Leica GS08 GNSS system), and quantified relative to Chart Datum. The elevation measurements were then expressed as a percentage of the regional tidal range (Balke et al., 2016); $[(\text{quadrat elevation}/\text{regional tidal range}) * 100 \text{ \%}]$.

Statistical Analyses

Linear mixed-effects models were used to determine the most important predictors influencing the following response variables: *salt marsh down-shore extent (% of the tidal range)* and *soil core erosion rates (% mass loss per minute)*. The complete list of predictor variables introduced in the models included categorical variables vegetation type (2 levels: *Spartina* marsh and not a *Spartina* marsh), exposure (2 levels: exposed and sheltered) and cliff (2 levels: cliffs and no cliffs) and continuous variables root biomass, soil organic matter, soil bulk density, soil conductivity (as a proxy for salinity), soil clay-silt content and wave forcing (measured with the pressure sensors). We used AIC and log-likelihood tests to evaluate the need to include the categorical random effects 'site' (20 levels) and

‘region’ (6 levels). Two types of models were used to carry out the analyses, one for the down-shore extent and another for the soil erosion rates response variables.

For the down-shore extent response variable, the full model included all model variables including the categorical variable exposure, which emerged from the design of selecting both sheltered and exposed marshes within each region. An additional model was performed to test the effect of wave forcing, as these measurements were only obtained from a sub-set of the study sites (see Table S3.1 for details). For the soil erosion rates response variable, the full model included all model variables. A binomial distribution in erosion rates (see Fig. S3.1) caused by differences in sediment grain size dominated the analysis with other predictors not featuring in the model outputs. We therefore subset the main erosion model into two models of high and low erosion rates given the presence of two clearly identifiable groups (cores with erosion rates <6% mass loss per minute and cores with erosion rates >6% mass loss per minute).

Model selection started with a full model including all predictor variables. Then, each predictor variable was dropped one by one, and the best model was inferred using Akaike Information Criterion (AIC) and the log-likelihood ratio statistic (Zurr et al., 2009). When necessary, variables were transformed to ensure normality and homogeneity of variance in model residuals. Refer to Table S3.2 for the model specifications.

The R package *nlme* (Pinheiro, 2019) was used to perform the mixed-effects models. All statistical analyses were performed in the open-source statistical software R (R Development Core Team 2017).

Results

Down-shore extent

As expected, marshes on the south-east coast of the UK had lower down-shore extents than marshes on the north-west coast (Fig. 3.5). Differences in down-shore extents were explained primarily by the continuous variable wave forcing at those sites where wave forcing was measured (Fig. 3.6; Table 3.1) (see Table S3.1 in the Supplementary Materials for details of the sites). The lower the wave forcing at the marsh edge, the lower down the marsh protruded into the tidal range (Fig. 3.6). As an example, the model predicted that the down-shore extents of marshes exposed to the lowest wave forcing would occur approximately 30% of the tidal range further down the shore than marshes exposed to the highest wave forcing (Fig. 3.6).

In the model with all sites, without the continuous variable ‘wave forcing’, sediment type (clay-silt fraction) and vegetation type (*Spartina* marsh and not a *Spartina* marsh) explained differences in salt marsh down-shore extents (Fig. 3.7; Table 3.1). Marshes with a higher percentage of fine-grained sediments at their edges protruded further into the tidal frame than marshes with a lower percentage of fine-grained sediments (Fig. 3.7). As an example, the model predicted that marshes with the highest fractions of clay-silts in their sediment (i.e. 90% of clay-silts in their sediment) would occur approximately 10% lower down-shore compared to the sandiest marshes (i.e. 0% of clay-silts in their sediment) (Fig. 3.7). In addition, the results showed that marshes with *Spartina* at their edges had lower down-shore extents than marshes without *Spartina* (Fig. 3.7; Table 3.1). The model predicted that the down-shore extent of marshes with *Spartina* at their edges would occur approximately 10% further into the tidal range than marshes without *Spartina* at their lower edges (Fig. 3.7).

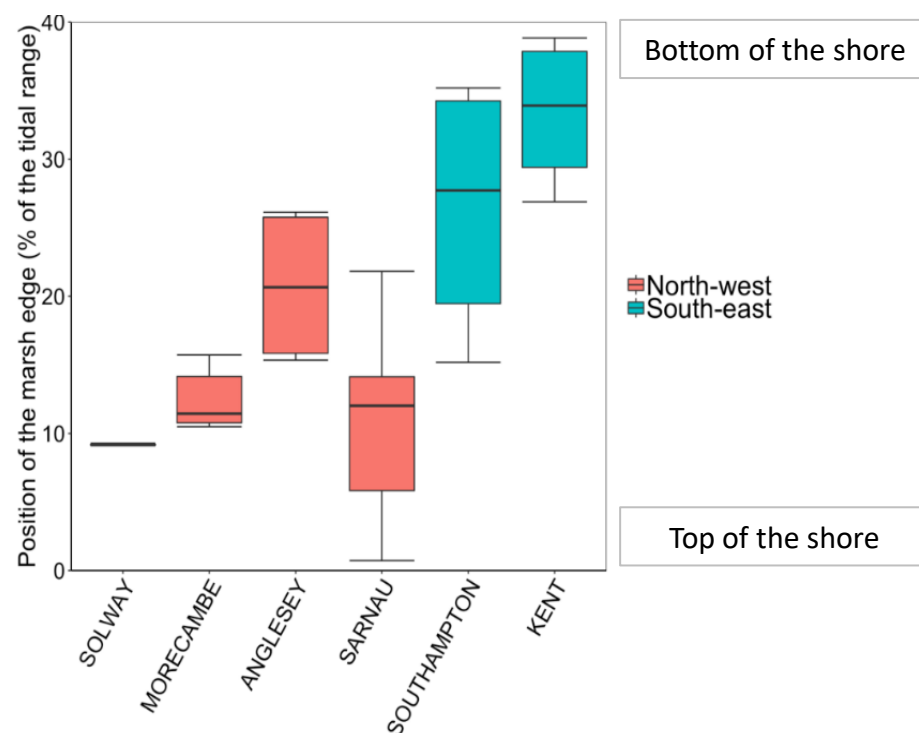


Fig 3.5. Positions of salt marsh edges in the tidal frame within six geographical regions of the UK, from the north-west to the south-east. Thick horizontal lines = median, box = interquartile range, vertical whiskers = full range, black circles = outliers.

Table 3.1. Outputs of the linear mixed effects models performed on the down-shore extent data. *ALL SITES* refers to the model without the wave forcing measurements, whilst *WAVE SITES* refers to the model with a sub-set of sites from which wave forcing measurements were obtained.

Response	Random effect	Effect	Df	Chi-squared	p-Value
ALL SITES: Marsh edge position (% of the tidal range)	Site	% Clay-silt	1	7.85	<0.01
		Vegetation type	1	6.49	<0.01
WAVE SITES: Marsh edge position (% of the tidal range)	Site	Wave height	1	7.49	<0.01

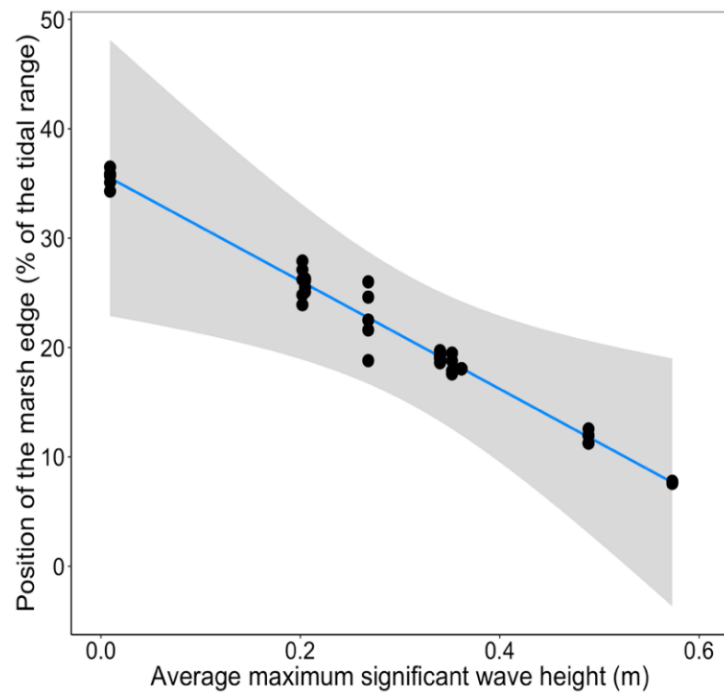


Fig 3.6. Linear mixed effects model fit showing the relationship between the average maximum significant wave height, which was used as a measure of wind-wave forcing between sites, and the percentage of the tidal range that the marsh has protruded into (i.e. the down-shore extent, DSE) for *WAVE SITES*. Solid blue line corresponds to the fitted values of the model ($n = 40$). Grey shading represents the 95% confidence intervals. Observations are the partial residuals of the observed data points (while the variance of the other variables in the model remain constant, Breheny & Burchett, 2013).

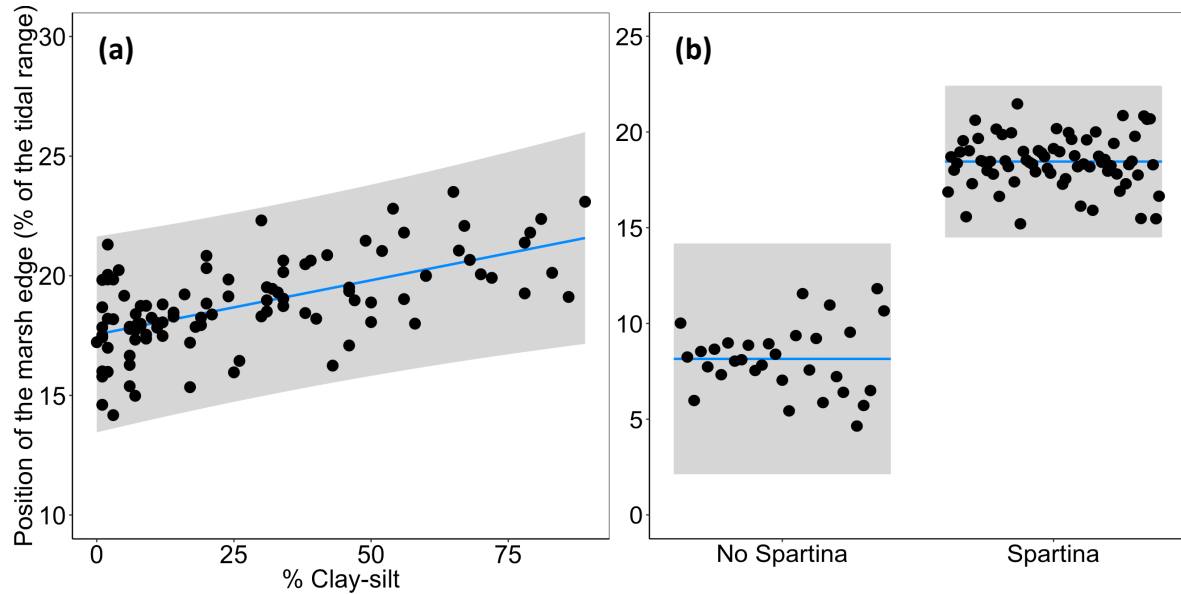


Fig 3.7. Linear mixed effects model fits showing the relationship between the percentage of the tidal range that the marsh has protruded into (i.e. the down-shore extent, DSE) and (a) the percentage of clay-silt in the sediment, and (b) vegetation type (no *Spartina*/*Spartina* marsh), for ALL SITES. Solid blue line corresponds to the fitted values of the model ($n = 110$). Grey shading represents the 95% confidence intervals. Observations are the partial residuals of the observed data points (while the variance of the other variables in the model remain constant, Breheny & Burchett, 2013).

Soil erosion rates

In the full model with all sites included, differences in soil erosion rates were explained by the clay-silt fraction in the sediment; erosion rates dropped non-linearly with increasing fractions of clay-silts in the sediment (Fig. 3.8; Table 3.2). The model predicted that the erosion rates of the sandiest soil cores (0% clay-silt, 2% of the core mass loss per minute) would be 2.5 times faster than the muddiest soil cores (80% clay-silt, 0.8% of the core mass loss per minute) (Fig. 3.8; Table 3.2).

Table 3.2. Outputs of the linear mixed effects models performed on the erosion rates data. *ALL SITES* refers to the full model with all sites included, whilst *MUDDY SITES* refers to the model with the cores which had low erosion rates (<6% mass loss per minute), and *SANDY SITES* refers to the model with the cores which had high erosion rates (>6% mass loss per minute) (refer to Table. S3.2 and Fig. S3.1 in the Supplementary Materials for details about the site selection).

Response	Random effect	Effect	Df	Chi-squared	p-Value
ALL SITES: sqrt (Erosion rate)	Site	sqrt (% Clay-silt)	1	39.79	<0.001
MUDDY SITES: sqrt (Erosion rate)	Site	log (% Clay-silt)	1	16.42	<0.001
SANDY SITES: sqrt (Erosion rate)	Site	Vegetation type	1	4.60	ns
		Root biomass	1	8.74	<0.05
		Bulk density	1	14.10	<0.01
		Organic content	1	37.82	<0.001

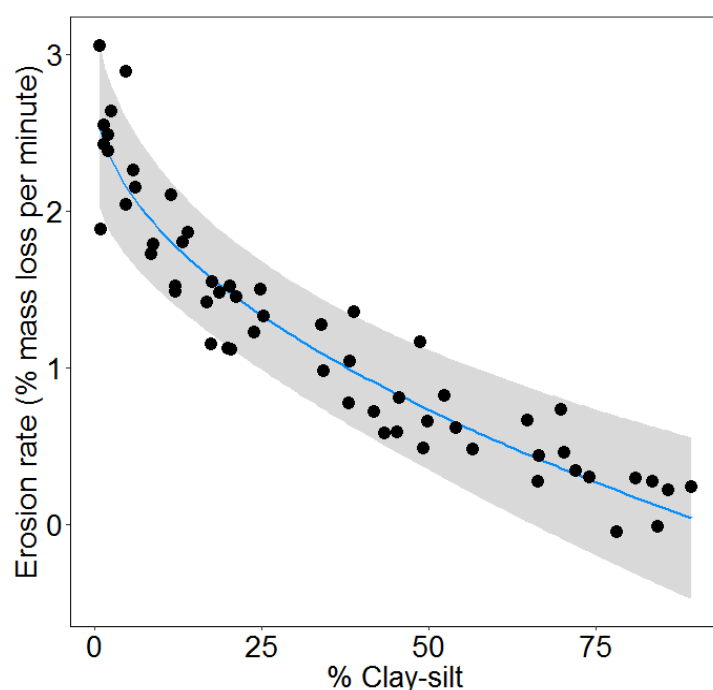


Fig 3.8. Linear mixed effects model fit showing the relationship between sediment core erosion rates and the percentage of clay-silt in the sediment for *ALL SITES*. Solid blue line corresponds to the fitted values of the model (n = 58). Grey shading represents the 95% confidence intervals. Observations are the partial residuals of the observed data points (while the variance of the other variables in the model remain constant, Breheny & Burchett, 2013).

In the model based solely on soil cores with high erosion rates (sandy sites), erosion rates were reduced by the presence of important biological variables (Fig. 3.9; Table 3.2). Soil cores with a higher density of roots and percentage of soil organic material resisted erosion better (Fig. 3.9; Table 3.2). In the model based on soil cores with low erosion rates (muddy sites), the biological variables were not important (Table 3.2). Differences in soil erosion rates at the muddy sites were explained only by the clay-silt fraction in the sediment (Fig. 3.10; Table 3.2).

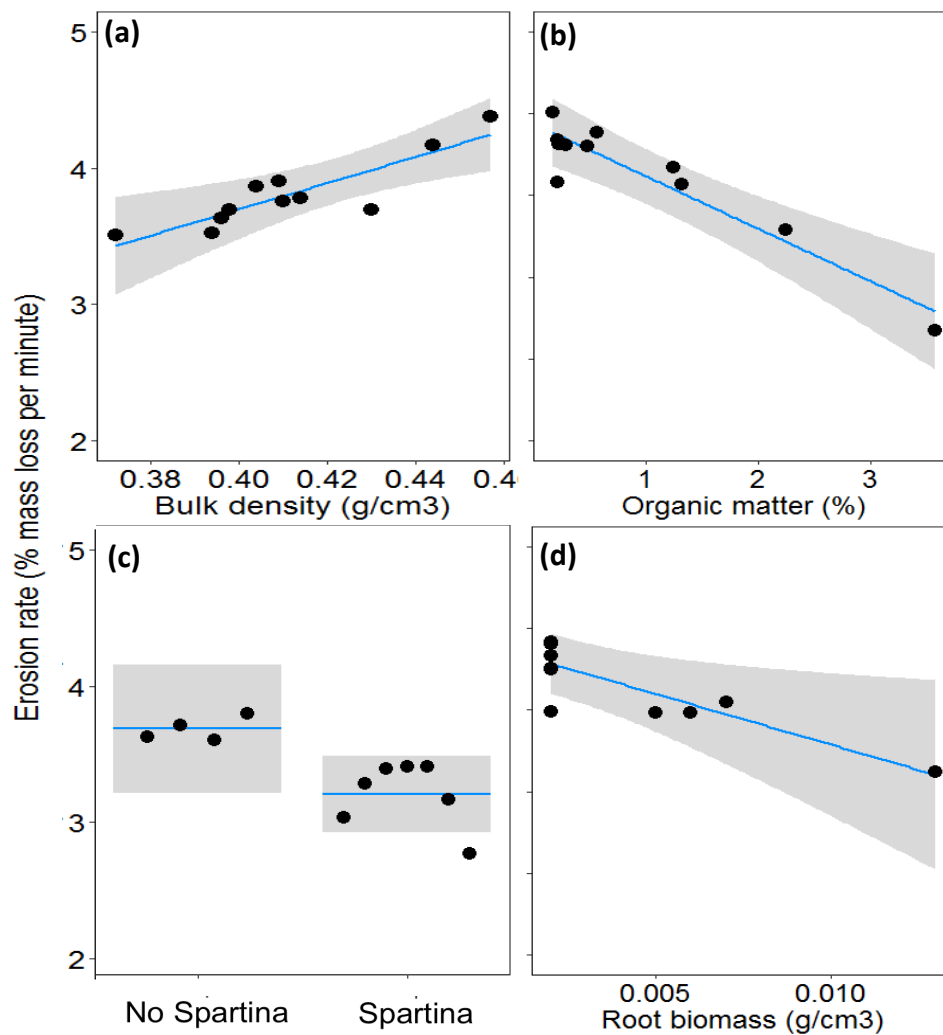


Fig 3.9. Linear mixed effects model fits showing the relationships between sediment core erosion rates and (a) soil bulk density, (b) soil organic matter content, (c) vegetation type and (d) soil root biomass, in *SANDY STES* (i.e. sediment cores with erosion rates of more than 6% mass loss per minute). Solid blue line corresponds to the fitted values of the model ($n = 11$). Grey shading represents the 95% confidence intervals. Observations are the partial residuals of the observed data points (after remaining variance of the other variables in the model, Breheny & Burchett, 2013).

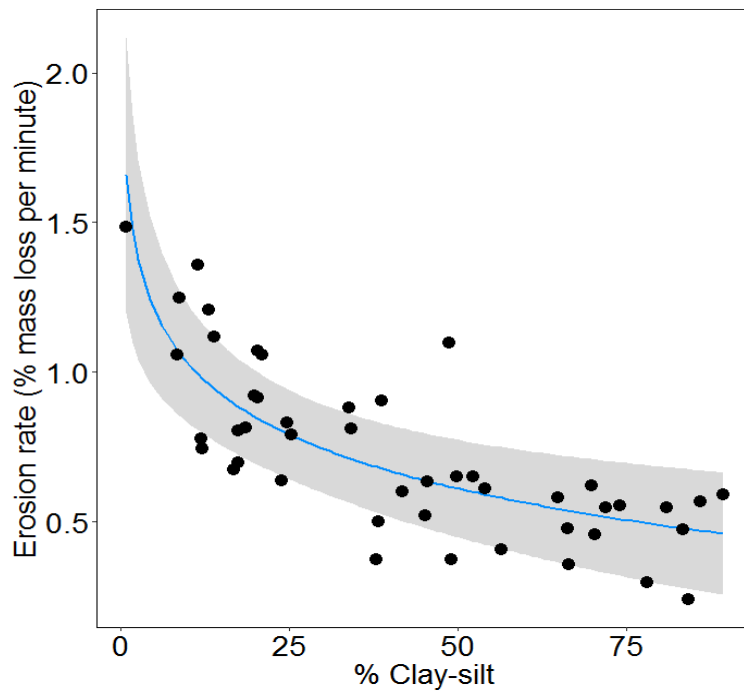


Fig 3.10. Linear mixed effects model fit showing the relationship between sediment core erosion rates and the percentage of clay-silt in sediment, in *MUDDY SITES* (i.e. sediment cores with erosion rates of less than 6% mass loss per minute). Solid blue line corresponds to the fitted values of the model ($n = 47$). Grey shading represents the 95% confidence intervals. Observations are the partial residuals of the observed data points (after remaining variance of the other variables in the model, Breheny & Burchett, 2013).

Discussion

This study shows that large-scale variation in wave forcing, a known threat to marsh growth and expansion at the lower edge (Callaghan et al., 2010), drives patterns of marsh resilience across the UK. It found that marsh down-shore extent increased from the north-west to the south-east coasts, consistent with large-scale gradients in wave forcing. Whilst previous studies have demonstrated the impact of wave forcing on cliff edge erosion (e.g. Callaghan et al., 2010; Mariotti & Carr, 2014; Silinski et al., 2016), the present study goes further. It shows that wave forcing also drives large-scale patterns of marsh down-shore extent, an outcome of long-term resilience and/or vulnerability to erosion at the lower marsh edge. However, this study also demonstrates that within regions (regional scale), patterns of marsh resilience are influenced by local sediment and vegetation properties, which mediate the

erodibility of the marsh cliff against local erosion. Marsh down-shore extent increased with the fraction of clay-silt in the sediment, and marshes occurred lower down the shore when the pioneer plant *Spartina anglica* was present at the lower marsh edge. At the sandy sites, biological variables including root density and soil organic matter content played fundamental roles in enhancing erosion resistance. At the muddy sites, the biological variables were not important and differences in soil erosion rates were explained only by the clay-silt fraction in the sediment.

Studies have previously shown that wave forcing is the main factor responsible for cliff erosion and hence landward retreat at the lower salt marsh edge (Callaghan et al., 2010; Marani et al., 2011; Mariotti & Fagherazzi, 2010; Tonelli et al., 2010). Marani et al., (2011) demonstrated that the erosion rate of the marsh edge increased positively with wave power density, which is a function of wind forcing (Marani et al., 2011). Therefore, it was unsurprising that marsh down-shore extents increased with decreasing wave forcing from north-west to south-east regions of the UK. The majority of studies model the responses of salt marshes to wave erosion without incorporating important bio-physical components of the marsh itself, which are known to play fundamental roles in regulating plant growth and expansion on tidal mudflats, in so called 'bio-physical feedbacks' (van Hulzen et al., 2007; van Wesenbeeck et al., 2008; Bouma et al., 2009). This study shows that cliff erosion at the lower marsh edge can be mediated by important intrinsic sediment and vegetation properties at a marsh scale (Feagin et al., 2009; Wang et al., 2017), which enable marshes to extend further down-shore. Our findings are similar to those of Balke et al., (2016), who showed that global-scale patterns of marsh down-shore extents could be explained by large-scale differences in tidal range and associated inundation stress, but that the same large-scale drivers could not explain regional variation in marsh down-shore extents. Balke et al., (2016) suggested that this regional-scale variability might be attributed to other properties that affect plant growth at the lower marsh edge, including soil salinities and plant traits, which operate at smaller, marsh scales.

This study shows, in agreement with Feagin et al., (2009), that sediment properties are more important than vegetation properties in mediating sediment erosion at the lower marsh edge. This is because in the present study, vegetation properties (including below-ground root biomass) did not explain any of the variation in soil core erosion rates across all of the UK sites, in contrast to the fraction of clay-silts in the sediment. Vegetation properties only played a significant role in reducing soil erosion rates at a smaller, regional-scale in the sandier, more erosion prone settings (Wang et al., 2016; Lo et al., 2017). This is because roots in the sediment help to bind the sandy substrate, and soil organic matter content acts as a glue to add cohesiveness, both of which increase the resistance of the otherwise erosion-prone sandy substrate. Similarly, Lo et al., (2017) showed that vegetation increased erosion resistance by 17% in muddy sediments, whilst it increased erosion resistance by 80% in sandier sediments. Although this study shows that sediment properties were more important than vegetation properties for provisioning erosion resistance in all of the salt marsh sites across the UK, vegetation type was an important driver of down-shore extents. Marshes with *Spartina anglica* at their edges extended further down the shore than marshes without *Spartina*. This was unsurprising, given that *Spartina* is extremely tolerant of harsh conditions at the lower marsh edge, including tidal inundation stress and high soil salinities (Adam, 1990). Thus, we suggest that vegetation type was linked to the tolerance of different plant species to environmental contexts including soil salinities and inundation stress, and not to the erosion-mediating effect of *Spartina* over other salt marsh plant species. Raposa et al., (2016) found that marshes on the east coast of the USA dominated by the formidable pioneer plant species *Spartina alterniflora* extended to lower positions in the tidal frame compared to west coast US marshes dominated by the high-shore species *Salicornia pacifica*, which cannot tolerate as much tidal inundation (Wasson et al., 2013; Janousek et al., 2016).

The findings of the present study highlight the complexities involved in making predictions about salt marsh down-shore extents, and hence about marsh resilience to erosion. At a large-scale, an extrinsic driver, wave forcing, determines patterns of marsh down-shore extents across a gradient from north-west to south-east coasts of the UK. At this large-scale, important intrinsic marsh

properties become redundant, but that at smaller regional scales, are important for mediating cliff edge erosion. In agreement with Balke et al., (2016) and Wang et al., (2017), we suggest a fundamental need to consider the scale of the observation when considering the resilience and/or vulnerability contexts of salt marshes (Fig. 3.11). Wang et al., (2017) showed that wave exposure strongly affected marsh retreat at a large, estuarine-scale, but that at a small, marsh-scale, important sediment and vegetation properties mediated the effects of the external forcing on marsh erosion. Similarly, Balke et al., (2016) showed that tidal range and associated tidal inundation stress explained global-scale patterns of marsh down-shore extents, but that the same driver, tidal range, could not explain regional-scale patterns of marsh down-shore extents. Similar scale-dependent interactions have been described in other systems, including coral reefs (Caselle & Warner, 1996; Oliver & Palumbi, 2009), as certain features of coral reef habitats predicted fish recruitment densities at the small, transect-scale, but that the same features could not explain patterns of fish recruitment at the large, reef-scale.

Our findings are highly relevant for the management and restoration of salt marshes, because they emphasise the need to consider to what extent, and at what scales the drivers and internal properties of salt marshes might influence marsh resilience against erosion. The majority of restoration projects fail before completion (Silliman et al., 2015), possibly because they do not consider the interactions between biotic and abiotic factors happening over a number of different spatial scales. This may be due to the difficulties in predicting the erosion drivers at a site, which affects the selection and application of restoration designs, in terms of selecting the most resilient vegetation and sediment traits, to minimise restoration failure due to exceeding erosional forces.

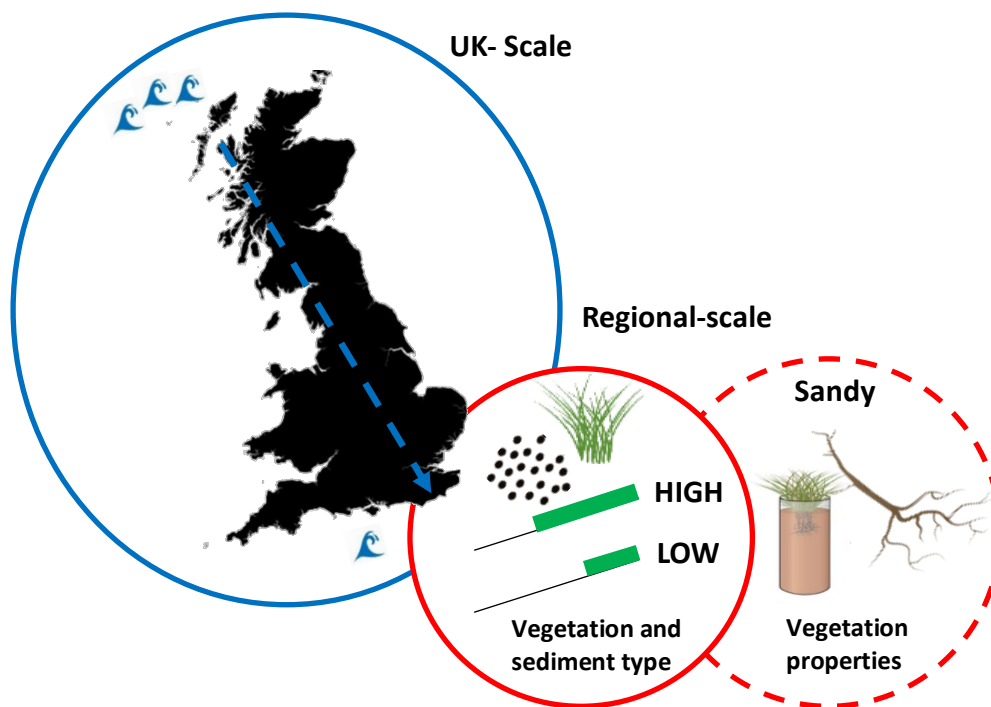


Fig 3.11. Wave forcing drives large-scale (UK-wide) patterns of marsh down-shore extents (blue circle), whilst regional-scale patterns of down-shore extents (red circle) are determined by local (marsh-scale) properties including vegetation type and sediment grain size, which mediate against local erosion. Marshes that extend to lower positions on the shore have high resilience to local wave forcing, whilst marshes that are restricted to higher positions have low resilience. Vegetation properties including root biomass (dashed red circle) mediate against erosion in sandy settings.

Although we make useful suggestions about considering the scales of the drivers and internal properties of salt marsh resilience, we acknowledge that this study did not consider temporal changes, which are highly relevant for management and conservation. Marshes are dynamic systems that regularly undertake dramatic switches between periods of lateral vegetation expansion followed by periods of lateral cliff retreat (Pringle, 1995; Cox et al., 2003). Yet, this study observes the down-shore extents of salt marshes at a single point in their evolutionary history, which may be during a longer-term period of seaward expansion or lateral retreat (Allen, 2000). Therefore, we suggest that managers must first consider whether the resilience that they are observing represents a short-term observation or is the outcome of a longer-term trend. This requires observing marshes and the drivers of resilience over temporal as well as spatial scales.

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SUPPLEMENTARY MATERIALS FOR CHAPTER 3

Supplementary Materials Section A

Additional tables and figures to support the main text.

Table S3.1. Details of the selected salt marsh sites within each geographical region of the United Kingdom.

Wider Region	Region	Marsh (<i>Spartina</i> /No <i>Spartina</i>)	Exposure	Co-ordinates	Wave data (Y/N)	Average maximum significant wave height (m)
North-west	Solway	Southernness (S)	Exposed	54.8792, -3.6596	Y	0.57
		Rough Firth (NS)	Sheltered	54.8552, -3.8135	N	N
	Morecambe	Sunderland Point (S)	Exposed	54.0038, -2.8967	N	N
		Grange-over-sands (NS)	Sheltered	54.1965, -2.8891	N	N
		Lades (S)	Sheltered	54.0011, -2.8746	N	N
	Red Wharf Bay	RWBE (S)	Exposed	53.2991, -4.1772	Y	0.35
		RWBS (S)	Sheltered	53.2977, -4.2119	Y	0.19
	Sarnau	Toll Bridge (NS)	Exposed	52.9238, -4.0640	N	N
		Morfa Harlech (NS)	Exposed	52.9016, -4.0955	N	N
		Glaslyn Cob (S)	Exposed	52.9157, -4.1112	Y	0.49
		Dyfi South (S)	Exposed	52.5256, -4.0359	N	N
		Talsarnau (S)	Sheltered	52.9186, -4.0598	N	N
		Penmaenpool (S)	Sheltered	52.7483, -3.9577	N	N
		Curian (S)	Sheltered	52.7329, -4.0193	N	N
		Fairbourne (NS)	Sheltered	52.7113, -4.0357	N	N
		Ynys Hir (NS)	Sheltered	52.7486, -3.9566	N	N
	South-east	Kent	Swale (S)	Sheltered	51.3576, 0.9181	Y
Elmley (S)			Exposed	53.3703, 0.7957	Y	0.35
Southampton		Hythe (S)	Exposed	50.8621, -1.3843	Y	0.27
	Exbury (S)	Sheltered	50.7853, -1.3889	Y	0.09	

Table S3.2. Details of the five models performed during the statistical analyses. Response and/or explanatory variables in **bold** represent those that are unique to the model.

Response	Model name	Explanatory variables	Number of Observations
Down-shore extent	ALL SITES	Vegetation type Exposure (E/S) Cliffs (C/NC) Soil organic matter Soil bulk density Soil conductivity (as a proxy for salinity) Soil clay-silt content	110
	WAVE SITES	Vegetation type Exposure (E/S) Cliffs (C/NC) Soil organic matter Soil bulk density Soil conductivity (as a proxy for salinity) Soil clay-silt content Wave forcing	40
Soil erosion rates	ALL SITES	Vegetation type Exposure (E/S) Cliffs (C/NC) Soil organic matter Soil bulk density Soil conductivity (as a proxy for salinity) Soil clay-silt content Root biomass	58
Soil erosion rates (>6% loss per minute)	SANDY SITES	Vegetation type Exposure (E/S) Cliffs (C/NC) Soil organic matter Soil bulk density Soil conductivity (as a proxy for salinity) Soil clay-silt content Root biomass	11
Soil erosion rates (<6% loss per minute)	MUDDY SITES	Vegetation type Exposure (E/S) Cliffs (C/NC) Soil organic matter Soil bulk density Soil conductivity (as a proxy for salinity) Soil clay-silt content Root biomass	47

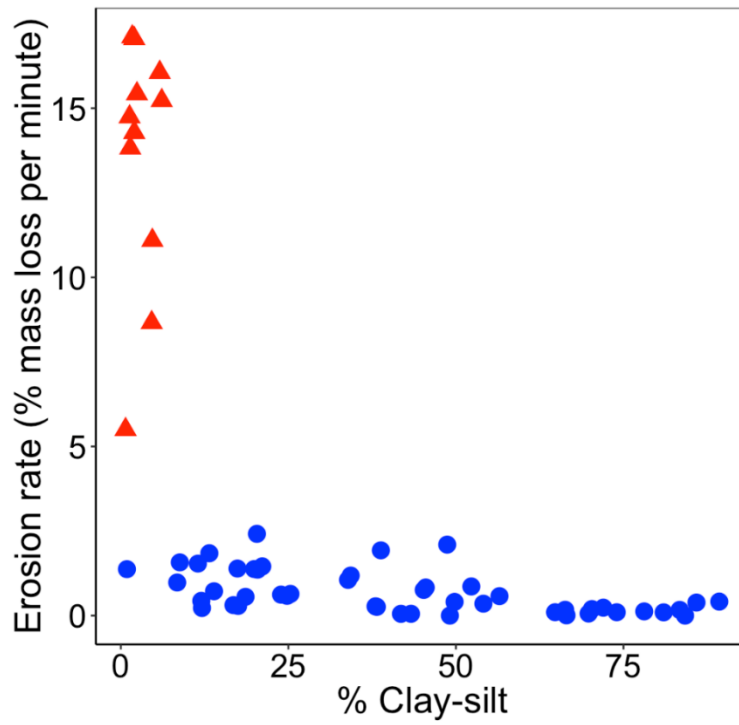


Fig S3.1. Relationship between sediment core erosion rates from the full erosion model ($n = 58$), showing two clearly identifiable groups. The red triangles represent sediment cores with high erosion rates (more than 6% mass loss per minute) and the blue circles represent sediment cores with low erosion rates (less than 6% mass loss per minute).

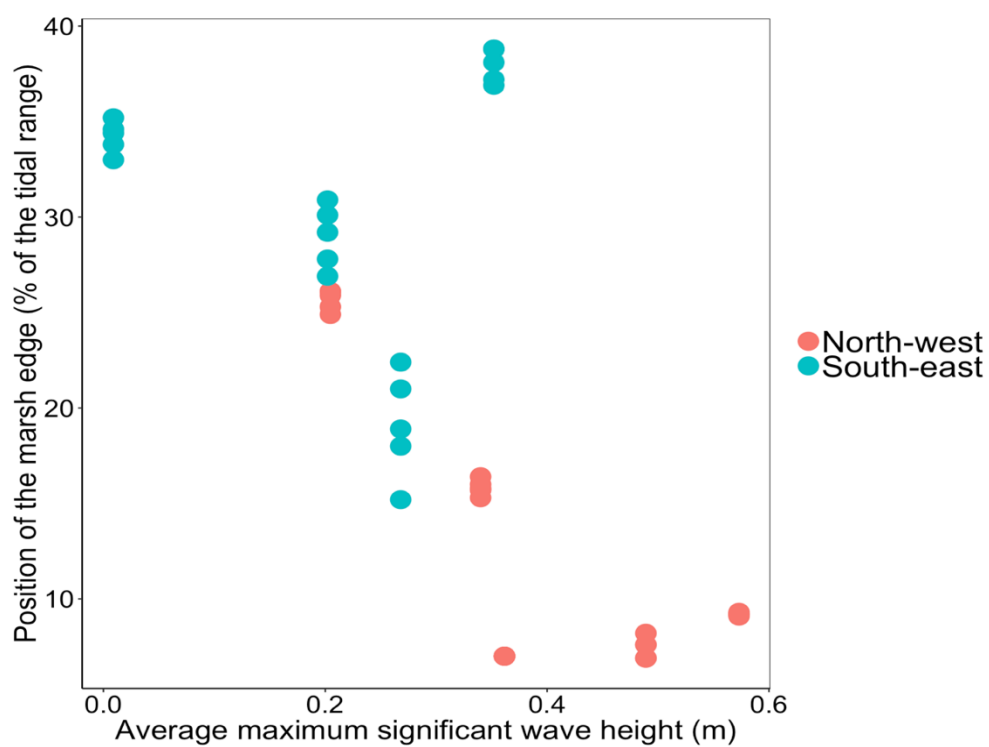


Fig S3.2. Relationship between the position of the marsh edge in the tidal frame and the significant maximum wave height which was used as a measure of wind-wave forcing between sites, at each site.

Supplementary Materials Section B

Wave forcing measurements

We quantified differences in wave forcing by deploying pressure sensors (OSSI-010-003C-01; Ocean Sensor Systems, Inc.) (Fig. S3.3) simultaneously at the sites over 1 month during September-October 2018. The pressure sensors were placed 0.05m above the seabed, and they measured at a burst frequency of 5Hz for 1-minute at 10-minute intervals, following methods by Willemsen et al., (2018). The mean water level in an interval was determined by averaging all of the data points. The wave analysis was based on pressure fluctuations. The attenuation of the pressure signals with water depths was corrected to derive bulk wave parameters, e.g. significant wave height (H_s) (Figs. S3.4- 11) (Tucker & Pitt, 2001). Mean maximum wave heights were used as an indicator of the wind-wave forcing at the study sites and it was used as a predictor variable in the statistical analyses. The results of the wave observations are shown in Figures S3.4- 11.



Fig S3.3. Pressure sensor deployed at one of the study sites.

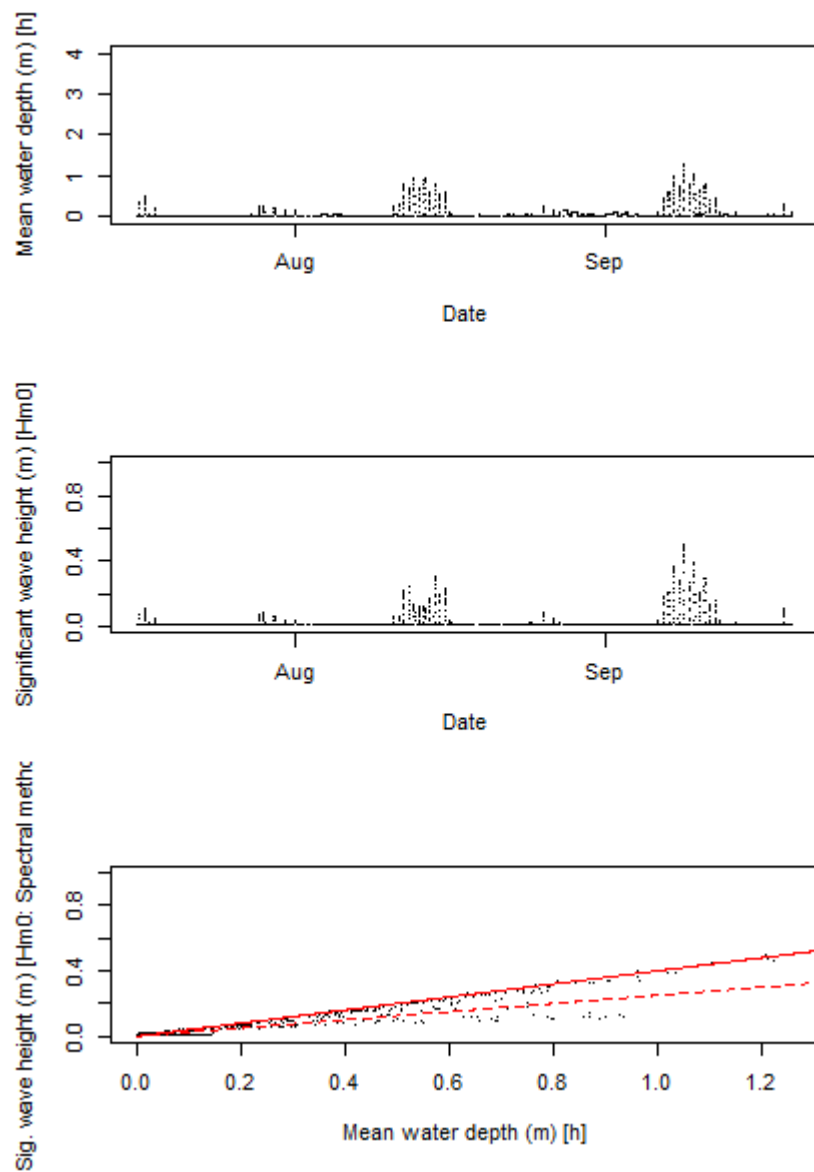


Fig S3.4. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Southernness site (Solway region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

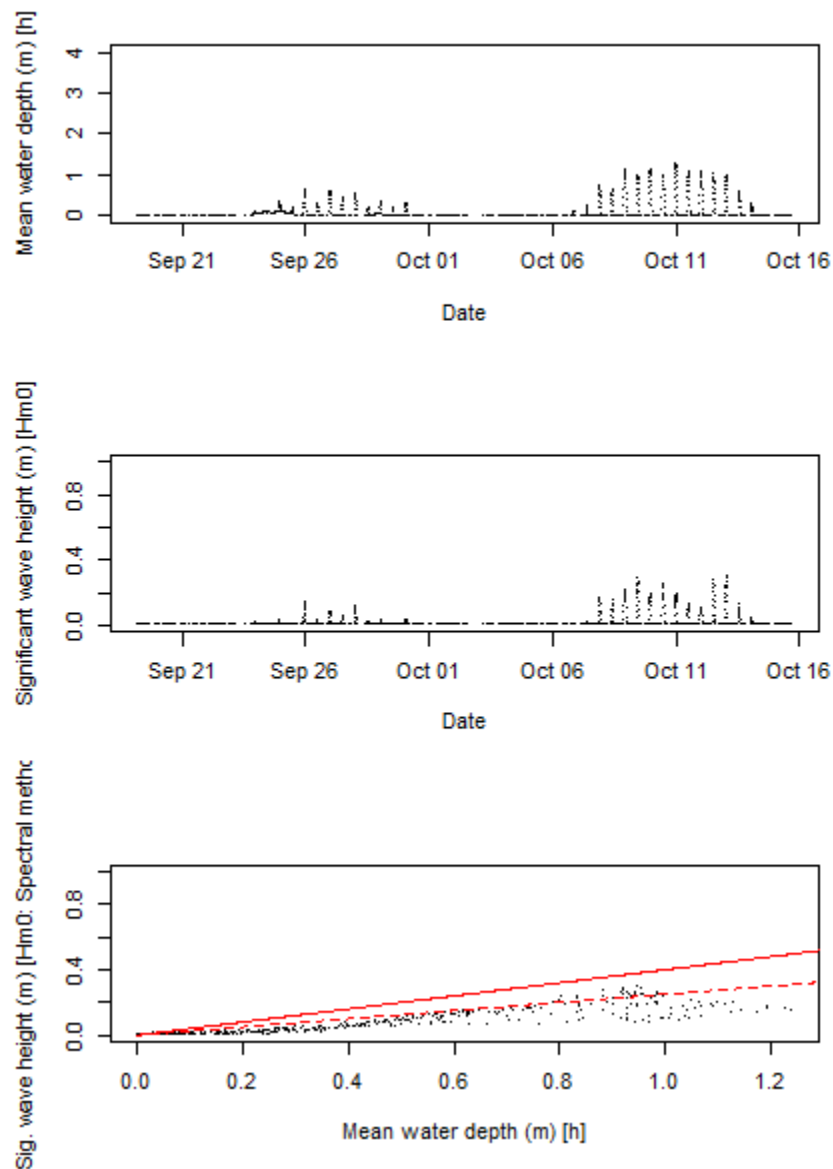


Fig S3.5. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Red Wharf Bay Exposed site (Anglesey region)** over the observation period (September-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

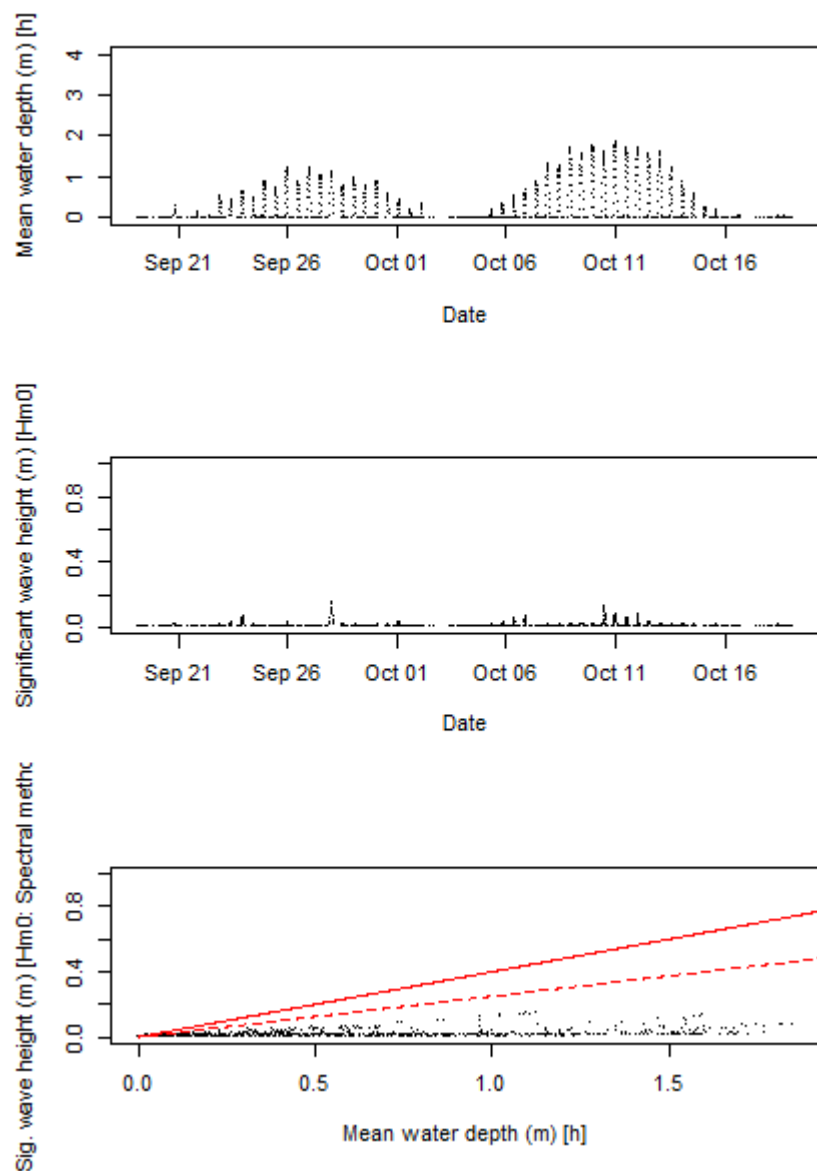


Fig S3.6. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Red Wharf Bay Sheltered site (Anglesey region)** over the observation period (September-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

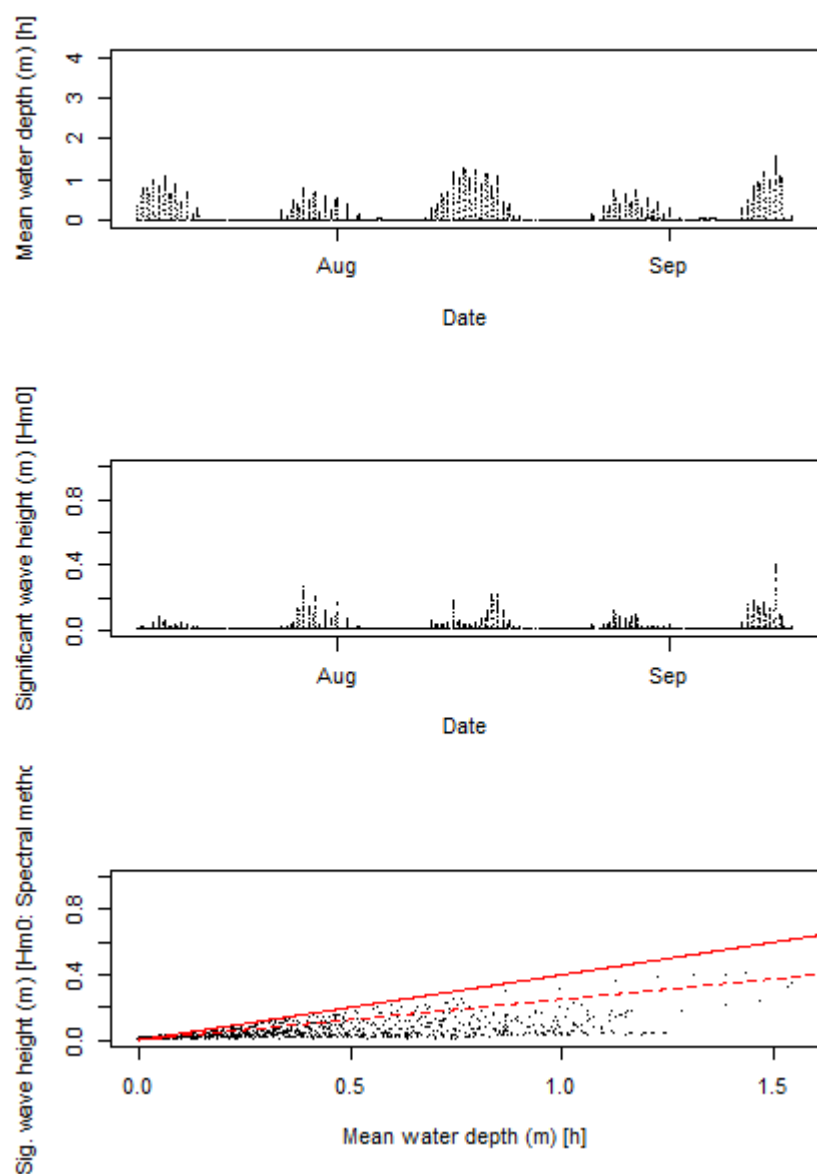


Fig S3.7. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Glaslyn Cob site (Sarnau region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

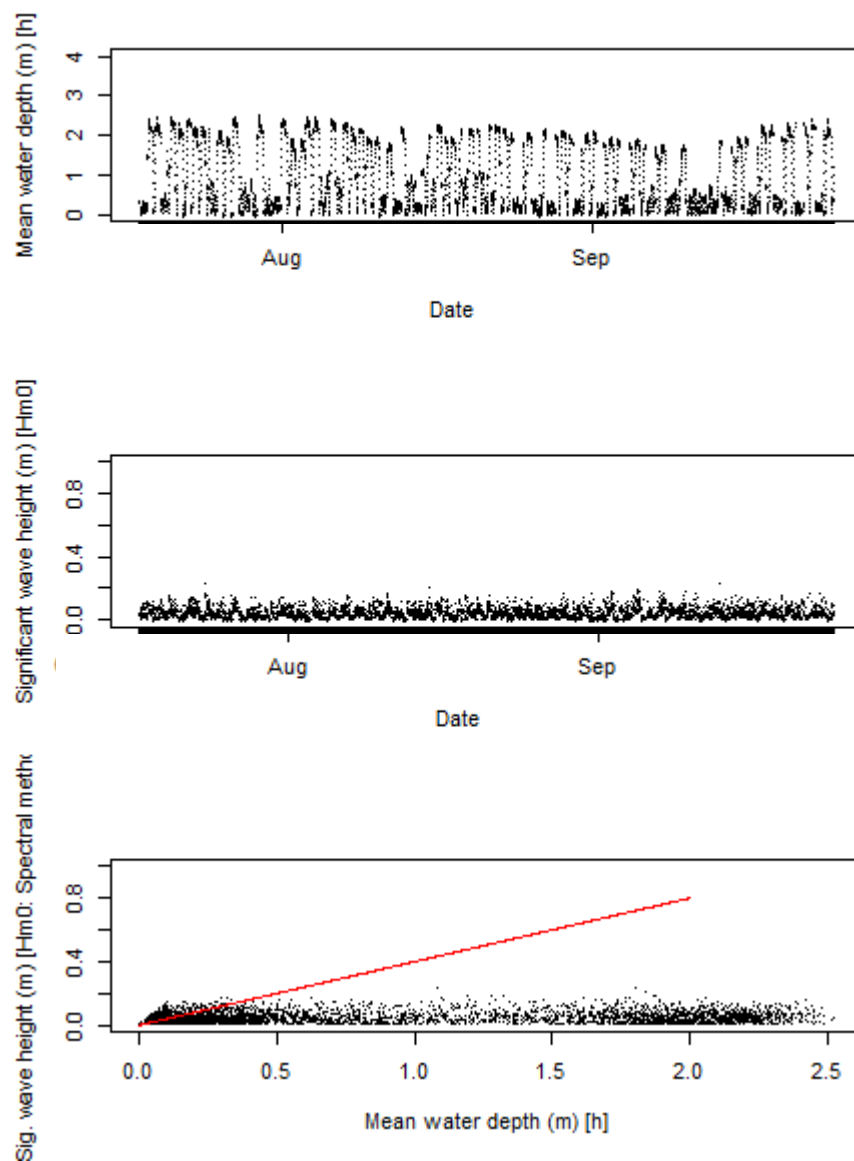


Fig S3.8. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Hythe site (Southampton region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

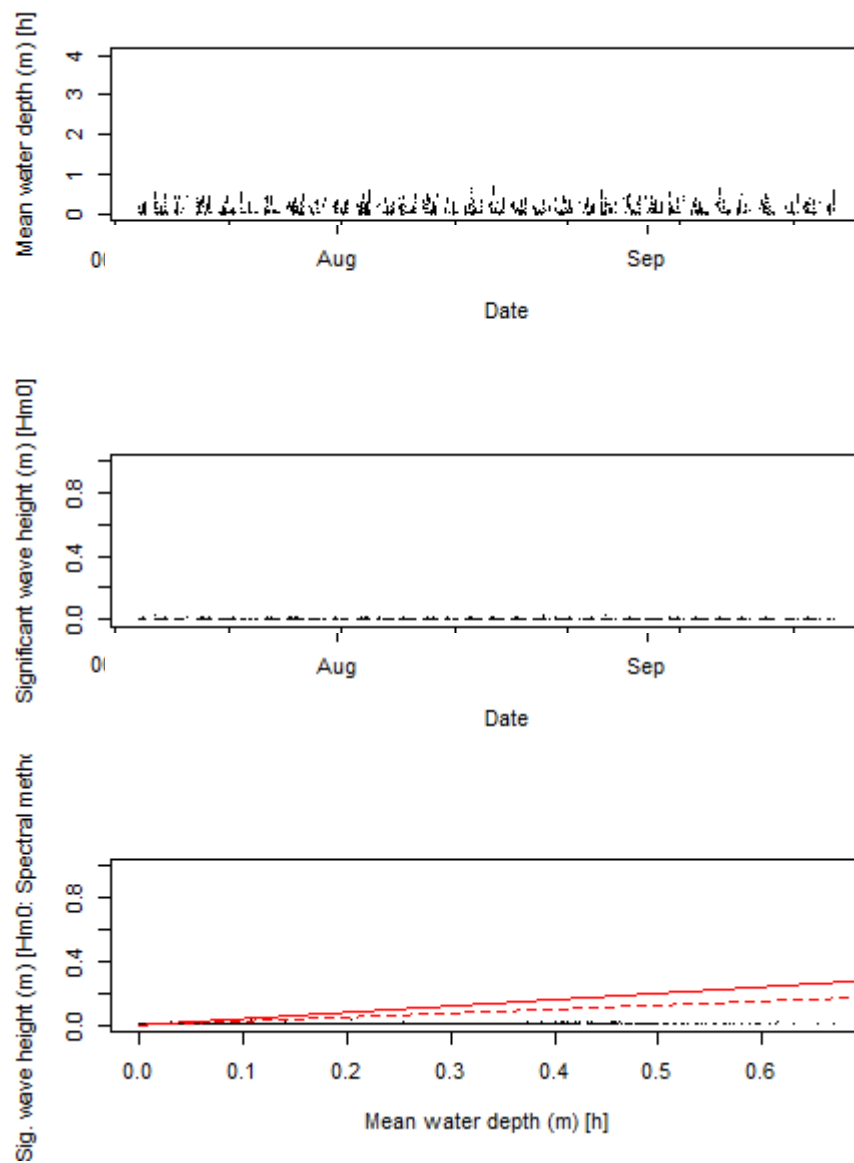


Fig S3.9. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Exbury site (Southampton region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

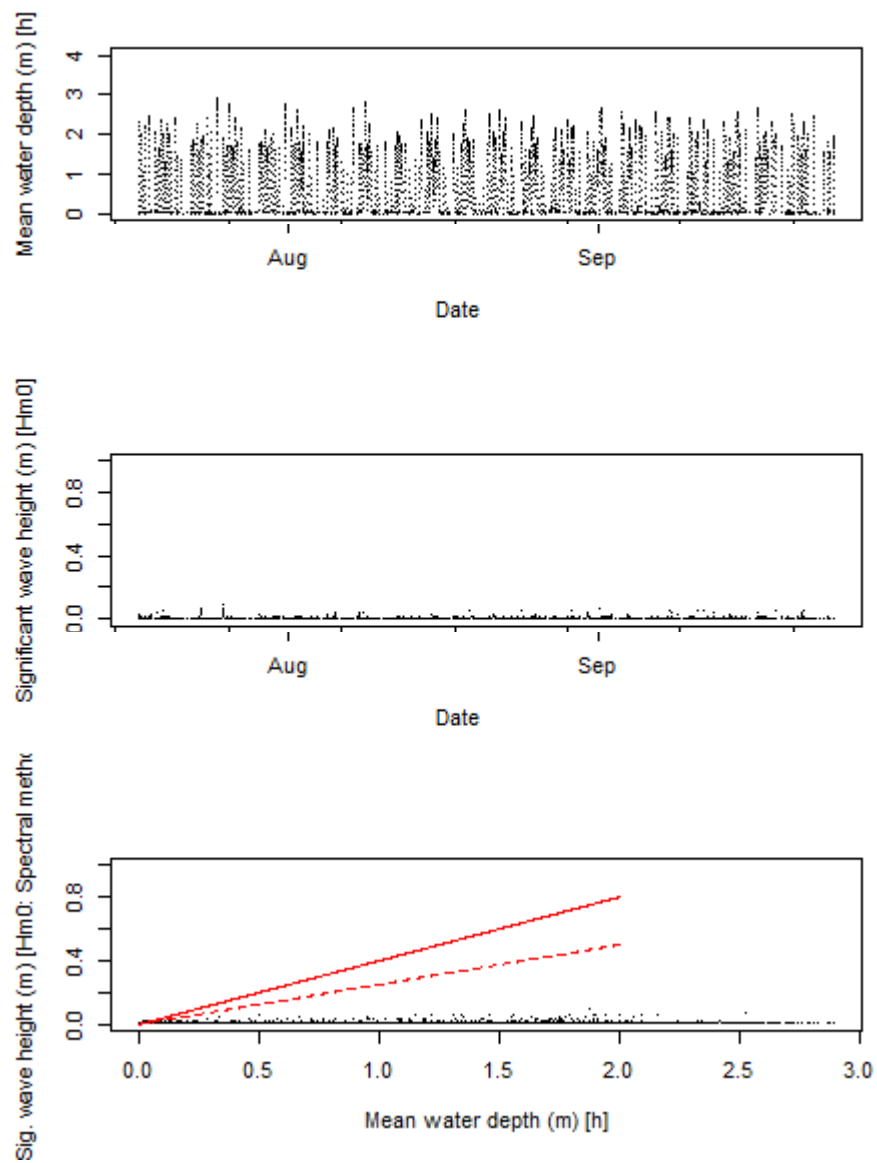


Fig S3.10. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Elmley site (Kent region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

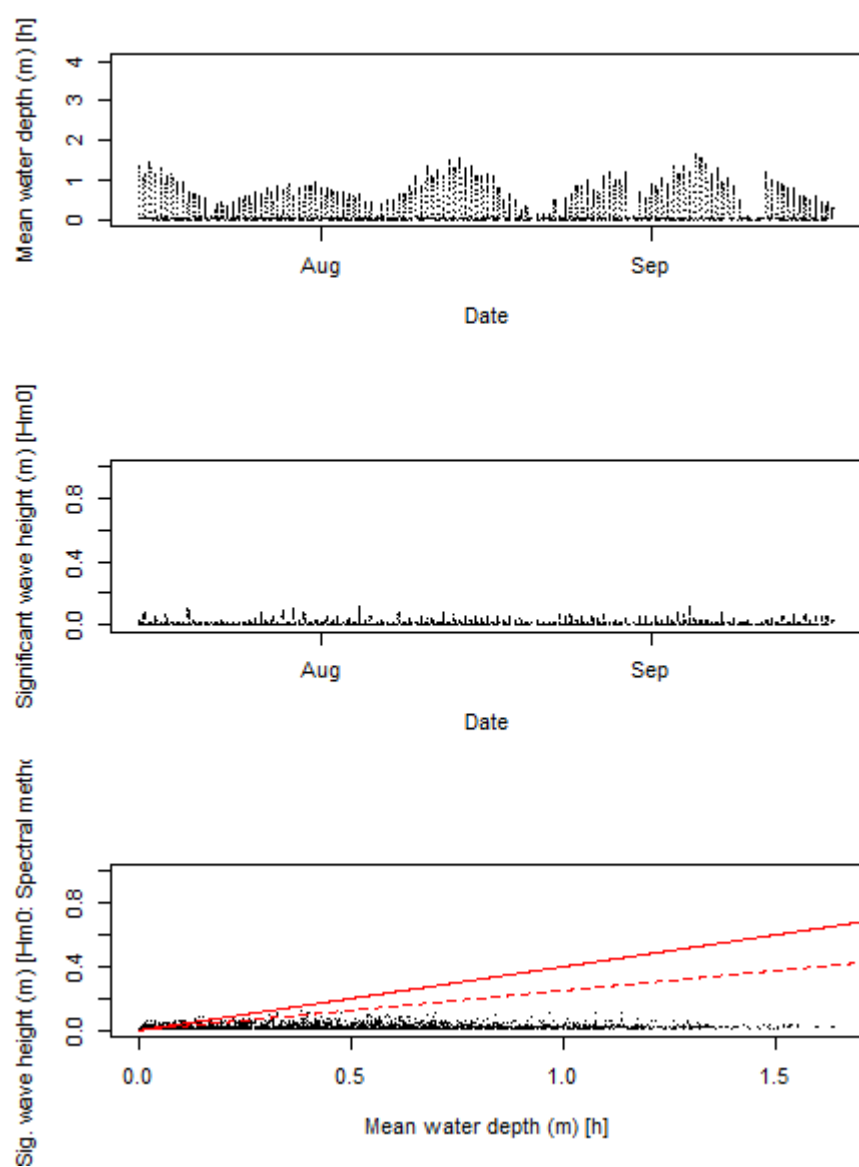


Fig S3.11. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Swale site (Kent region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

CHAPTER 4

Bio-physical drivers of large-scale variation in salt marsh resilience

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Status: Prepared for Submission

Author Contributions:

MDE conceived the research ideas and designed the methodology with assistance from MS, AG and TB. MDE conducted the fieldwork with assistance from MS and various undergraduate and postgraduate students. MDE performed the statistical analyses with guidance from JFP. MDE led the writing of the paper and all of the co-authors contributed critically to the drafts.

Abstract

Resilience of ecosystems can vary systematically between geographical regions, but the mechanistic reasons for large-scale variations are often unclear. Coastal salt marshes have declined to fifty percent of their historical cover in the last century, and they are threatened by emergent sea level rise and increased storminess. Geographical variation in marsh resilience and their underlying mechanistic causes are poorly understood, but there is a growing need to better understand the drivers and traits of resilience if we are going to continue benefitting from their valuable ecosystem services. We experimentally disturbed above- and below-ground patches of *Spartina anglica* marshes in twelve locations of six regions in the UK, to test how vegetation recovery was affected by contexts in climate, wave forcing, inundation period, shore elevation, sediment stability, sediment accretion rates, and vegetation and sediment properties. Vegetation recovery was poorer in the north marshes than the south, and was explained (48% of the variation) by a north to south trend of increasing sediment accretion and clay-silt content (which boost soil stability), mean temperature (which increases plant growth) and plant above-ground biomass (which is symptomatic of growth vigour). These variables varied systematically with a latitudinal gradient from the north-west to the south-east coasts of the UK. The study shows that salt marshes have geographical resilience contexts which are driven by large-scale variation in climate and geology. Large-scale variation in resilience is likely to be common across other ecosystems, and although the intrinsic bio-physical properties behind resilience contexts will be system specific, climate is likely to be a common driver.

Introduction

Coastal salt marshes provide valuable ecosystem services, including sequestering and storing 'blue carbon' (Himes-Cornell, Pendleton, & Atiyah, 2018), regulating coastal nutrient cycles (Mitsch & Gosselink, 2000), delivering natural coastal protection (Nicholls et al., 2007; Barbier et al., 2008; Möller et al., 2014) and providing habitat for a range of wildlife and fisheries species (Kneib et al. 1997; Gedan et al., 2009). Current patterns of change indicate strong global losses in salt marsh extent, which threaten the delivery of these important services (Gedan et al., 2009). Salt marshes were reduced to fifty percent of their historical cover over the last century (Moreno-Mateos, Power, Comín, & Yockteng, 2012) due to human-induced stressors including land reclamation, waste pollution, channel dredging and coastal defence construction, which diminishes sediment supply to marshes (Gedan et al., 2009). These historical losses, in combination with emergent erosional risks from climate-change induced sea level rise and increasing storminess (Mariotti & Fagherazzi, 2010; Kirwan & Megonigal, 2013; Leonardi, Ganju, & Fagherazzi, 2016), are fuelling significant global efforts to conserve and restore marshes (Gedan et al., 2009; Silliman et al., 2015). Patterns of marsh change, and the successes of protection and restoration schemes, vary substantially with contextual setting (Silliman et al., 2015). Finding common causes for this variation is further complicated by the inherently dynamic nature of salt marshes, where natural switching between periods of expansion and retreat at lower marsh edges can be commonplace (van de Koppel et al., 2005; Van der Wal, Wielemaker-Van den Dool, & Herman, 2008) (Fig. 4.1). Here we explore the extent to which spatial variation in salt marsh vegetation recovery in response to disturbance can be explained by large-scale variation in environmental context and the properties of marsh resilience, as influenced by change in environmental context.

Resilience can be expressed as the capacity of an ecosystem to resist change by maintaining a stable state in the face of disturbance (i.e. resistance); it can also be expressed in terms of recovery, as the capacity of the system to return to its pre-disturbed state following disturbance (Odum, 1969; Holling, 1973; Tilman & Downing, 1994; Stone & Wolfe, 1996). Most studies on salt marsh resilience have focused on investigating the mechanisms of resistance (Feagin et al., 2009; Ford, Garbutt, Ladd,

Malarkey, & Skov, 2016; Wang et al., 2017), even though recovery is key to successful restoration and a main predictor of marsh persistence in a changing climate (van Belzen et al., 2017).

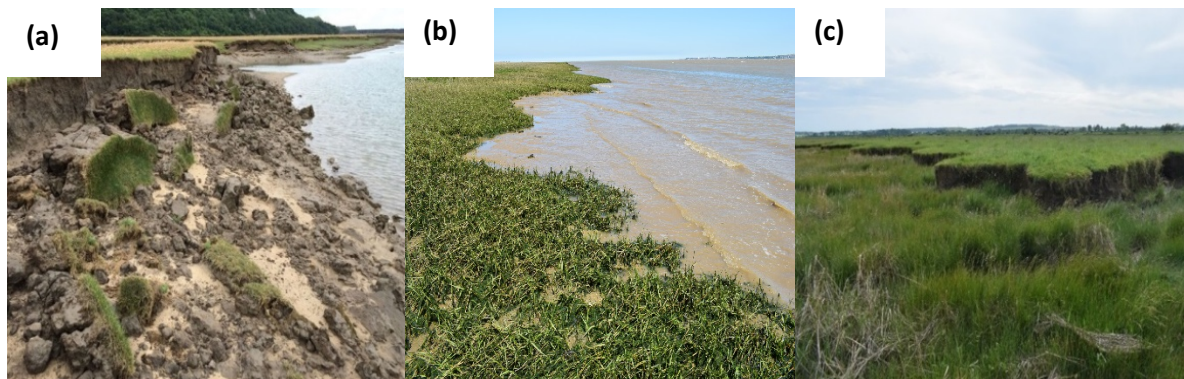


Fig 4.1. Three different states of salt marsh expansion and erosion. (a) Cliffed marshes are either in the process of erosion or have reached the threshold exposure to wave forcing whereby further down-shore extension of the marsh is inhibited (van de Koppel et al., 2005). (b) Un-cliffed marshes are generally in the process of expansion. Note, there is no erosion cliff, but a gentle transition between vegetated marsh and un-vegetated mudflat. (c) A vista of a marsh that historically eroded back to an erosion cliff, but which since expanded (recovered) and added new marsh in front of the remnant erosion cliff. Such historical erosion cliffs are common in salt marshes and indicative of the temporal dynamics of salt marsh seaward edges.

There are indications that salt marsh recovery from disturbance varies systematically over large spatial scales, and that these differences are explained by large-scale variation in forcing agents and marsh-scale resilience properties that influence sediment stability and plant establishment and growth (Fig. 4.2) (Moor et al., 2017). The forcing agents for salt marshes may be categorised as hydrologically mediated disturbances, or climatic drivers (Fig. 4.2). Hydrological disturbances include wave forcing and tidal inundation (Callaghan et al., 2010; Hu et al., 2015), which stress plant establishment and growth – directly, by inducing mechanical stress on newly settled seedlings, or indirectly by influencing sediment dynamics (i.e. erosion and accretion) (Fig. 4.2) (Balke et al., 2016). In a recent study, van Belzen et al., (2017) showed that inundation stress was the main driver of the variation in vegetation recovery, as marshes exposed to lower inundation recovered quicker than

marshes exposed to higher inundation. In addition to these hydrological disturbances, climatic drivers, including temperature and rainfall, have been shown to influence key metabolic functions, which consequently affects plant growth rates (Fig. 4.2) (Kirwan & Mudd, 2012).

Recovery-resilience may also be influenced by intrinsic marsh properties (properties at the patch scale, within marshes) that fall into two major groups; (1) Properties that influence sediment stability, and thus indirectly affect the capacity for seedlings to establish and grow, and (2) properties that directly affect plant establishment and growth (Fig. 4.2). In order for plant seedlings to establish successfully on intertidal mudflats, the sediment dynamics (i.e. erosion and accretion) must remain below a critical level to avoid dislodgement and/or smothering (Fig. 4.2) (Balke et al., 2011; Hu et al., 2015). As demonstrated in Figure 4.2, sediment dynamics are strongly influenced by hydrological regimes, and there is an interaction with sediment type (Komar, 1976). Sandy sediments are indicative of more energetic settings and they tend to be more dynamic, and hence less stable, than muddier sediments, which are indicative of calmer settings (Huckle, Potter, & Marrs, 2000; Feagin et al., 2009; Ford et al., 2016). Furthermore, sediment type affects plant establishment because the roots of the seedlings find it difficult to penetrate coarse sand, whilst the enhanced capacity of the seedlings to anchor their roots into the muddier sediment makes it a better substrate for promoting establishment and growth (Huckle, Potter, & Marrs, 2000; Balke et al., 2011).

Intrinsic marsh properties that are known to affect plant growth and vegetation expansion include elevation in the tidal frame, which determines a number of other important variables including inundation period, wave forcing and soil salinity, all of which are known stressors of plant establishment and growth (Fig. 4.2) (Huckle et al., 2000; Marani et al., 2011; Wang & Temmerman, 2013). Soil salinity has the capacity to restrict the seaward expansion of marsh vegetation by interfering with plant metabolic functions, because excessive salts in the soil can cause inhibition of plant growth (Fig. 4.2) (Huckle, Potter, & Marrs, 2000). Plant growth may also be reduced by the compaction of the soil (measured by bulk density), because compaction hinders root penetration and

thus the soil volume for plant uptake of water and nutrients (Fig. 4.2) (Kooistra et al., 1992). Another factor that has been shown to influence plant growth is the amount of organic material in the soil, given that organic materials play an important role in carbon and nutrient cycling, which are key components of plant growth (Fig. 4.2) (Herrick & Wander, 1998).

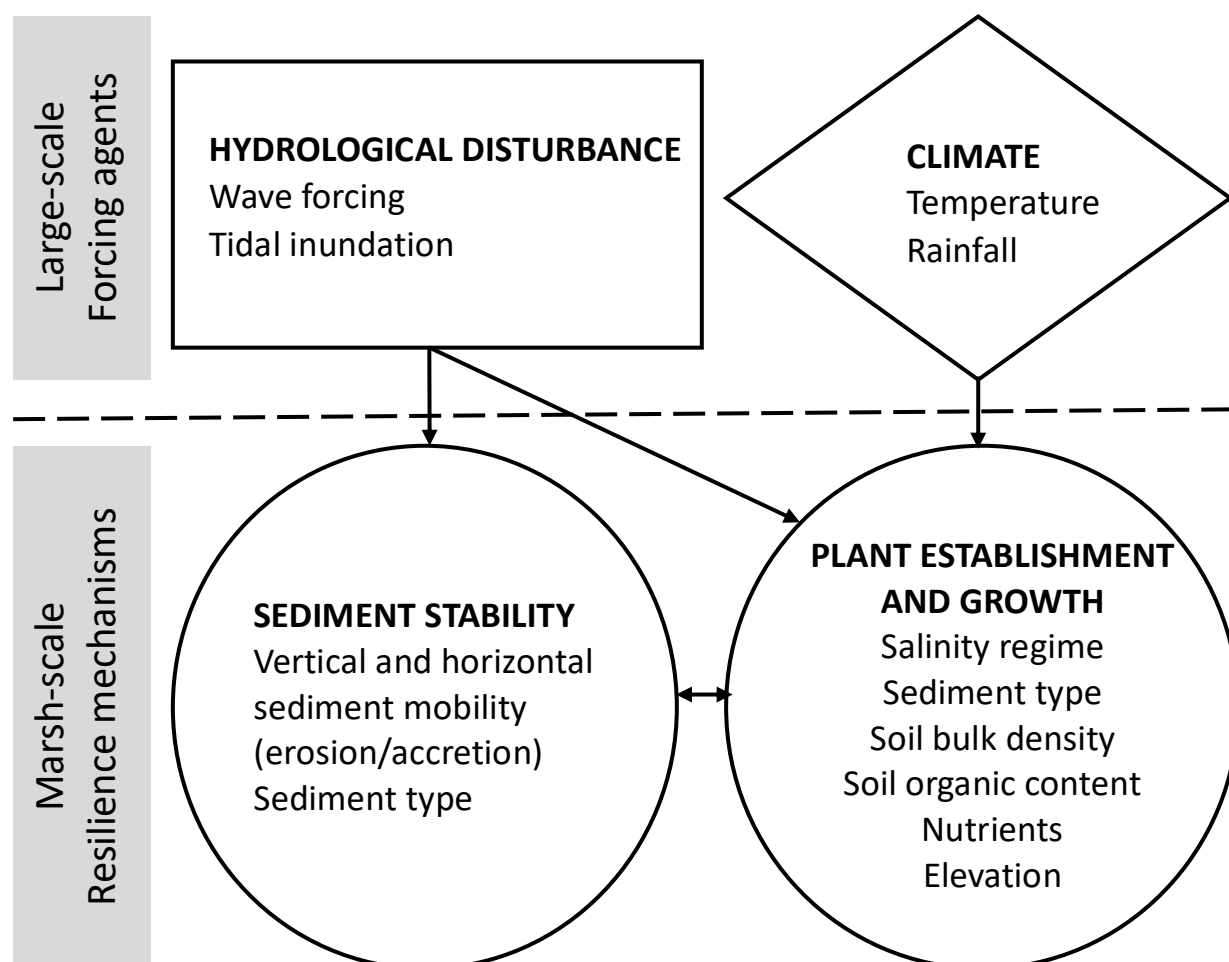


Fig 4.2. Conceptual figure showing the clustering of large-scale forcing agents and marsh-scale resilience properties that ultimately affect plant establishment and growth. Forcing agents operate over large spatial scales and may be categorised as hydrological disturbances, which mainly have mechanical/physical influences on the plants, and climatic stressors including temperature and rainfall, which impede on plant metabolic processes. Large-scale forcing agents can have direct impacts on plant establishment and growth (indicated by arrows), but they can also indirectly affect plant growth and establishment by modifying sediment properties, which are important for growth. At a local, marsh-scale, properties of marsh resilience are linked to characteristics that influence sediment stability and the ability of the plants to establish and grow.

We explored the extent to which large-scale, geographical variation in salt marsh recovery-resilience is governed by geographical differences in forcing agents and/or internal marsh properties that affect sediment stability, plant establishment and growth (Fig. 4.2). Incorporating six geographical regions in the UK, and associated variation in wind and hydrological forcing, temperature and soil characteristics, we experimentally disturbed natural populations of the marsh pioneer species, *Spartina anglica*, and assessed the recovery over two growing seasons. We hypothesised that large-scale variation in salt marsh recovery would be principally explained by regional differences in soil characteristics, in particular grain size, and secondarily by temperature, which affects marsh re-growth after disturbance. These predictions put into a resilience-recovery context the findings of recent studies that show soil stability explains variation in marsh down-shore extent (Willemsen et al., 2018; findings of Chapter 3) and that marsh growth rate can be influenced by geographical differences temperature (Kirwan & Mudd, 2012). The study is the first to test for the influences of multiple abiotic and biotic drivers of resilience on large-scale variation in marsh recovery; the work therefore advances recent work focused on single variables, such as tidal inundation (van Belzen et al., 2017).

Methods

Study sites

Manipulative field experiments were conducted in six well-known regions for salt marshes around the United Kingdom (Fig. 4.3). The Solway (north-west Scotland), Morecambe (north-west England), Anglesey (Red Wharf Bay) and Sarnau (west Wales) regions on the west coast in the Irish Sea, as well as Southampton (south England) and Kent (south-east England) regions on the south-east coast in the English Channel and North Sea. These regions were selected to represent the widest possible range of expected drivers and properties of salt marsh resilience in the UK (Fig. 4.2). The latitudinal gradient from 55° (Solway) to 50° (Southampton) represented a 2.3 °C difference in mean annual temperature – a sufficient range in temperature to affect vegetation growth rates (Megonigal et al., 2016). Previous work indicated that wave forcing and sediment characteristics, both of which are likely to affect vegetation recovery after disturbance (Huckle, Potter, & Marrs, 2000; Callaghan et al., 2010), vary systematically from the north-west to the south-east coasts of the UK (Ladd et al., in review). Sediment stability is likely to vary systematically between regions, given that sandy mobile sediments characterise the north-western regions, while muddy and stable sediments dominate south-eastern regions (Chapman, 1974). The study focused on mono-specific marshes dominated by *Spartina anglica* (hereafter *Spartina*), as this species is the dominant pioneer in western European marshes and a globally important genus for initiating marsh recovery following disturbance (Bouma et al., 2009). The choice of study regions represented the maximal geographical spread of this species in the UK; *Spartina* reaches its northern limit in the Solway estuary (Chapman, 1974) and so this region was chosen as the highest latitudinal limit of the study.

Wave forcing was expected to be an important driver of vegetation recovery because it directly affects plant colonisation and establishment by causing uprooting and dislodgement of seedlings (Balke, Herman, & Bouma, 2014; Hu et al., 2015), and it influences important sediment characteristics which might impinge on resilience associated with sediment dynamics (Fig. 4.2) (Balke, Herman, & Bouma, 2014; Hu et al., 2015). Six well-spread study regions offered the opportunity to detect the

effect of large-scale variation in wind-wave forcing on vegetation recovery. Yet, wave forcing can also vary on a local scale, for example between marshes within the same regions, depending on their relative fetch distances, i.e. the distance of open water in front of a site over which wind can build up wave energy (Denny et al., 2004), and the orientation of the marsh towards prevailing wind conditions (Burrows, Harvey, & Robb, 2008). To unravel the large-scale (UK-wide) versus local-scale (within regions) effects of wind-wave forcing, the study incorporated one wave-exposed and one wave-sheltered site per region (Fig. 4.3) (full detail in Supplementary Materials Table S4.1). Categorisation of exposure was based on wind-fetch following methods by Silinski et al., (2016); sheltered sites had restricted fetch and open water windows, whilst exposed sites had long fetch distances and open water windows. As it happened, two regions ended up with no observational data from wave-exposed sites; in the Southampton region, the experimental plots at the wave-exposed site were completely eroded away by the end of the experiment. In the Solway, we failed to find an exposed site, probably because *Spartina* is at its northern distribution limit (Chapman, 1974), where the additional stress of wave erosion may prevent plant establishment.

Experimental design

At each site, in early May 2017, manipulative disturbance experiments were set-up inside the *Spartina* vegetation, along a 50m stretch of the seaward edge of the marsh (defined as the boundary between marsh plants and the commencement of the bare mudflat). Normally, the boundary between marsh plants and the commencement of the bare mudflat is defined by having >10% (marsh) or <10% (mudflat) plant cover, but in this study much sharper transitions defined the boundary between the marsh and the commencement of the bare mudflat, with a shift from >80% (marsh) to 0% (mudflat) plant cover. Areas near creek edges or depressions were avoided because these were unrepresentative of the sampled marsh platform and hence might have caused variation in vegetation recovery between the plots. The experimental area was represented by fifteen 0.3 x 0.3m plots (n = 15 per site), which

were randomly allocated 1-4m landward of the seaward edge on the vegetated marsh platform. Plots were a minimum of 5m apart and were marked with bamboo sticks (Fig. 4.4).

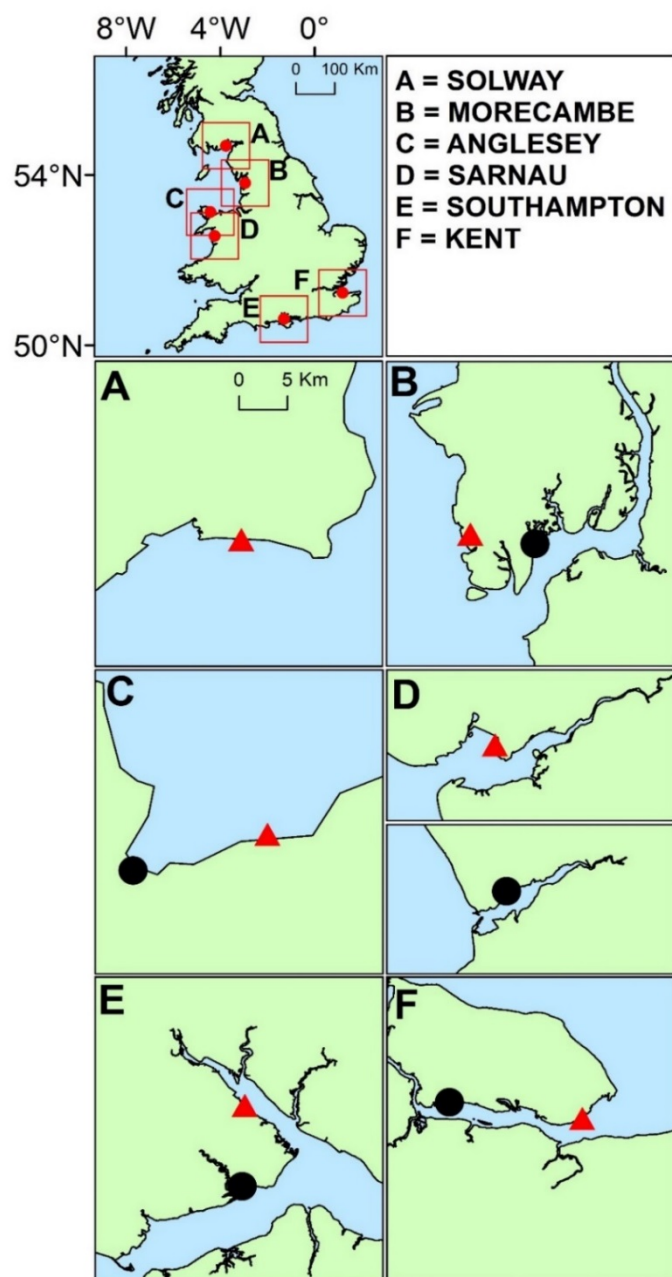


Fig 4.3. Six sampled geographical regions in the United Kingdom. Red triangles represent wave-exposed sites and black circles represent wave-sheltered sites.

Two disturbance treatments were randomly allocated to ten of the plots (5 plots per treatment), while the remaining five plots were left as un-disturbed controls. The two disturbance treatments were (1) above-ground vegetation removal only (hereafter 'AG removal') and (2) both

above- and below ground vegetation removal (hereafter 'ABG removal') (Fig. 4.3). For the ABG removal treatment, all of the above- and below ground vegetation biomass was removed by digging the soil to a depth of ~0.4m and discarding the sediment. The removal depth of 0.4m was chosen because plant roots in UK salt marshes typically occupy the top 0.3m of the sediment (Ford et al., 2016). The empty holes were re-filled with unvegetated sediment from the mudflat in front of the marsh. For the AG removal treatments, the vegetation above the sediment surface was removed by clipping. The clipped vegetation from the five AG removals was dried (60°C, 48 h) and used as a measure of the mean initial above-ground biomass per site, and a predictor variable in the subsequent statistical analyses.

Vegetation biomass

The re-grown above-ground vegetation was harvested by clipping in all plots in September-October 2018, two growing seasons after the disturbances were first executed. The vegetation was then dried (60°C, 48 h) and weighed to calculate a dry-weight biomass. Plant dry-weight biomass at the close of the experiment represented the 'absolute recovery' of the vegetation inside the disturbed plots, and it was used as the response variable in all the subsequent statistical analyses. *Spartina* patches can extend laterally through below-ground extension of the root-rhizome network, from which plants emerge above-ground (Bertness & Hacker, 1994). Thus, the *Spartina* biomass harvested from inside the plots at the close of the experiment could have originated from rhizome extensions of established plants within or next to the experimental plots, or through the germination of seeds, and thus new colonisation into the bare plots (Adam, 1990). The study was not able to distinguish between biomass originating from lateral rhizome growth or newly colonised seeds in the assessment of absolute recovery.

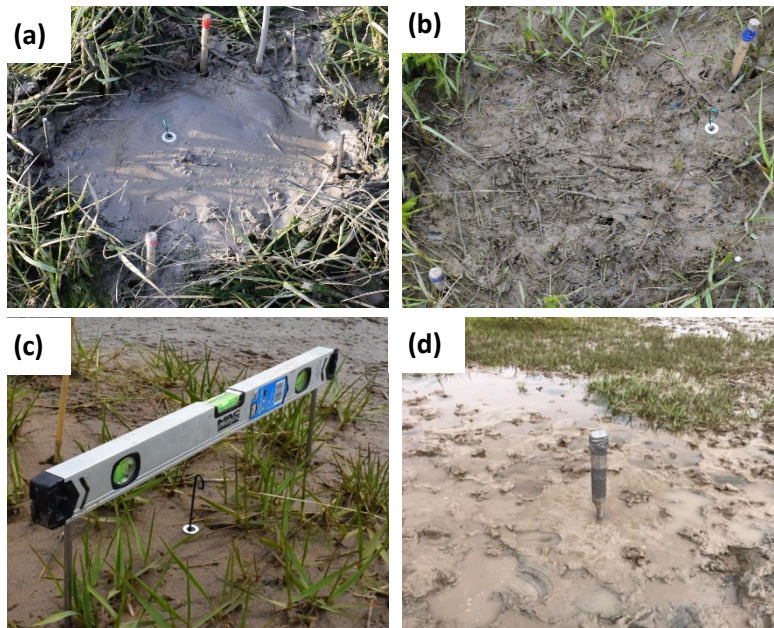


Fig 4.4. (a) Above- and below- ground vegetation removal ('ABG removal'), (b) above-ground vegetation removal only ('AG removal'), (c) Sedimentation-Erosion Bars (SEB's) and (d) Surface Elevation Dynamics (SED) sensor.

Measurements per plot

Soil characteristics

The following variables were measured due to their known influence on vegetation establishment and growth. Soil salinity is a stressor of plant growth and it has the capacity to restrict seaward marsh expansion (Huckle et al., 2000; Raposa et al., 2016). Soil samples of ~10g were extracted from the top 10cm of the soil in the five ABG plots, and these were measured for electrical conductivity (EC) (as a proxy for salinity) after diluting with distilled water according to methods by Ford et al., (2016). Soil bulk density, which is a measurement of soil density and a proxy for soil compaction, affects the capacity of plant roots to penetrate the soil and take up water and nutrients that are vital for growth (Kooistra et al., 1992). Bulk density was measured by removing soil samples centrally from the top 10cm in the five ABG plots using a stainless-steel ring (3.1cm height, 7.5 cm diameter) and then drying (105°C, 72 h) to remove all moisture following methods by Emmet et al., (2008). Organic material in salt marsh soils plays an important role in carbon and nutrient cycling, which are key components of

plant growth (Herrick & Wander, 1998). The percentage of organic matter was estimated by loss-on-ignition (375°C, 16 h) (Ball, 1964; Schumacher, 2002) using the dried sediment from the bulk density analyses. Sediment grain size can affect seedling establishment and growth on intertidal mudflats (Willemsen et al., 2018), and it is thought to be the most important factor affecting soil stability against hydrological forcing (Feagin et al., 2009). Sediment grain size affects plant colonisation and establishment because it influences the potential for the seedlings to anchor their roots into the sediment; a factor influencing the likelihood of dislodgement by waves and currents (Huckle, Potter, & Marrs, 2000). Soil grain size was measured from sub-samples (~1g) of the soil from the organic content analyses, after removal of any remaining organic material by hydrogen peroxide (Blott et al., 2004). Grain size was measured using a Beckman Coulter LS 13 320 laser diffraction particle size analyser, in which the sediment samples were classified into 33 size fractions ranging from 0.2-2000.0 μm . Grain size classes were then expressed as the percentage inside each sample (e.g. the % of the sand class, >63 μm , and the % of the clay-silt class, 0.02-63 μm). The percentage of the clay-silt class in the sediment samples was used as a predictor variable in all of the statistical analyses.

Elevation

Marsh elevation is an important driver of plant growth because it determines the effect of other influential variables on plants, including tidal inundation, wave forcing and soil salinity, all of which have been shown to increase with decreasing elevation (Ford et al., 2016; Raposa et al., 2016; Willemsen et al., 2018). The elevation of each plot was recorded to within $\pm 0.1\text{m}$ with a differential GPS (Leica GS08 GNSS System) and expressed relative to local tidal datum.

Down-shore extent

The degree to which the marsh edge protrudes into the intertidal (i.e. its down-shore extent; Chapter 3) is indicative of the marsh's inherent resistance to erosional forces, and the tolerance of the plants to harsh environmental conditions (Balke et al., 2016; Raposa et al., 2016). Down-shore extent is known to vary significantly from north-west to south-east regions of the UK (findings from Chapter 3). To measure marsh down-shore extent, the elevation of each plot was quantified relative to Chart Datum and then expressed as a percentage of the regional tidal range (Balke et al., 2016); [(plot elevation/regional tidal range) *100 %] (Fig. S4.1 in the Supplementary Materials).

Tidal inundation period

The percentage of tidal inundation per plot was estimated by referencing the elevation measurements taken in the field to daily annual tidal height records from the nearest tidal gauges at each study site (Fig. S4.2 in the Supplementary Materials) (downloaded from the British Oceanographic Data Centre, <https://www.bodc.ac.uk>). This method was used to estimate the percentage of time that the plots were under water over twelve months. A mean of the per plot inundation period (percent per year) was used as a predictor variable in the statistical analyses.

Sediment accretion

Sediment accretion can promote plant growth, by maintaining substrate elevation and inundation period, or can bury or smother seedlings when sediment accretion is high; conversely, sediment erosion can cause seedling uprooting and dislodgement, both of which negatively affect plant establishment and growth (Hu et al., 2015). Sediment accretion inside each plot was quantified using Sedimentation-Erosion-Bars (SEB's) (Nolte et al., 2013) (Fig. 4.4). For each plot, two 0.6m long metal rods were inserted into the sediment with 0.15m above ground in opposite corners. During observations of sediment elevation, a spirit level was slotted onto the metal rods to create a trestle

(Fig. 4.4) and sediment elevation was quantified as the vertical distance from the spirit level to the sediment surface at five random intervals. SEB measurements were taken at the start of the experiment (May 2017), and at the end of the experiment in September 2018. Sediment accretion was calculated by subtracting the mean initial height measurements (May 2017) from the mean final measurements in September 2018.

Measurements per site

Temperature

Temperature affects key plant metabolic functions, and thereby plant growth (Kirwan & Mudd, 2012). Daily mean annual temperatures were obtained from local weather stations nearest to the study sites (Met Office, <https://www.metoffice.gov.uk>). All of the weather stations were within 10 Km of the study sites. The daily mean temperatures were then used to calculate an average annual mean temperature per site, which was used as a predictor variable in the statistical analyses.

Wave forcing

Wave forcing induces mechanical stress on newly settled seedlings and also affects sediment dynamics, which influences plant establishment and growth (Callaghan et al., 2010; Balke et al., 2011). Observations of wave height and wave periods were done in eight of the eleven sites (Supplementary Materials Table S4.1) over a two-month period during July-September 2018, by use of water pressure sensors (OSS1-010-003C-01; Ocean Sensor Systems, Inc.). Following Willemsen et al., (2018), sensors were placed on the fronting mudflats 0.05m above the seabed and set to record pressure fluctuations at 5Hz with 1-minute bursts every 10 minutes. Pressure readings were converted to water level fluctuations and used to derive bulk wave parameters, including significant wave height (H_s) and peak wave period (T_p) (Tucker & Pitt, 2001). Refer to Section B in the Supplementary Materials for more detail on the extraction of bulk wave parameters. Mean maximum wave height per site was derived

from the pressure readings, as a standard indicator of potential erosional forcing from wind-generated waves (Tonelli et al., 2010). Mean maximum wave heights were used as an indicator of the wind-wave forcing at the study sites and it was used as a predictor variable in the statistical analyses.

The presence or absence of a cliff at the lower edge of a salt marsh may be indicative of the erosional state of the site (Fig. 4.1). Given that the erosional condition of a marsh might well influence its capacity to recover from experimental disturbance, it was important to account for its effect here. We noted whether the marsh edge was cliffed or un-cliffed and entered this information into the subsequent analyses. It was not possible to simplify the overall study design by focusing only on cliffed or un-cliffed marshes, as in some regions cliffed or un-cliffed marshes were rare or absent. Clipping was not confounded by wave exposure: it occurred in both wave-exposed and wave-sheltered sites.

Mudflat sediment dynamics

To estimate sediment bed level dynamics, Surface Elevation Dynamics (SED) sensors (Hu et al., 2017) (Fig. 4.4) were deployed on the fronting mudflats in eight out of the eleven sites over the duration of the experimental period. SED's measured sediment bed level dynamics (see Supplementary Materials Section C for details). The sensors used an array of light-sensitive cells (phototransistors) to detect and measure sediment surface positions at 30-minute intervals (Hu et al., 2017). The instrument (1.1m in length) was installed firmly in the sediment, with 0.7m below and 0.4m (including phototransistors) above the sediment surface, and the ground around the instrument was checked for scouring effects. The first observation after deployment of the SED's was designated to zero-level, against which the subsequent temporal variance in sediment bed levels were expressed (Willemsen et al., 2018) (Supplementary Materials Section C).

Statistical Analyses

The analyses sought to establish which predictor variables best explained most of the variation in vegetation recovery in marshes around the UK. 'Absolute vegetation recovery' (hereafter referred to as 'AR'), which was the total re-grown plant biomass inside each of the disturbed plots at the end of the experiment (refer to 'Vegetation biomass' section of the methods for details), was used as the response variable in all statistical analyses. After careful exploratory data analyses, AR was chosen as the response variable instead of 'relative vegetation recovery' (absolute vegetation recovery divided by the initial above-ground biomass, hereafter referred to as 'RR'), due to the complex distribution of the RR variable (Supplementary Materials Fig. S4.3). One of the main disadvantages of using AR over RR is that it does not account for the natural variance in above-ground biomass between sites, which changes due to contextual variation in growth conditions. This contextual variation in growth condition could bias comparisons of vegetation recovery between sites, because biomass recovery would be greatest in the areas where above-ground biomass naturally was greater. To account for this potential bias of AR, the variable 'initial above-ground biomass' was included as a predictor in all of the analyses.

The complete list of predictor variables introduced in the model included the categorical variables 'marsh exposure to wind-generated waves' (2 levels: wave-exposed and wave-sheltered) and 'cliff' (2 levels: with a cliff or without a cliff); plus the continuous variables 'initial above-ground biomass', 'soil organic content', 'soil bulk density', 'soil conductivity' (as a proxy for salinity), 'soil clay-silt content', 'tidal range', 'elevation', 'inundation period', 'down-shore extent', 'sediment accretion' (from SEBs) and 'mean annual temperature'.

Initial exploratory data analyses using linear regression models revealed that most predictors were highly correlated (strong collinearity). Multicollinearity produces erratic signs in linear regression coefficients, thus increasing the chances of type II error and complicates the interpretation of linear regression results (Carrascal et al., 2010). Therefore, we used Partial Least Squares Regression (PLSR), which is an extension of multiple regression analysis especially suited to analyse data sets where the

set of predictors are highly correlated. PLSR is strongly shielded against both type I and type II errors (Carrascal et al., 2010). In PLSR models, associations are established with latent factors (i.e. summary variables extracted from predictors) that maximize the explained variance in the response variables. These latent factors are defined as linear combinations constructed between predictor and response variables, such that the original multidimensionality is reduced to a lower number of orthogonal factors to detect the structure in the relationships between predictor variables and between these latent factors and the response variables. The extracted factors account for successively lower proportions of original variance (Carrascal et al., 2010).

An iterative approach was used whereby, in each loop, a PLSR model was fit to a training data set, including a random sample of the 80% of the original data set. The remaining 20% of data points were used as a validation data set. For each iteration the Variable Importance in Projection (VIP) was also calculated. VIP scores are useful in understanding which predictor variables are the ones that best explain the variance in the response variable (Farrés et al., 2015). The entire procedure was repeated 1000 times (with a new random sample of the 80% of the original data set in each iteration), after which we calculated average model coefficients, average variance explained by the models, average number of components retained and average VIP scores for each variable.

The R packages *p/s* (Mevik et al. 2019) and *caret* (Kuhn, 2008) were used to perform the PLSR models. All statistical analyses were performed in the open-source statistical software R (R Core Development Team 2017).

Results

Plot disturbance treatment (AG vs ABG) did not contribute significantly to the PLSR explanation of absolute vegetation recovery (Figs. 4.5- 6). Absolute vegetation recovery was most strongly influenced by four predictor variables, as indicated by the Partial Least Squares Regression (PLSR) (Fig. 4.5): sediment accretion, mean annual temperature, initial above-ground biomass and the clay-silt fraction in the sediment, all of which positively influenced vegetation recovery (Fig. 4.5). The PLSR fit two components in 72% of 1,000 model runs (Supplementary Materials Fig. S4.4), and both components together explained an average of 48% of the variance in absolute vegetation recovery across the UK (Figs. 4.5- 6). There was evidence of geographical variation in marsh resilience (Fig. 4.7). Given that PLSR component 1 was positively related to sediment accretion, mean annual temperature, initial above-ground biomass and the clay-silt fraction in the sediment (Fig. 4.6), the relationship depicted in Figure 4.7 can be interpreted as a north-west to south-east gradient in marsh resilience due to these four marsh characteristics.

The influence of two additional predictor variables 'wave forcing' and 'mudflat sediment dynamics' on absolute vegetation recovery were tested in a separate PLSR model, because these were only obtained from a subset of the study sites (Supplementary Materials Table S4.1). Wave forcing and mudflat sediment dynamics had a limited effect on absolute vegetation recovery, as indicated by their low VIP scores (Supplementary Materials Section D). Sediment accretion mean annual temperature, initial above-ground biomass and the clay-silt fraction in the sediment were once again amongst the most important factors influencing absolute vegetation recovery, and hence the 1st component on the PLSR (Supplementary Materials Section D), similarly to the PLSR with the full data set. For this subset, tidal inundation period, soil salinity and soil bulk density were also important predictors of absolute vegetation recovery (Supplementary Materials Section D). The north-west to south-east gradient in absolute vegetation recovery to predictor variables was even more marked (Supplementary Materials Section D) than in the main analysis (Fig. 4.7).

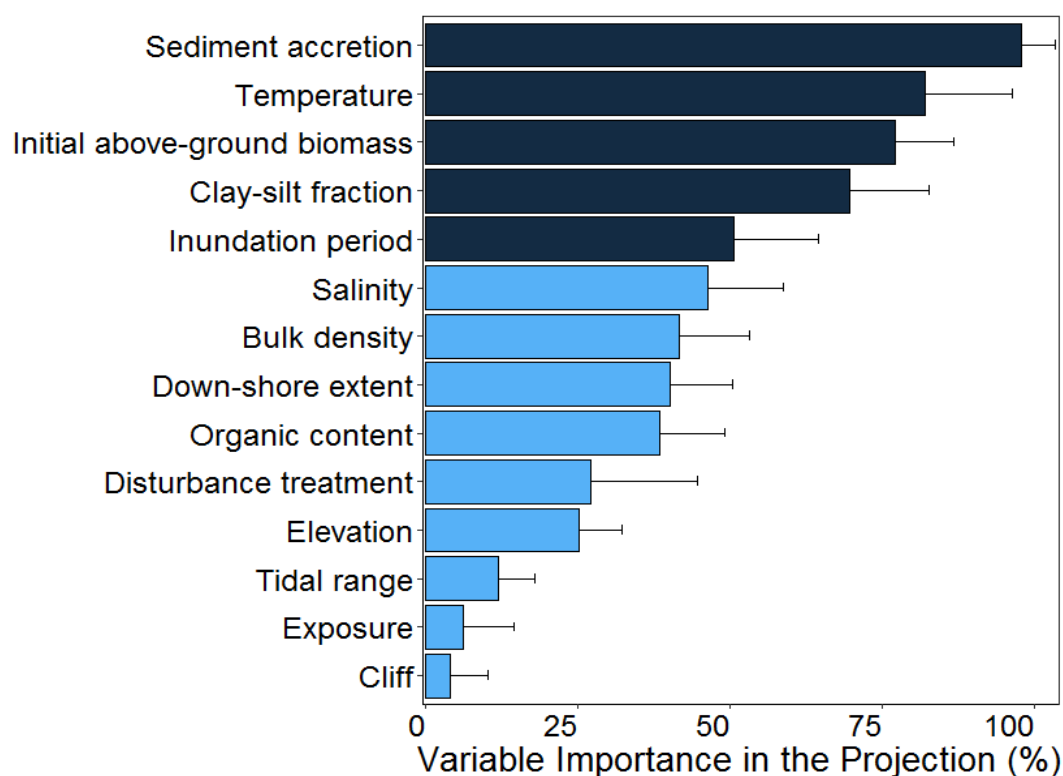


Fig 4.5. Influence of the predictor variables on absolute vegetation recovery, as indicated by the Partial Least Squares Regression (PLSR). Bars show the mean \pm std. error Variable Importance in the Projection (VIP) (% of importance) for each predictor variable in 1,000 PLSR model runs. Variables with large VIP values were consistently relevant to explaining absolute vegetation recovery in the 1,000 PLSR model runs. Dark blue bars represent predictor variables with a VIP >50%, whilst the pale blue bars represent predictor variables with VIP <50%.

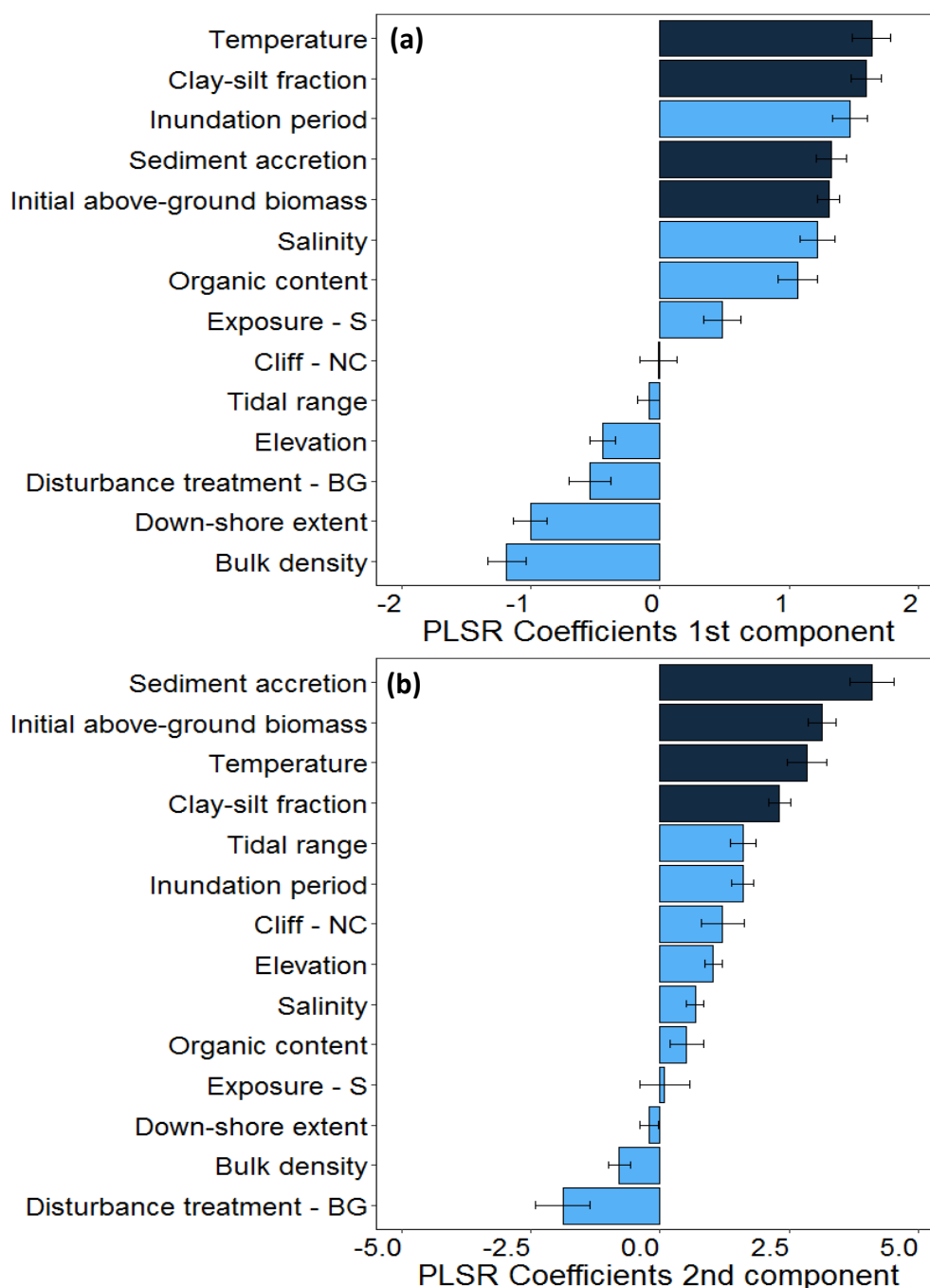


Fig 4.6. The mean \pm std. error regression coefficients of each predictor variable in the (a) first and (b) second components of the PLSR analysis, after 1,000 PLSR model runs. Bars show that positive coefficients loaded positively with absolute vegetation recovery, whilst negative coefficients contributed negatively to the loading of the response variable (Fig. 4.7). Dark blue bars represent the most important predictor variables (VIP>50%), whilst the pale blue bars represent less important predictor variables (VIP <50%). For categorical variables cliff, exposure and disturbance treatment, the appropriate levels are shown. For example, BG disturbance treatments contributed negatively to the loading of the response variable, whilst marshes with no cliffs contributed positively.

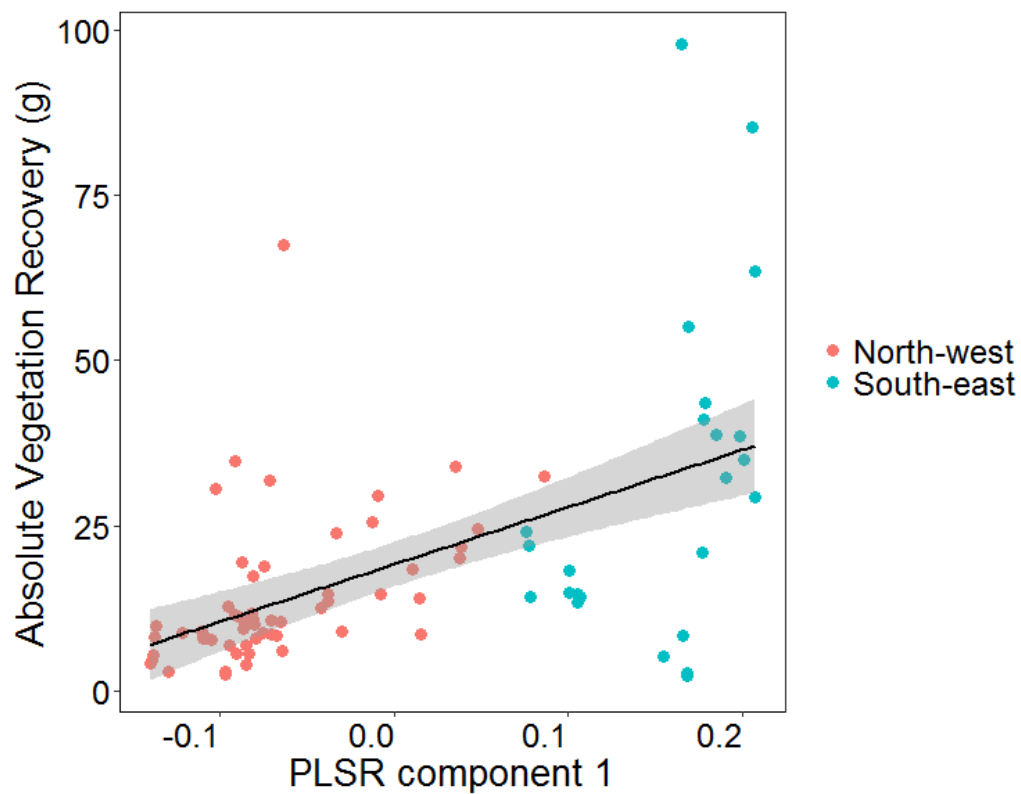


Fig 4.7. Relationship between absolute vegetation recovery and component 1 of PLSR analysis. PLSR component 1 was positively related to sediment accretion, mean annual temperature, initial plant above-ground biomass and the clay-silt fraction in the sediment, the higher the value of these variables the better the vegetation recovered after disturbance. Every observation represents a single 0.3m² vegetation removal plot. Grey shading represents the 95% confidence intervals.

Discussion

This study shows that salt marsh resilience, in the form of vegetation recovery after disturbance, can vary predictably over large scales due to geographical changes in extrinsic and intrinsic system characteristics. Variation in salt marsh vegetation recovery across the UK was explained by geographical differences in sediment accretion, mean annual temperature, initial above-ground biomass and the clay-silt fraction in the sediment. Disturbed patches of *Spartina* recovered better at sites with greater sediment accretion, higher annual mean temperatures, muddier sediments and bigger initial above-ground biomass, which were characteristics that increased from north-west to south-east regions of the UK, implying that resilience was boosted by a decreasing latitude. Our findings have important implications for predicting marsh resilience to large-scale climatic drivers including warming temperatures and sediment dynamics.

Whilst marsh resilience to climate threats, including sea level rise and storminess, are discussed extensively in the literature (Kirwan et al., 2016; Leonardi et al., 2016; Mariotti & Carr, 2014), few studies have considered the direct effects of global warming on marshes (Gray & Mogg, 2001; Loebl, Van Beusekom, & Reise, 2006; Charles & Dukes, 2009). Warming experiments in vegetated systems including salt marshes (Gray & Mogg, 2001; Loebl, Van Beusekom, & Reise, 2006; Charles & Dukes, 2009), seagrasses (Olsen et al., 2012) and mangroves (Alongi, 2015; Coldren et al., 2016), consistently reveal that higher temperatures can have a positive influence on vegetation. Temperature directly affects metabolic rates and plant primary productivity, which ultimately affects the overall plant biomass production at a site (Megonigal et al., 2016). Temperature effects on vegetation biomass have been observed across latitudinal gradients in coastal wetlands, including salt marshes (Kirwan, Guntenspergen, & Morris, 2009), seagrasses (Soissons, 2013) and mangroves (Saenger & Snedaker, 1993). For example, biomass production of the salt marsh plant *Spartina alterniflora* increased along a north to south latitudinal gradient in North America (Kirwan et al., 2009). We also found the same to be true in our study, but in addition, we show that temperature and its effect on vegetation biomass,

in combination with other factors, also explain large-scale differences in vegetation recovery after disturbance, which to our knowledge has not yet been discussed in the literature.

This study found that the sediment accretion (or erosion) inside the disturbed plots had an effect on vegetation recovery. Previous studies have shown that net sediment changes have significant implications for seedling establishment and growth (Balke et al., 2014; Bouma et al., 2016; Willemssen et al., 2018), and in the present study we build on this by suggesting that, in combination with other factors, they also affect vegetation recovery after disturbance. Marshes with sediment accretion inside the disturbed plots recovered better after disturbance than marshes with eroding sediments. This is not surprising, as sediment erosion poses one of the greatest threats to seedling establishment by uprooting and dislodging the newly settled seedlings (Balke et al., 2013; Bouma et al., 2016; Cao et al., 2018). In addition, sediment accretion has also been shown to negatively impact seedling establishment and growth by causing smothering of the newly settled seedlings (Balke et al., 2013), but in this study we found that it had a positive effect on vegetation recovery after disturbance. As sediment elevation changes are driven by important interactions between the biological and physical processes (so called 'bio-physical interactions'), it is important to note the important role that the vegetation plays in influencing sediment elevation changes (Mariotti & Fagherazzi, 2010; Corenblit et al., 2011; Deegan et al., 2012).

Vegetation biomass stimulates sediment build-up and hence accretion, the effect of which is illustrated in Figure 4.8. Studies have previously shown that marshes with denser vegetation canopies dissipate wave energy more effectively, which may lead to the potential for more sediment build-up, given sufficient sediment supply (Bouma et al., 2005, 2009; Van Hulzen, Van Soelen, & Bouma, 2007; findings of Chapter 2). In contrast, marshes with lower vegetation densities may be more prone to sediment erosion (Fig. 4.8) (Bouma et al., 2005, 2009; Van Hulzen, Van Soelen, & Bouma, 2007).

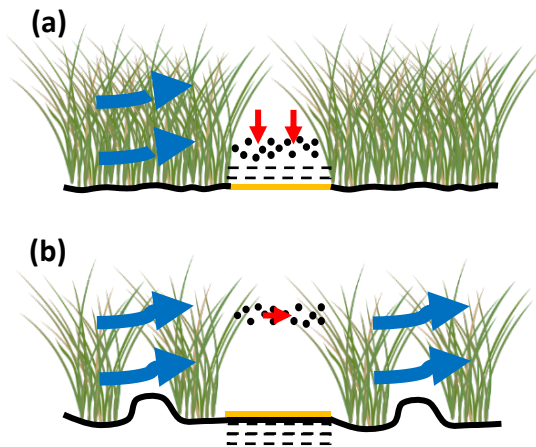


Fig 4.8. Schematic representation of the bio-physical feedbacks that might have led to vegetation recovery inside the disturbed patches. (a) Dense vegetation; wave energy is attenuated leading to sediment capture and accretion inside the disturbed patches. (b) Sparse vegetation; limited wave attenuation and as a result the energy carries through the canopy leading to less sediment capture and consequent erosion inside the disturbed patches. Orange lines represent the disturbed patches inside the vegetation. Blue arrows represent the energetic water flow and red arrows represent the direction of the suspended sediment (settlement in dense patches but movement in sparse patches). Dashed black lines represent the sediment dynamics (build-up in dense vegetation but erosion in sparse vegetation).

Salt marshes with higher fractions of clay-silts in their sediments were more resilient than marshes with lower fractions of clay-silts in their sediments. Salt marsh plants grow better in muddier sediments, in contrast to sandier sediments (Huckle et al., 2000; Van Hulzen et al., 2007). For example, Huckle et al., (2000) found that coarse-grained sandy sediments mostly inhibited plant growth, whilst fine-grained muddy sediments encouraged plant growth because individual plants found it difficult to anchor their roots into the looser sandy sediment. Other studies have demonstrated that muddier sediments tend to be more organically rich than sandier sediments, again promoting plant growth (Ford et al., 2016). As well as aiding the growth of individual plants, muddier sediments (i.e. with higher fractions of clay-silts) also tend to be more stable than sandier sediments (Defew et al., 2002; Bouma et al., 2016; Willemsen et al., 2018), which is an important factor controlling marsh growth (Balke et

al., 2014). Van Hulzen et al., (2007) found that denser *Spartina* canopies occurred lower down the shore in muddier sediments, whilst Willemsen et al., (2018) showed that marsh plants extended lower down the shore in more stable muddy sediments, both of which indicate greater resilience to disturbance. Sediment type is the main factor determining the erodibility of the sediment making marshes with higher clay-silt sediments more resistant and therefore stable in the face of erosional stressors (Deegan et al., 2012). Sediment type is typically the result of the hydrodynamic setting at a site, as marshes in more energetic settings tend to have coarser sediments whilst marshes under low forcing tend to have finer sediments (Komar, 1976). However, differences in sediment type between sites may also be indicative of the source of the sediment (May & Hansom, 2003). Marshes on the south-east coast of the UK receive most of their muddy sediment from fluvial sources, whilst marshes on the north-west coast receive most of their coarse sediments from offshore sources (May & Hansom, 2003). Apart from the known influence of sediment type on the resistance of salt marshes to erosion, with this study we show that sediment type further influences another component of salt marsh resilience, in this case salt marsh vegetation recovery.

We found a limited effect of tidal inundation on vegetation recovery in this study, despite the fact that inundation periods ranged up to 47% between sites (Supplementary Materials Fig. S4.5). Even though the regression coefficients from PLSR analyses for inundation were small (Fig. 4.6), they were positive, suggesting a positive relationship of vegetation recovery with tidal inundation period. This is surprising, given that previous studies have suggested that inundation is the main stress operating against salt marsh growth (Balke et al., 2016; Willemsen et al., 2018) and recovery (van Belzen et al., 2017). In our study, tidal inundation period increased along the same latitudinal gradient as mean annual temperature (Supplementary Materials Fig. S4.6), sediment accretion, the clay-silt fraction in the sediment and initial above-ground biomass from the north to the south of the UK, as marshes on the south-east coast extend lower down the shore than marshes in the north-west (Supplementary Materials Fig. S4.5; findings of Chapter 3). It is possible that by having a higher vegetation biomass, salt marshes in the south (where tidal inundation is highest) are more resilient to tidal inundation stress

by having denser vegetation. Another explanation for our results is that the combination of mean annual temperature, sediment accretion, initial above-ground biomass and the clay-silt fraction in the sediment override the effect of inundation period as an important stressor of salt marsh recovery. In addition, van Hulzen et al., (2007) suggested that sediment accretion is strongly related to inundation time, as marshes that are inundated for longer accrete more sediment, as a result of increased availability of suspended sediment concentrations (Temmerman et al., 2003). It might well be that sediment elevation change is a more proximal driver of salt marsh recovery, while inundation period is merely a distal driver.

In conclusion, our results indicate that a combination of abiotic (sediment accretion, mean annual temperature, clay-silt fraction in the sediment) and biotic variables (initial above-ground biomass) drive vegetation recovery in salt marshes along the coasts of the UK. In our study sites, these predictor variables cannot be seen as independent since they all change concomitantly along a latitudinal gradient. Therefore, the combination of sediment accretion, mean annual temperature, clay-silt fraction in the sediment and initial above-ground biomass can be understood together as a latitudinal effect on vegetation recovery potential following a disturbance. Our findings therefore have important implications for predicting vegetation recovery potential in other ecosystems exposed to large-scale gradients in bio-physical drivers.

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SUPPLEMENTARY MATERIALS FOR CHAPTER 4

Supplementary Materials Section A

Additional tables and figures to support the main text.

Table S4 .1. Details of the selected salt marsh sites within each geographical region of the United Kingdom.

Wider Region	Region	Marsh	Exposure	Co-ordinates	Wave data (Y/N)	Average maximum significant wave height (m)	Sediment data (Y/N)
North-west	Solway	Southerness	Exposed	54.8792, -3.6596	Y	0.57	N
			Sheltered	54.0038, -2.8967	N	N	Y
	Morecambe	Sunderland Lades	Exposed	54.0011, -2.8746	N	N	Y
			Sheltered	53.2991, -4.1772	Y	0.35	Y
	Red Wharf Bay	RWBE	Exposed	53.2977, -4.2119	Y	0.19	Y
			Sheltered	52.9157, -4.1112	Y	0.49	Y
	Sarnau	Glaslyn Cob Curian	Exposed	52.7329, -4.0193	N	N	Y
			Sheltered				
South-east	Kent	Swale Elmley	Exposed	51.3576, 0.9181	Y	0.20	Y
			Sheltered	53.3703, 0.7957	Y	0.35	N
	Southampton	Hythe	Exposed	50.8621, -1.3843	Y	0.27	N
			Sheltered	50.7853, -1.3889	Y	0.09	Y

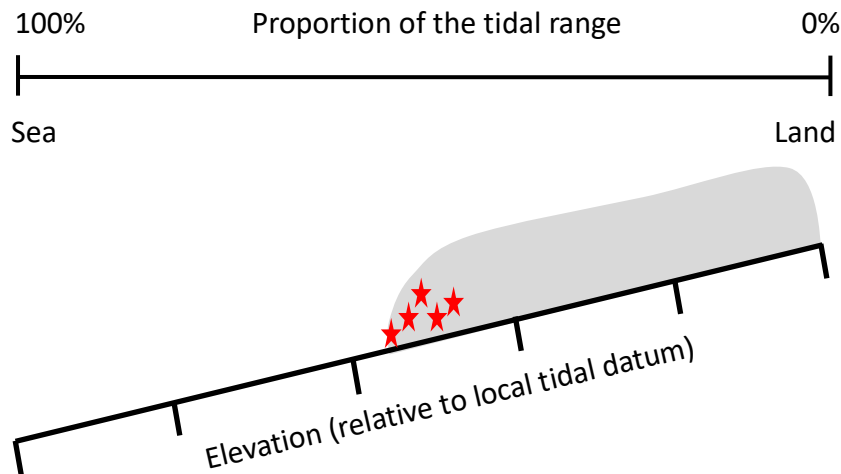


Fig S4.1. Method for calculating the 'down-shore extent (DSE)' predictor variable. Red stars represent the position of the plots on the lower marsh (greyed area). The measured elevation of the plots (relative to local tidal datum) was divided by the regional tidal range and used to calculate their positions in the tidal frame.

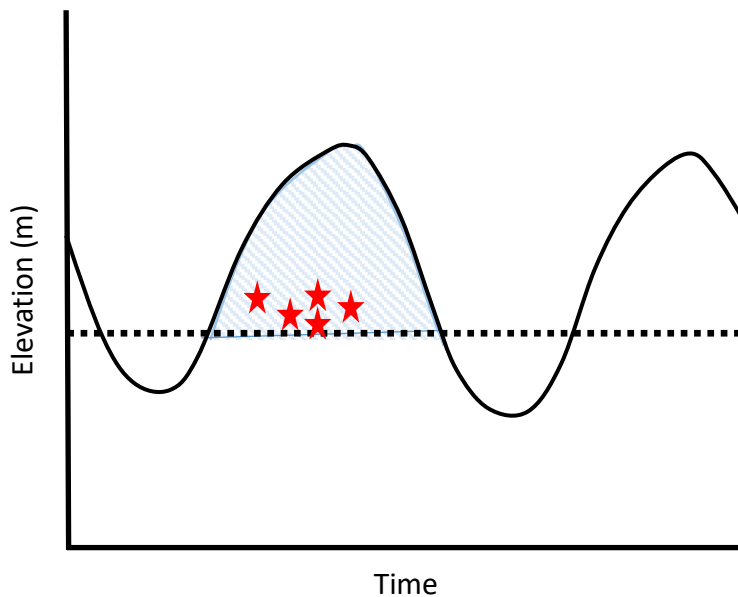


Fig S4.2. Method for calculating the 'inundation period' predictor variable. Red stars represent the position of the plots in the tidal frame. The measured elevation of the plots was referenced to local tidal charts over twelve months to estimate the percentage of time that the plots were inundated (blue hatched area).

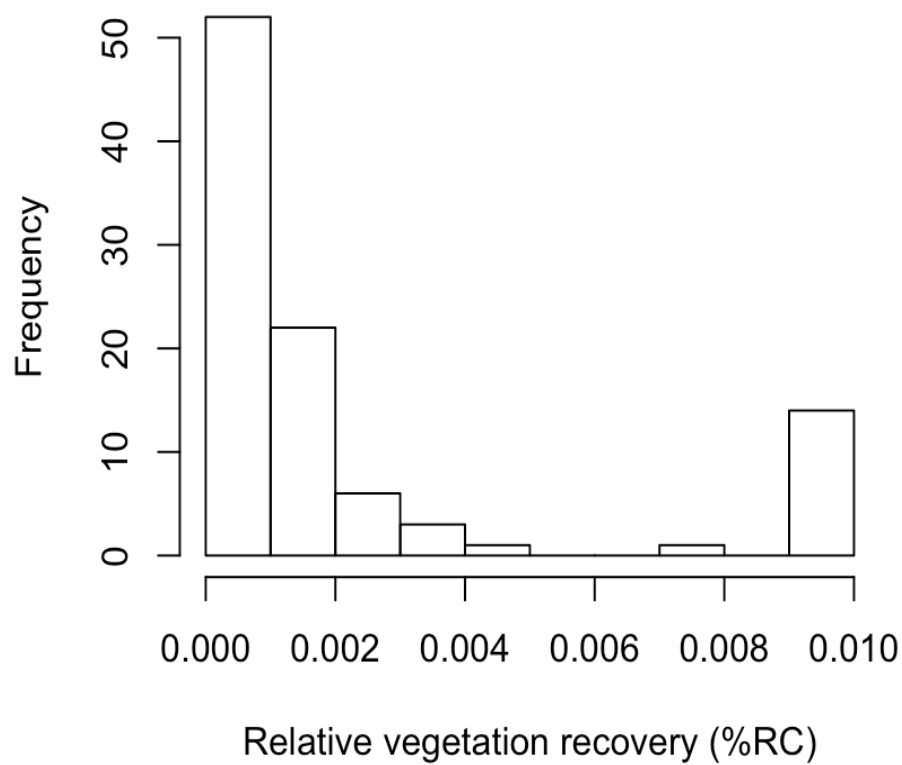


Fig S4.3. Histogram of the distribution of the 'relative vegetation recovery (RR)' response variable.

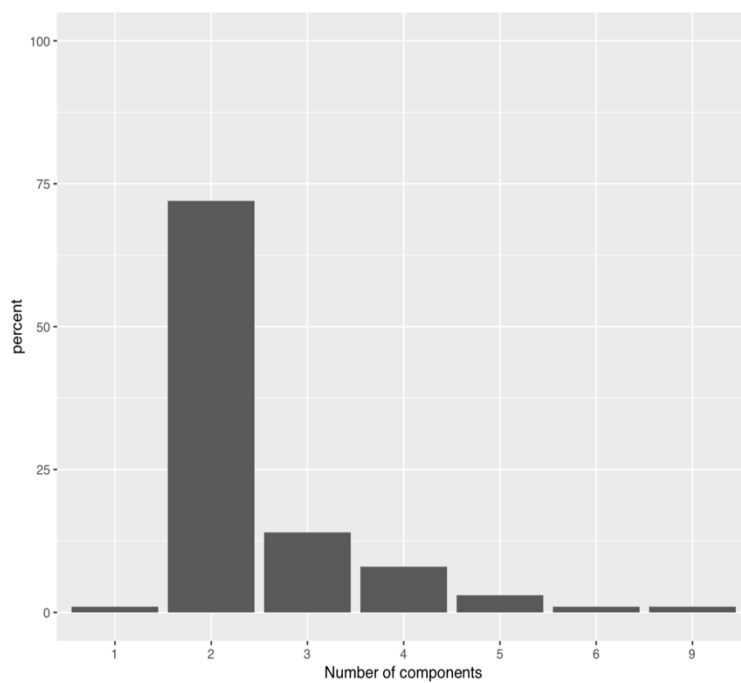


Fig S4.4. Percent frequency of one to nine components in the PLSR analysis after 1,000 model runs. The great majority of models included two PLSR components.

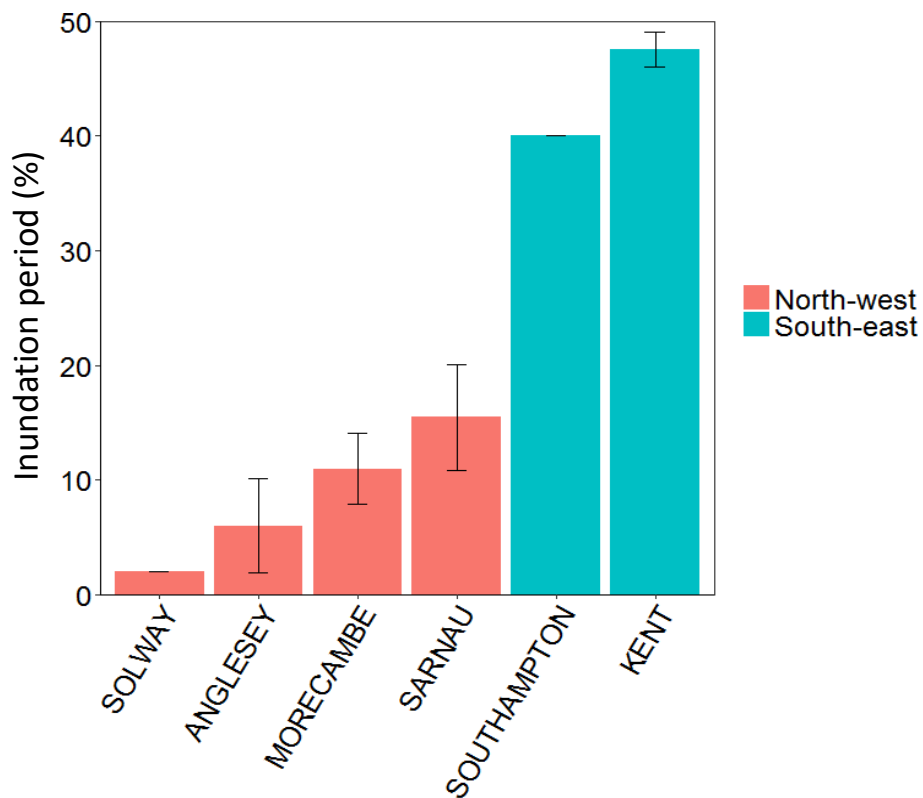


Fig S4.5. The mean \pm std. error inundation period at the marsh edge within the six geographical regions of the UK, from the north-west to the south-east. Means represent two salt marsh sites per region, except in the Solway and Southampton regions where there was only one study site at the end of the experiment (hence lack of error bars).

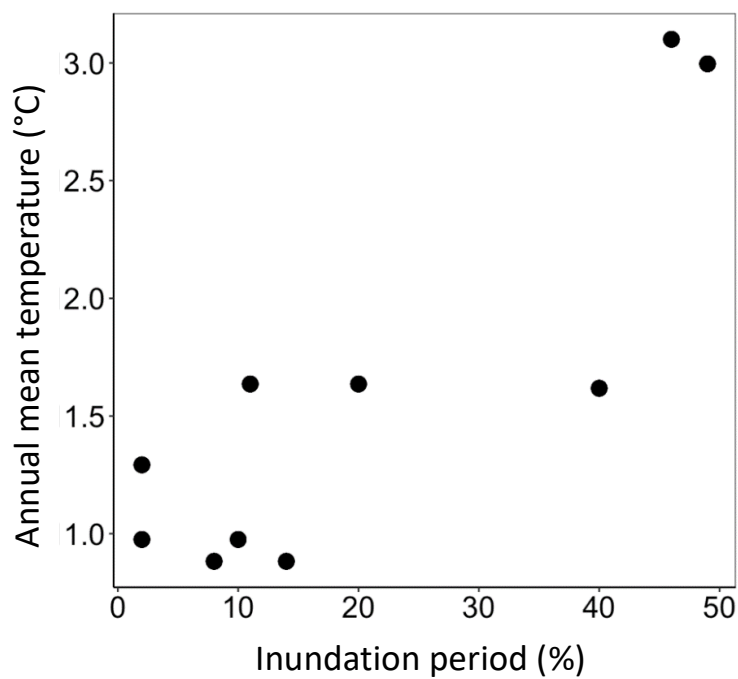


Fig S4.6. Relationship between inundation period and the mean annual temperature across the UK study sites.

Supplementary Materials Section B

Wave forcing measurements

We quantified differences in wave forcing by deploying pressure sensors (OSSI-010-003C-01; Ocean Sensor Systems, Inc.) (Fig. S4.7) simultaneously at the sites over 1 month during September-October 2018. The pressure sensors were placed 0.05m above the seabed, and they measured at a burst frequency of 5Hz for 1-minute at 10-minute intervals, following methods by Willemsen et al., (2018). The mean water level in an interval was determined by averaging all of the data points. The wave analysis was based on pressure fluctuations. The attenuation of the pressure signals with water depths was corrected to derive bulk wave parameters, e.g. significant wave height (H_s) (Figs. S4.8- 15) (Tucker & Pitt, 2001). Mean maximum wave heights were used as an indicator of the wind-wave forcing at the study sites and it was used as a predictor variable in the statistical analyses. The results of the wave observations are shown in Figures S4.8– 15.



Fig S4.7. Pressure sensor deployed at one of the study sites.

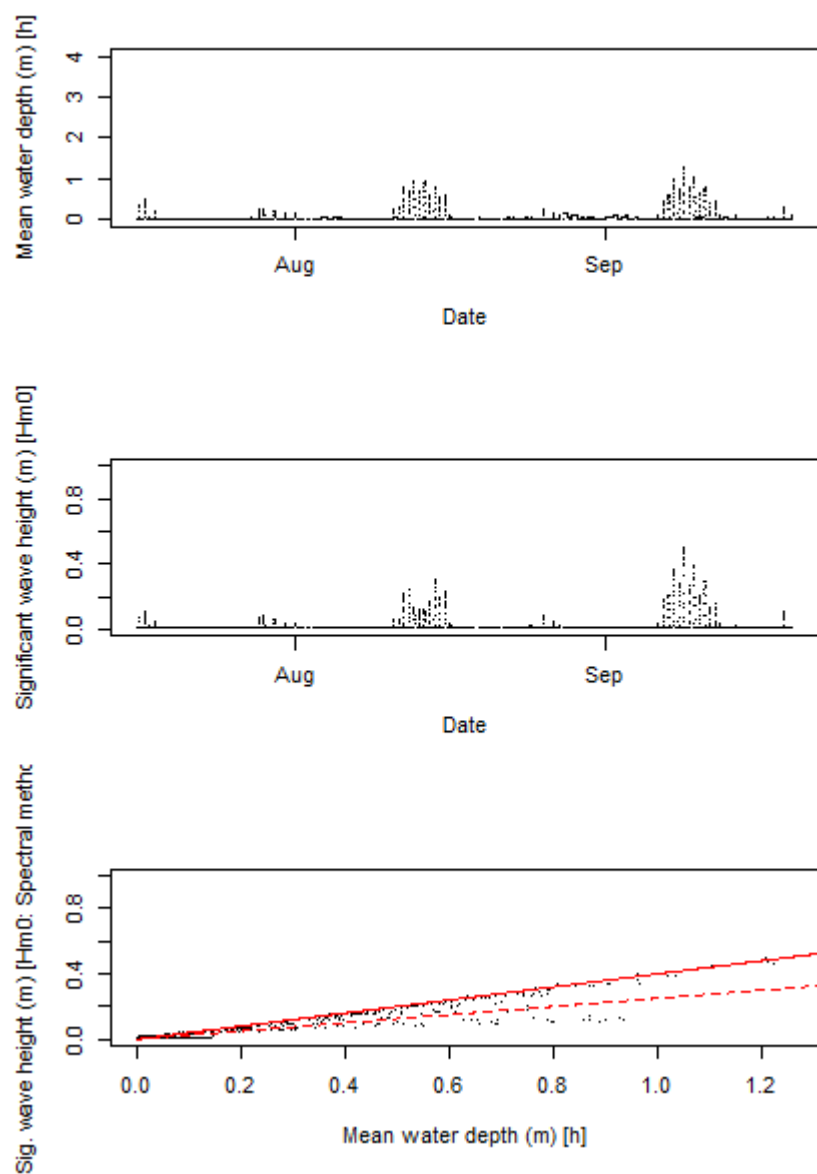


Fig S4.8. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Southernness site (Solway region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

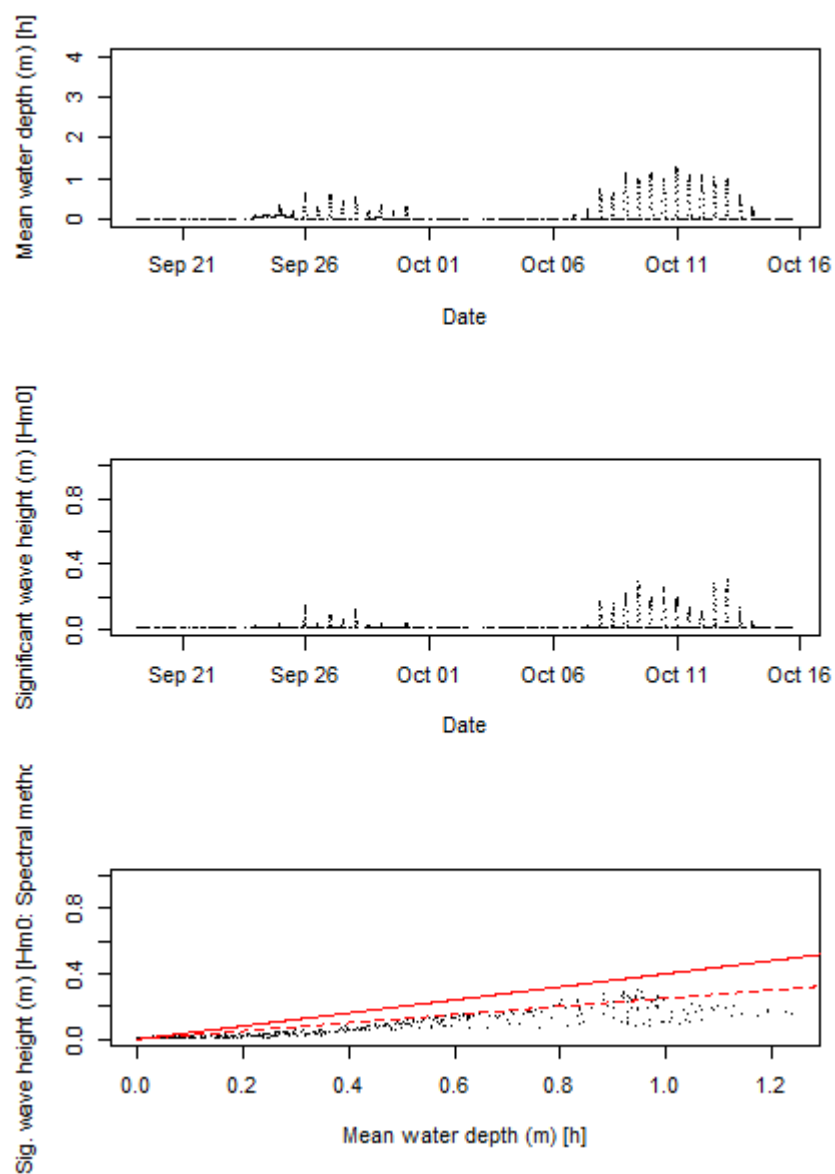


Fig S4.9. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Red Wharf Bay Exposed site (Anglesey region)** over the observation period (September-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

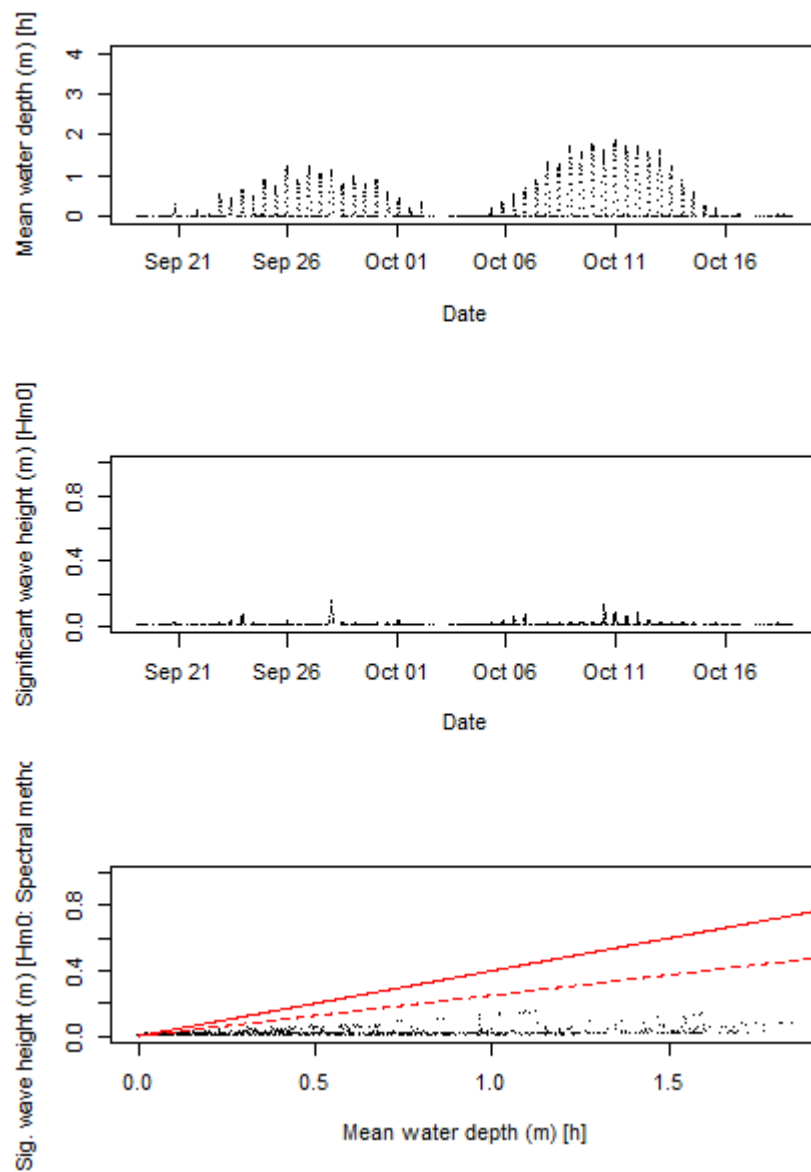


Fig S4.10. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Red Wharf Bay Sheltered site (Anglesey region)** over the observation period (September-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

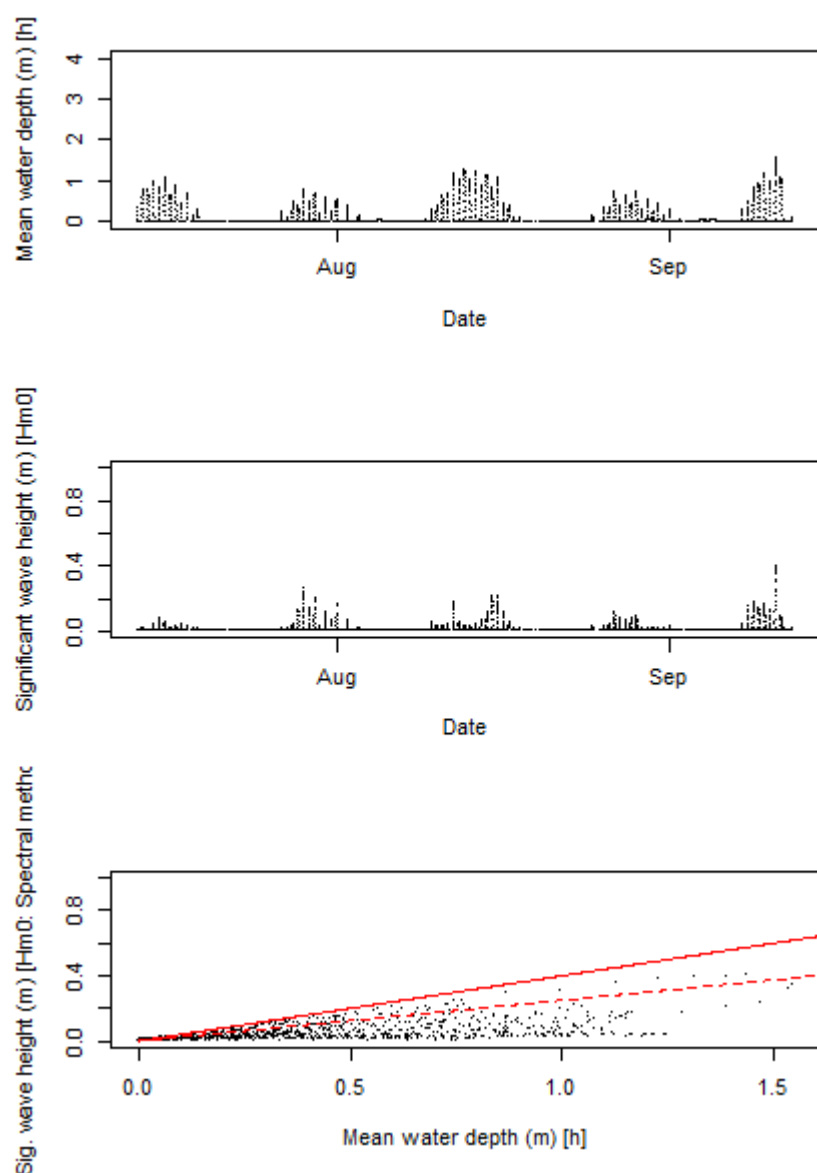


Fig S4.11. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Glaslyn Cob site (Sarnau region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

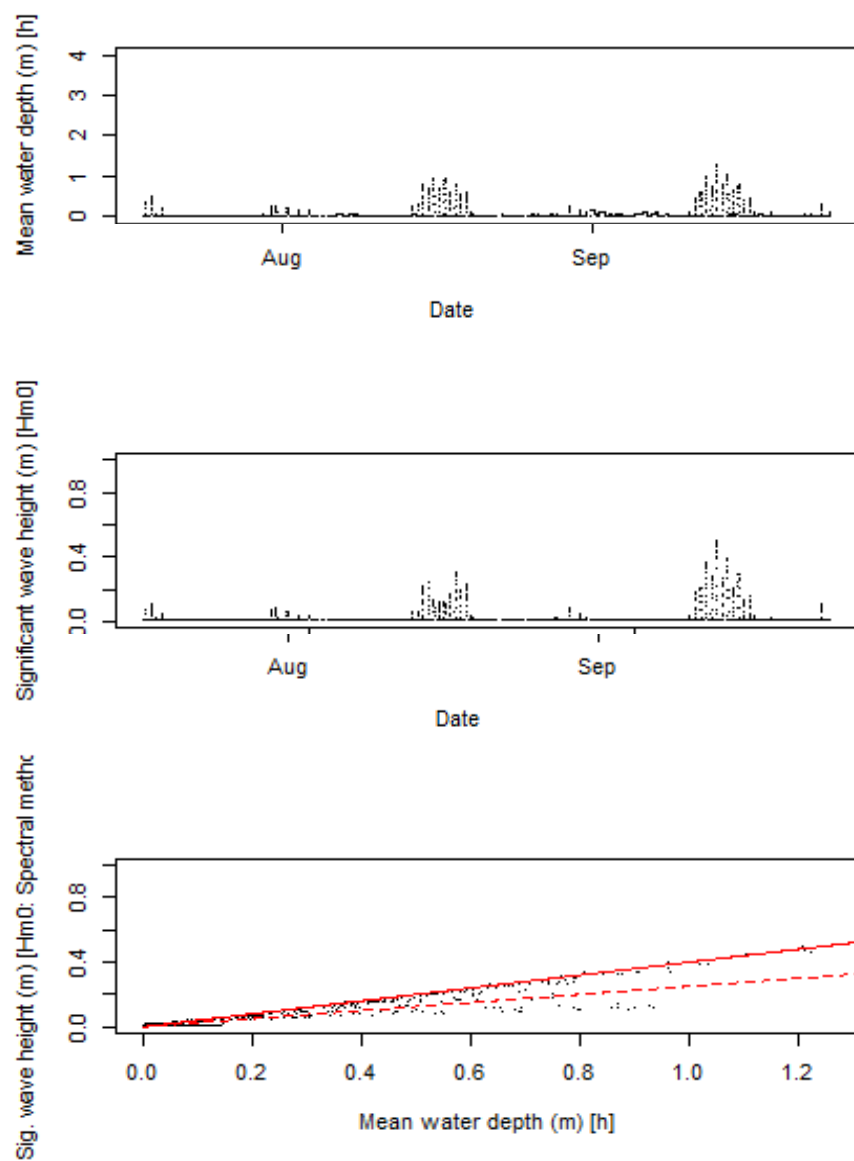


Fig S4.12. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Hythe site (Southampton region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

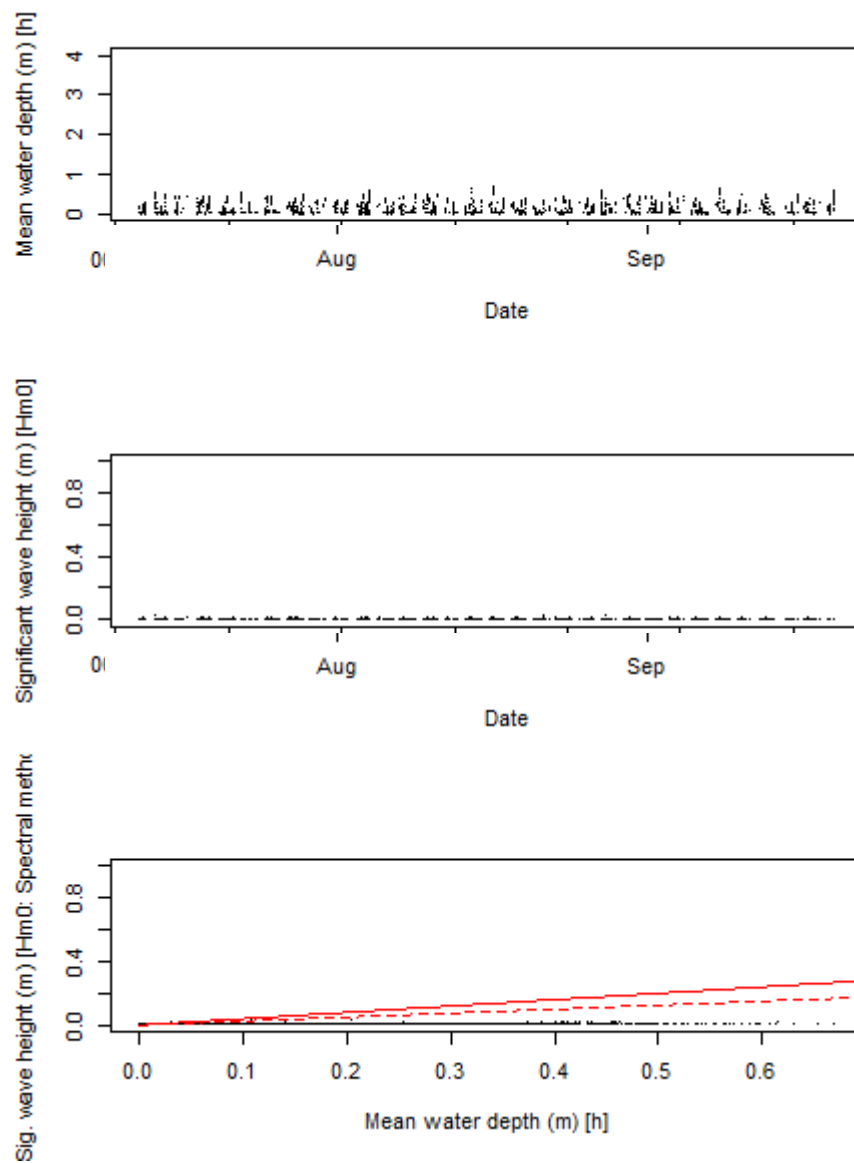


Fig S4.13. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Exbury site (Southampton region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

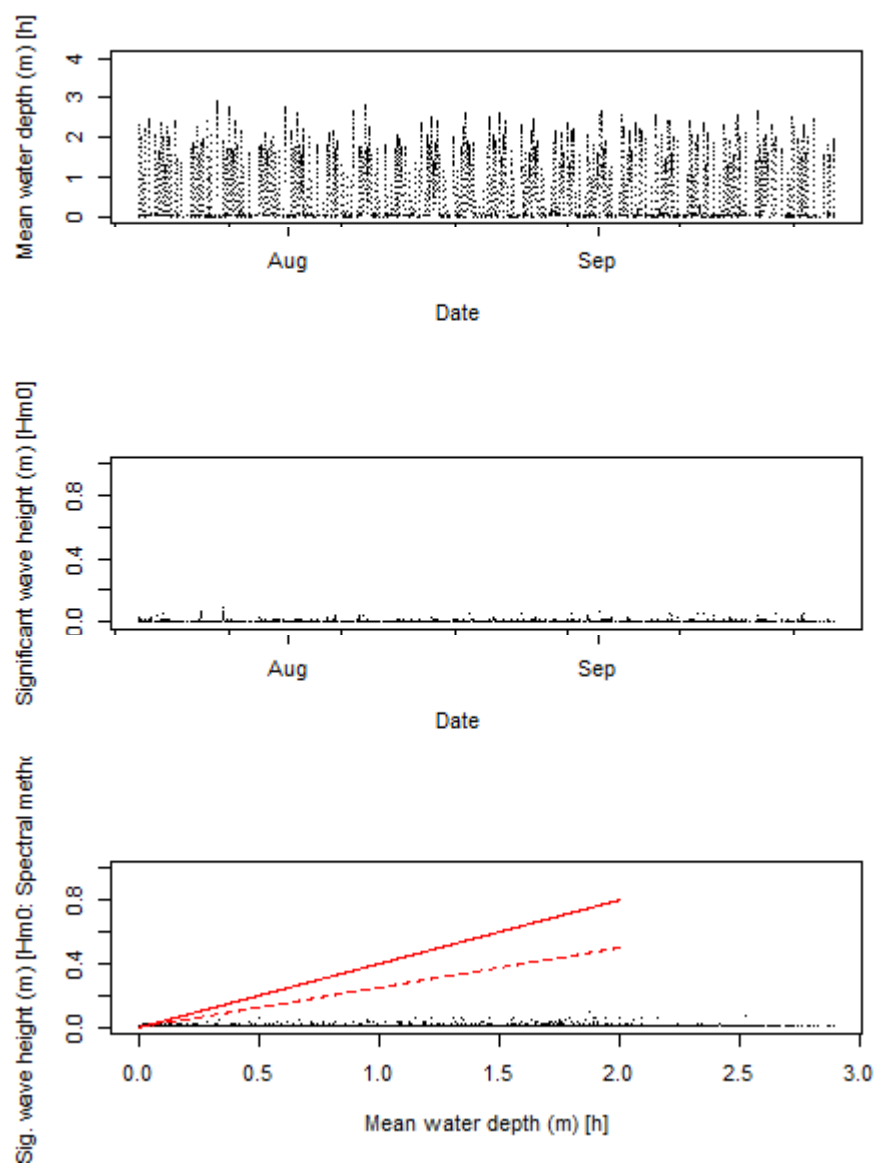


Fig S4.14. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Elmley site (Kent region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

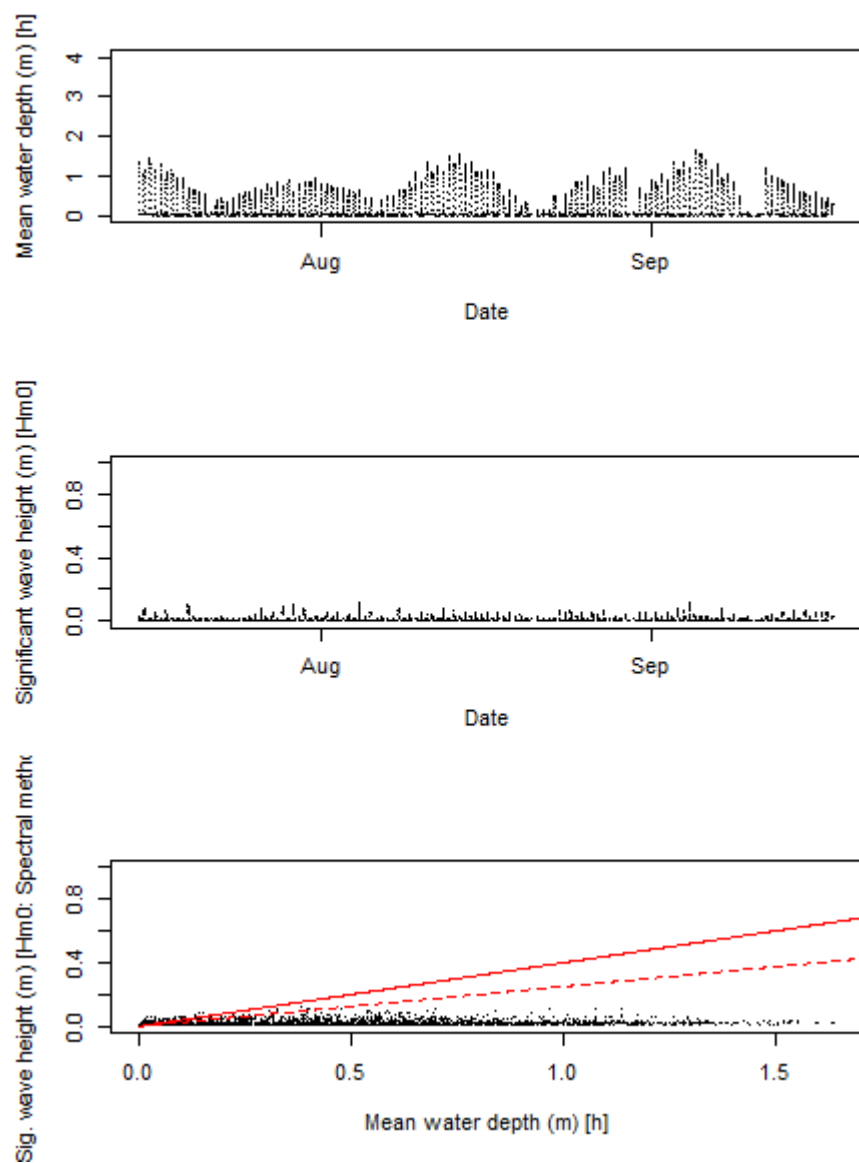


Fig S4.15. Mean water depths and significant wave heights, which was used as a measure of wind-wave forcing between sites, measured at the **Swale site (Kent region)** over the observation period (July-October 2018). The solid red line represents the interquartile range (IQR) and the dashed red line represents the median of the data in the wave heights plot.

Supplementary Materials Section C

Mudflat sediment dynamics measurements

We quantified differences in mudflat sediment dynamics by deploying SED (Surface Elevation Dynamics) sensors (Hu et al. 2017) (Fig. S4.16) on the mudflats in front of the marsh-mudflat boundaries in seven out of the eleven sites over the duration of the experimental period (Table S4.1 for details). The sensor, measuring 1.1m, used an array of light sensitive cells (phototransistors) to detect and measure sediment surface positions (Hu et al., 2015). The instrument was installed firmly in the sediment, with 0.7m below and 0.4m (including phototransistors) above the sediment surface. Sediment surface positions were measured every 30 minutes. Following methods by Willemsen et al. (2018), we made the first obtained measurement equal to zero and referred all other bed measurements to this first point to calculate the variance of the sediment measurements (Figs. S4.17-20). The results of the SED observations are shown in Figures. S4.17– 20.



Fig S4.16. SED sensor deployed on the mudflat at one of the study sites.

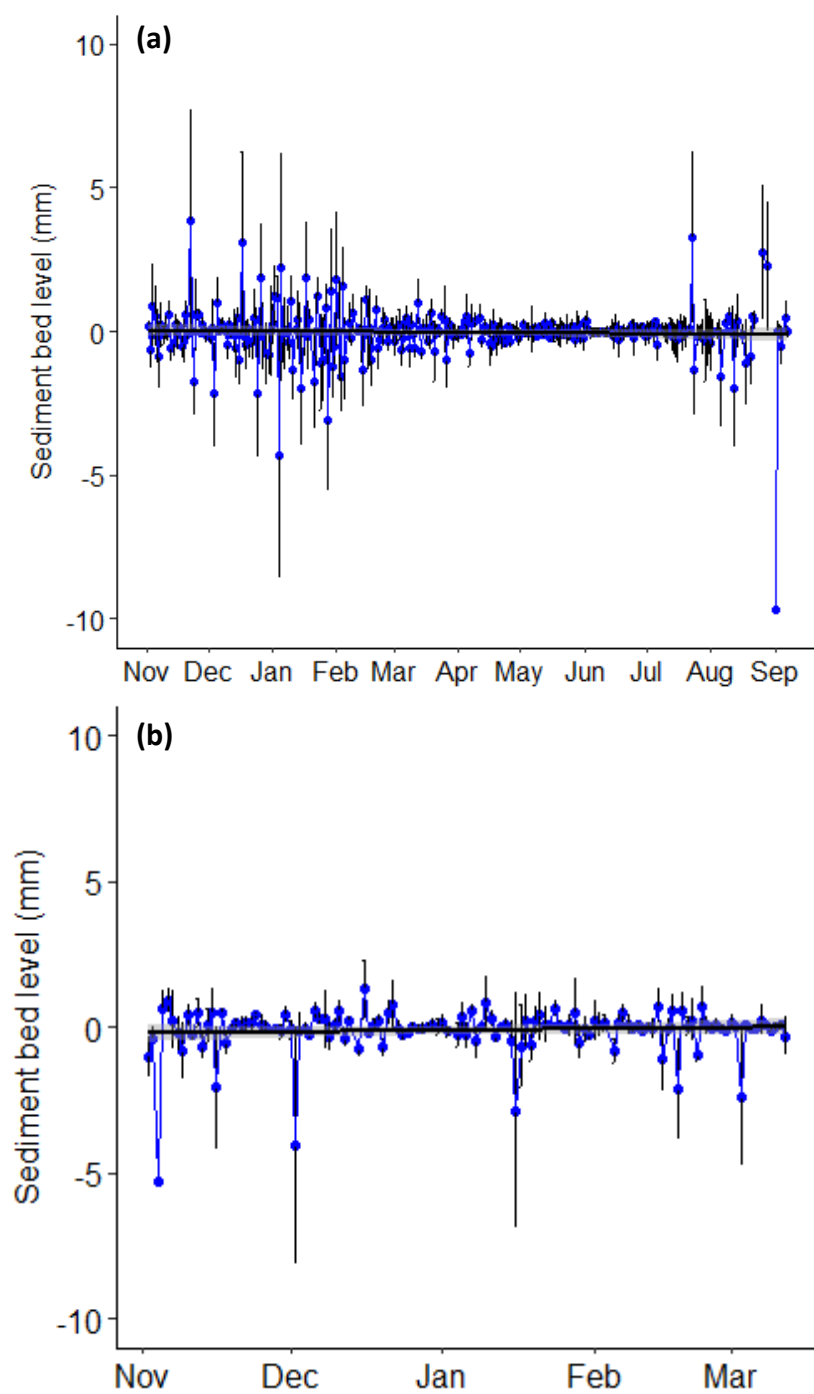


Fig S4.17. Sediment bed level changes measured by SED sensors on the fronting mudflat at the **(a) Lades** and **(b) Sunderland sites in the Morecambe region** over the observation period. Each solid circle represents the daily mean \pm sd.error.

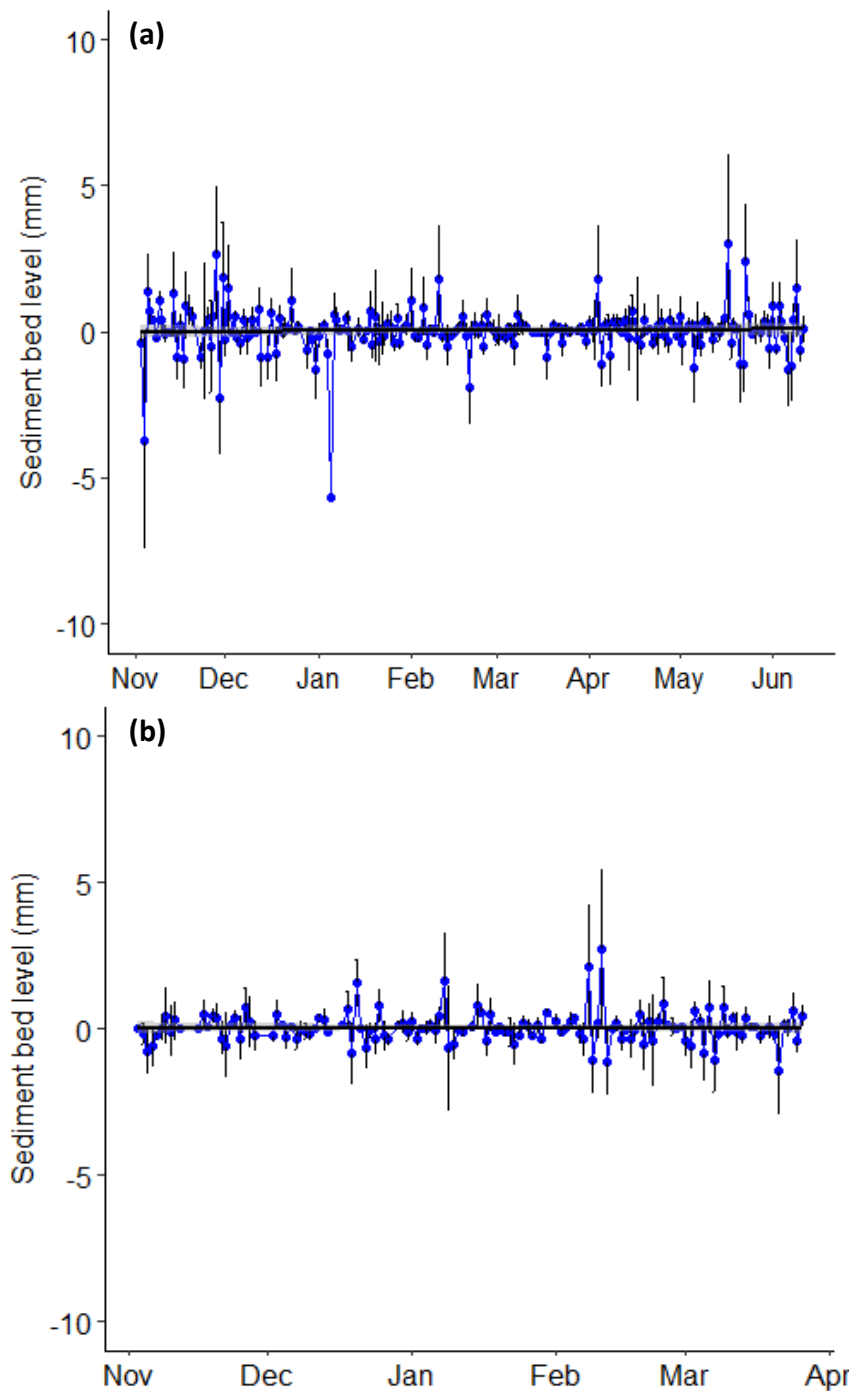


Fig S4.18. Sediment bed level changes measured by SED sensors on the fronting mudflat at the **(a) Curian** and **(b) Glaslyn Cob** sites in the **Sarnau region** over the observation period. Each solid circle represents the daily mean \pm sd.error.

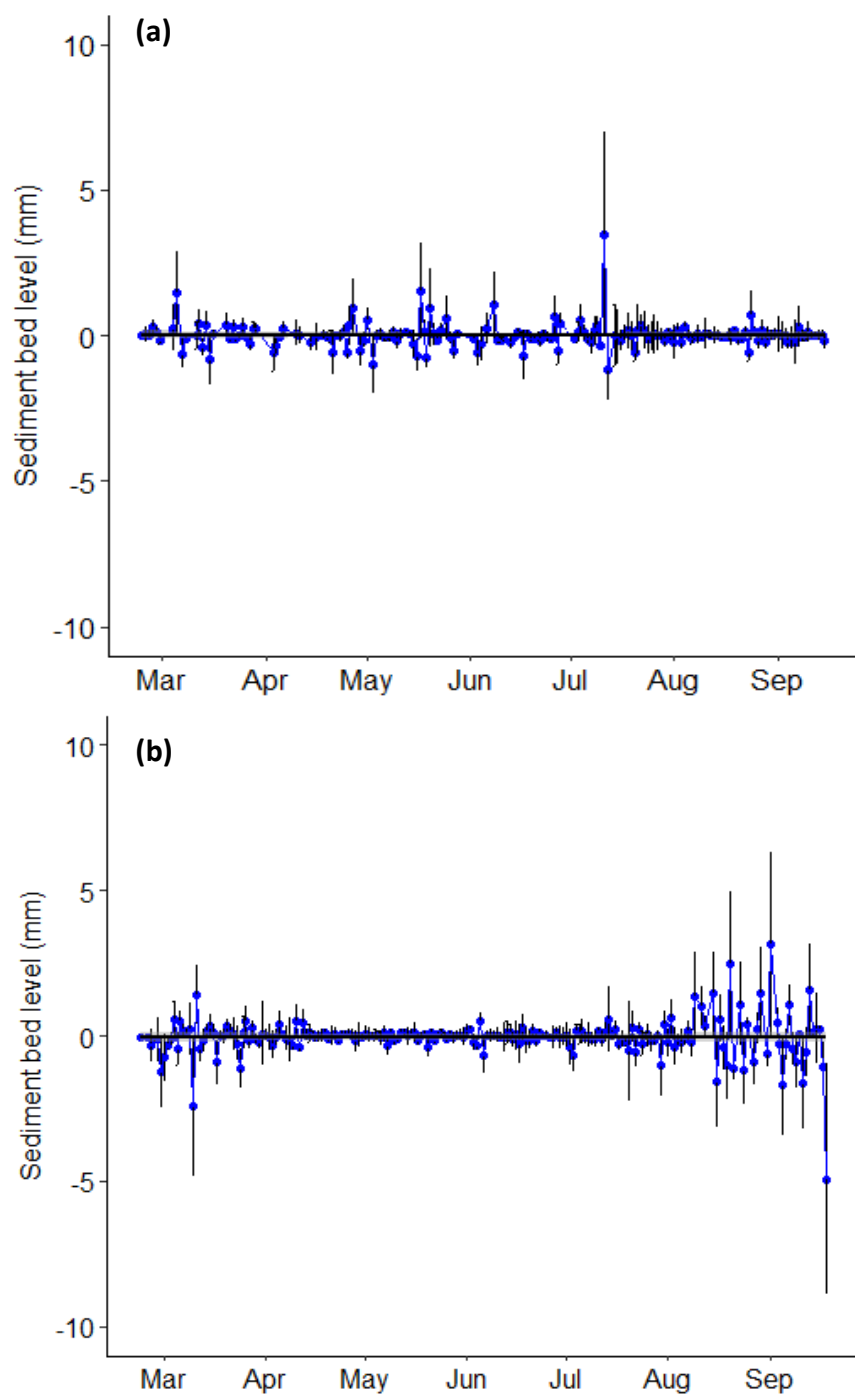


Fig S4.19. Sediment bed level changes measured by SED sensors on the fronting mudflat at the **(a) Exbury site (Southampton region)** and **(b) Swale site (Kent region)** over the observation period. Each solid circle represents the daily mean \pm sd.error.

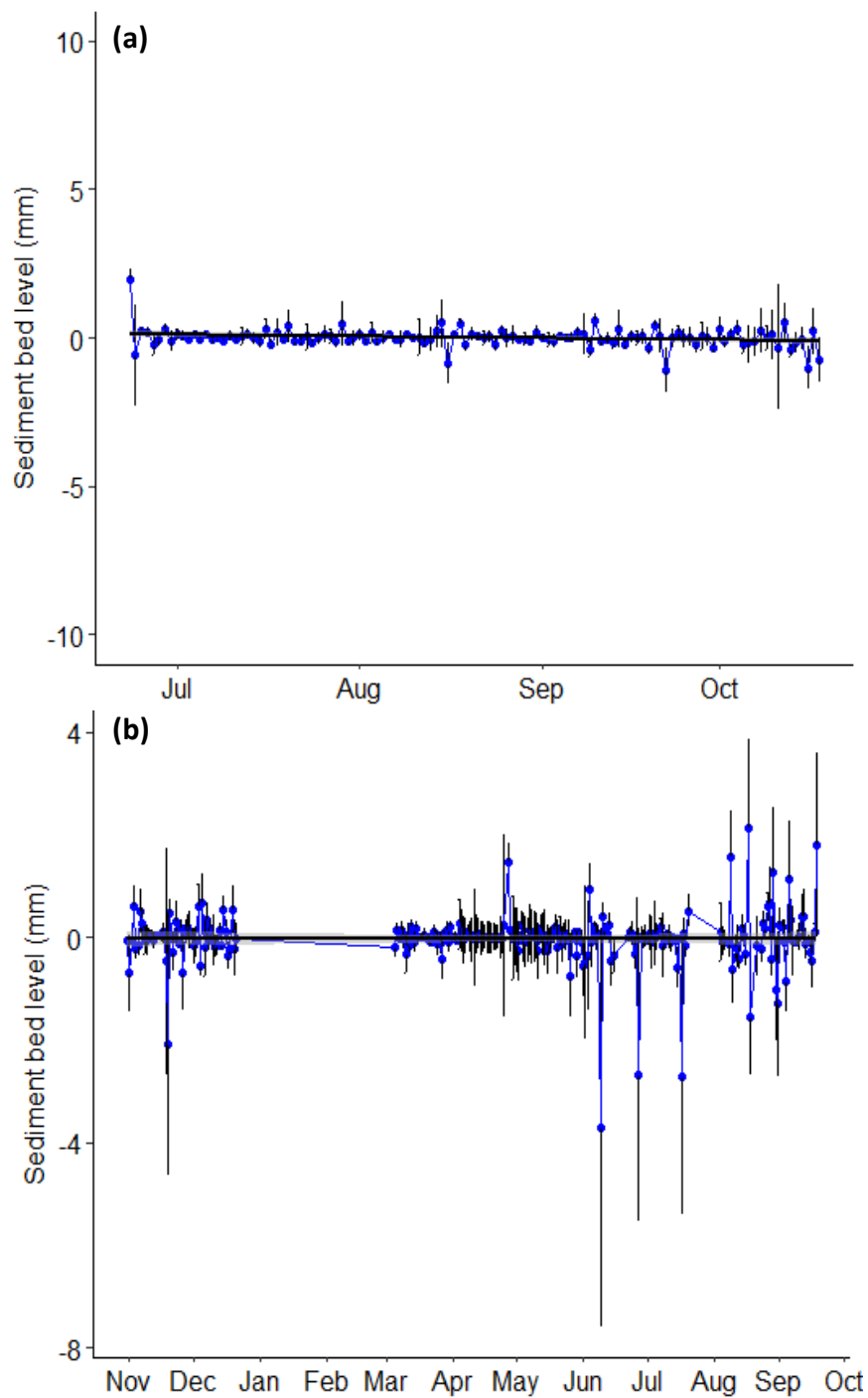


Fig S4.20. Sediment bed level changes measured by SED sensors on the fronting mudflat at the **(a) Red Wharf Bay Sheltered site** and **(b) Red Wharf Bay Exposed site (Anglesey region)** over the observation period. Each solid circle represents the daily mean \pm sd.error.

Supplementary Materials Section D

Partial Least Squares Regression (PLSR) analyses performed on the sites from which wave and mudflat sediment dynamics data were obtained.

Wave and mudflat sediment dynamics data were only obtained from seven out of the eleven study sites (Supplementary Materials Section A, Table S4.1) and so these predictors were included and tested for their effects on the response variable (absolute vegetation recovery) in a separate PLSR model. The results of this PLSR analyses are shown in Figures S4.21- 23.

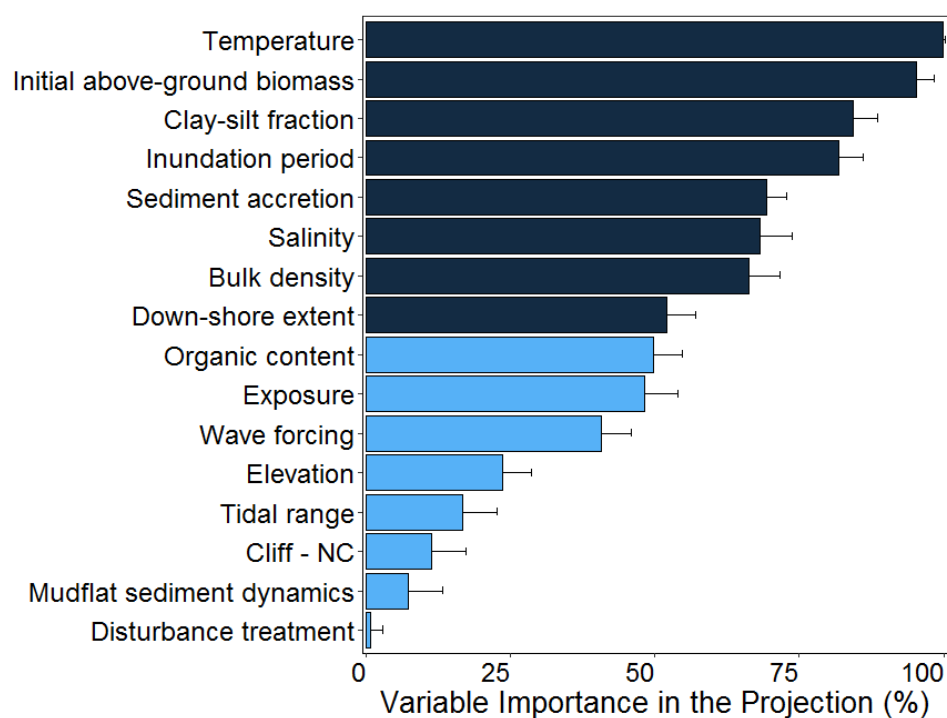


Fig S4.21. Influence of the predictor variables on absolute vegetation recovery in **sites with wave and mudflat sediment dynamics data**, as indicated by the Partial Least Squares Regression (PLSR). Bars show the mean \pm std. error Variable Importance in the Projection (VIP) (% of importance) for each predictor variable in 1,000 PLSR model runs. Variables with large VIP values were consistently relevant to explaining absolute vegetation recovery in the 1,000 PLSR model runs. Dark blue bars represent predictor variables with a VIP >50%, whilst the pale blue bars represent predictor variables with VIP <50%.

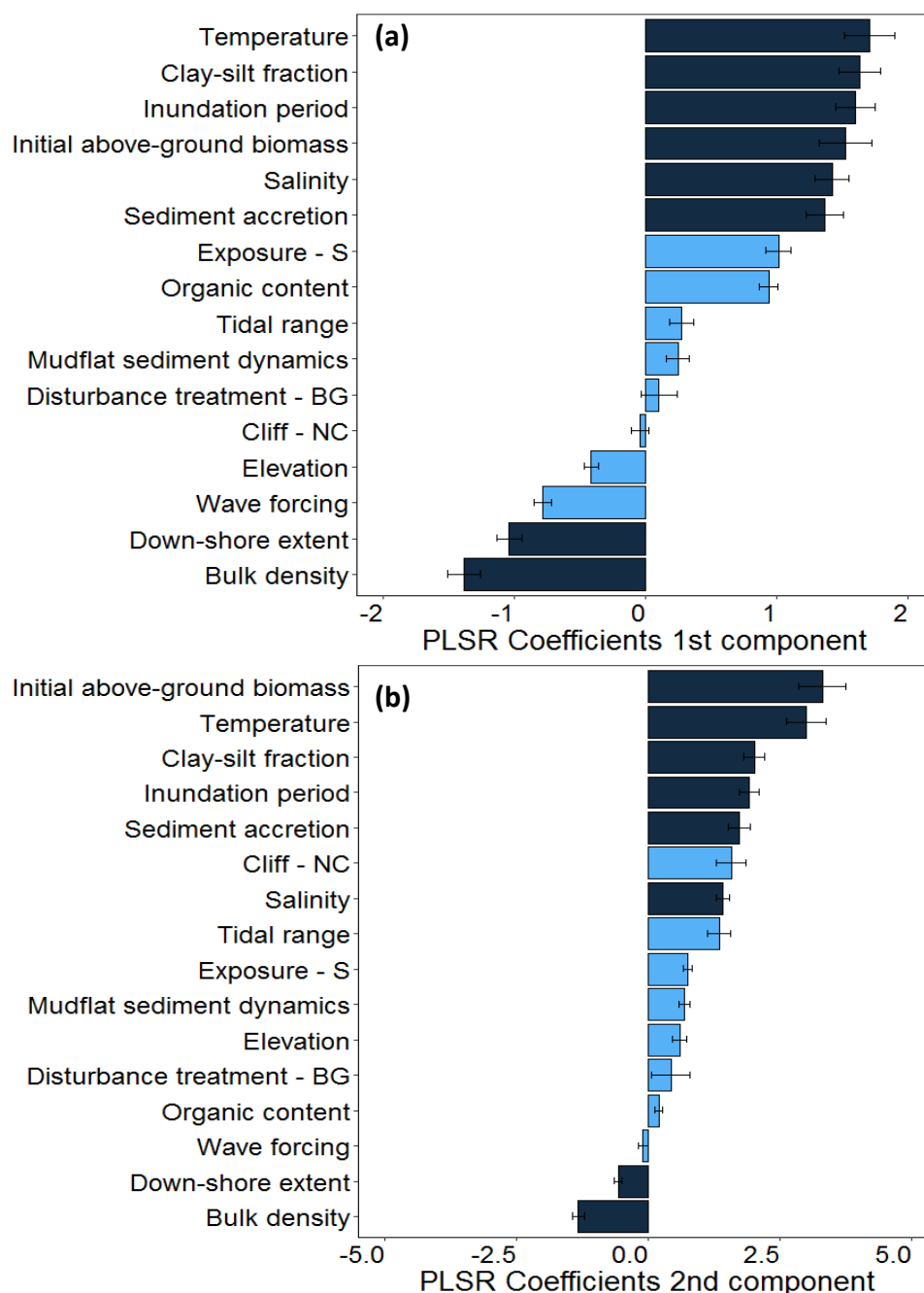


Fig S4.22. The mean \pm std. error regression coefficients of each predictor variable in the (a) first and (b) second components of the PLSR analysis **performed on the sites with wave and mudflat sediment dynamics data**, after 1,000 PLSR model runs. Bars show that positive coefficients loaded positively with absolute vegetation recovery, whilst negative coefficients contributed negatively to the loading of the response variable (Fig. S4.23). Dark blue bars represent the most important predictor variables (VIP>50%), whilst the pale blue bars represent less important predictor variables (VIP <50%). For categorical variables cliff, exposure and disturbance treatment, the appropriate levels are shown. For example, BG disturbance treatments contributed negatively to the loading of the response variable, whilst marshes with no cliffs contributed positively.

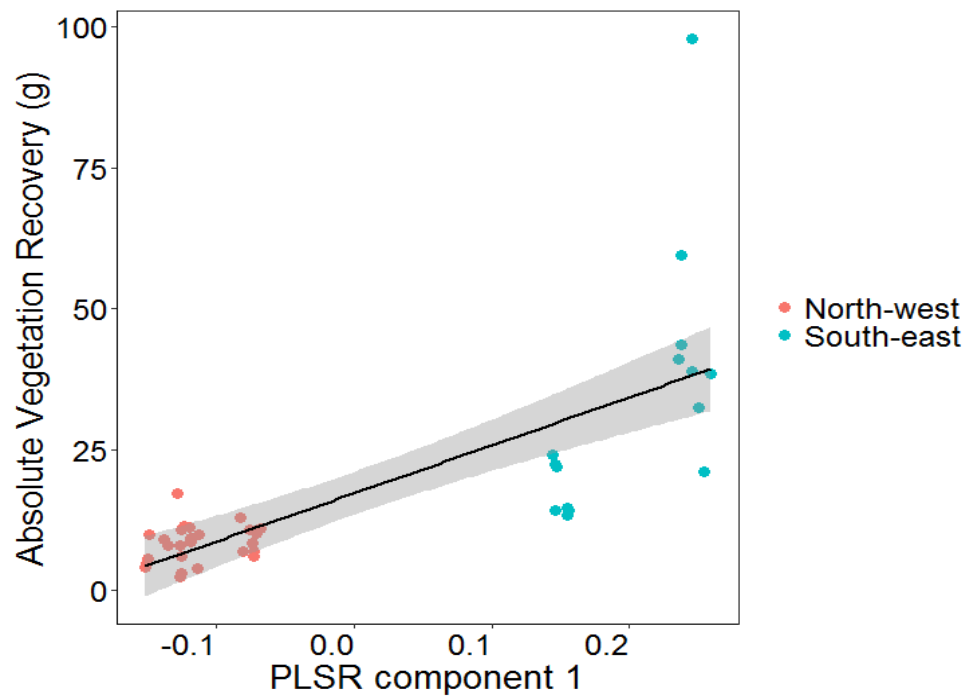


Fig S4.23. Relationship between absolute vegetation recovery and component 1 of the PLSR analysis **performed on the sites with wave and mudflat sediment dynamics data**. PLSR component 1 was positively related to sediment accretion, mean annual temperature, initial plant above-ground biomass, the clay-silt fraction in the sediment, inundation period, salinity, bulk density and marsh down-shore extent. Every observation represents a single 0.3m² vegetation removal plot. Grey shading represents the 95% confidence intervals.

CHAPTER 5

General Discussion

Mollie F. Duggan-Edwards

This thesis has investigated the mechanisms and traits that allow salt marshes to resist stress and to recover after disturbance to provide understanding on what underpins the resilience of coastal ecosystems. Fundamentally, the thesis has examined how gradients in environmental and climatic conditions (i.e. extrinsic factors) drive differences in marsh resilience. In the proceeding sections of this chapter I discuss my main findings and consider how they might be used to inform salt marsh management. I argue that scale is a particularly important element to consider in observations of resilience, because different spatial scales influence interactions between the extrinsic drivers and intrinsic properties of marsh resilience.

5.1 Spatial scales of resilience: extrinsic drivers and intrinsic marsh properties

One of the main knowledge gaps identified at the beginning of this thesis was that we lack understanding of how certain properties of salt marshes, which can act to enforce resilience, change across gradients in environmental and climatic conditions. Here I have shown, for the first time, that marsh resilience varies geographically, as large-scale changes in intrinsic marsh properties, such as sediment characteristics, overlay with gradients in extrinsic environmental and climatic conditions. Thus, Chapters 3 and 4 both showed that marsh characteristics and geographical gradients in climatic conditions generated north to south differences in salt marsh resilience, as marshes in the south-east were more resilient than marshes in the north-west. This north to south variation in resilience was evidenced in two different ways. (1) Marshes in the south-east of the UK extended further down the shore than marshes in the north-west (Chapter 3), and (2) marshes in southern regions recovered better from experimental disturbance than marshes in northern regions (Chapter 4).

The observed large-scale differences in marsh resilience were linked to extrinsic factors, in particular latitude-linked differences in wave forcing and mean annual temperature, which are important for regulating salt marsh establishment and growth (Balke et al., 2013; Callaghan et al., 2010; Kirwan & Mudd, 2012). Thus, higher latitude marshes were less resilient than lower latitude

marshes, because the former experienced greater wave forcing and were exposed to lower ambient temperatures to limit rates of vegetation re-growth following disturbance. Yet, the study also found systematic changes across the UK in intrinsic marsh traits that boost resistance to erosion and enhance vegetation establishment and growth. These traits included above-ground vegetation biomass and sediment grain size. Vegetation biomass increased systematically from north to south regions of the UK (Chapter 4), partially due to latitudinal variation in growth-promoting temperature, as also indicated for North American marshes (Kirwan & Mudd, 2012). As for sediment grain size, I observed that marshes in northern regions tended to have coarser sediments than southern marshes and I suggested this was likely the result of large-scale variation in wave forcing and geological processes. Sediment type is partially the result of local hydrodynamic context, as marshes in more energetic settings tend to have coarser sediments whilst marshes under low forcing tend to have finer sediments (Komar, 1976). However, differences in sediment type between sites may also be indicative of large-scale differences in the source of the sediment (May & Hansom, 2003). Marshes on the south-east coast of the UK receive most of their sediment from fluvial sources, whilst marshes on the north-west coast receive most of their coarse sediments from offshore sources (May & Hansom, 2003). The coarser the sediments, the less erosion resistant and stable the marshes are (Ford, Garbutt, Ladd, Malarkey, & Skov, 2016), as also demonstrated in Chapters 3 and 4.

Thus, patterns of salt marsh resilience that I observed across the UK might be driven by larger-scale, latitudinal gradients in environmental factors such as wave forcing and mean annual temperature. Gradients in wave forcing and temperature affect marsh resilience by mediating erosive forces which regulate marsh lateral expansion/retreat, and by impacting vegetation growth rates. As well as the direct effect of these environmental gradients on resilience, they also affect the intrinsic resilience properties of marshes, such as sediment grain size and above-ground vegetation biomass, which are known to affect marsh stability and expansion. Thus, complex interactions between extrinsic drivers and intrinsic traits regulate large-scale patterns in salt marsh resilience across the UK.

Spatial variation in environmental drivers and the complex way resilience traits interact with environmental context has been observed across other ecosystems, for example in Neotropical dry forests and seagrasses (Soissons, 2013; Poorter et al., 2016). Poorter et al., (2016) showed that vegetation density, an important resilience trait in Neotropical dry forests, was driven by local rainfall across a number of sites in South America. Forests exposed to higher rainfall tended to have higher vegetation densities compared to those exposed to lower rainfall, and consequently forests with higher vegetation densities recovered better after severe drought events than those with lower densities (Poorter et al., 2016). In another example, Soissons (2013) showed that differences in seagrass resilience properties, including mechanical plant traits, were driven by a latitudinal gradient in nutrient status. Seagrasses in nutrient-rich southern regions presented stiffer leaves whilst those in nutrient-deficient northern regions had more flexible leaves, and these differences in mechanical traits ultimately made the plants more or less resistant to physical disturbances (Soissons, 2013).

At smaller-scales, i.e. within geographical regions (north/south) or individual estuaries, other factors which operate at local scales gained importance in driving the observed differences in resilience between individual marshes. For example, I showed in Chapter 3 that biological properties, including vegetation type and the below-ground root biomass in the sediment, were important for increasing marsh resistance to erosion and their capacity to extend down-shore. Below-ground root biomass and the associated organic matter content in the sediment increased marsh resistance to erosion in the sandier, more erosion prone marshes (Ford et al., 2016; Wang et al., 2017). In addition, marshes with *Spartina anglica*, an important pioneer species in western European marshes (Adam, 1990), enabled marshes to extend further down the shore than marshes without *Spartina* at their edges. Similar scale-dependent relationships have been shown in other studies (Balke et al., 2016; Wang et al., 2017). Balke et al., (2016) showed that inundation durations drove differences in down-shore extents (a proxy for resilience) across the globe, but that the same large-scale driver could not explain all of the variation in down-shore extents within the same estuaries or bays. Instead, Balke et al., (2016) concluded that localised factors, such as soil salinity, must be driving patterns of resilience, and hence these localised

factors must be taken into consideration when determining salt marsh resilience at smaller scales (Balke et al., 2016; Wang et al., 2017). My findings suggest that external factors such as wave forcing and mean annual temperature regulate large-scale patterns of marsh resilience, but at smaller scales when the effects of these large-scale drivers are compressed, the importance of the internal properties of the marsh become most important. This is because the internal properties of the marsh regulate sediment erodibility and marsh resilience to environmental stressors, including local variation in soil salinity. I suggest that scale-dependent patterns, such as those demonstrated here, will have important implications for interpreting patterns of resilience across other ecosystems and that they might affect salt marsh management decisions, which will be discussed in the next sections.

In the previous sections I have demonstrated the utility of large-scale studies to examine how climatic/environmental gradients drive differences in internal marsh properties to affect large- and small-scale patterns of resilience across multiple study sites. Yet, this thesis also demonstrates the utility of small-scale, controlled experimentation for understanding larger-scale patterns of resilience. In Chapter 2, I observed that pioneer vegetation was resilient in dense patches at the tussock scale, but that this tussock-scale resilience might ultimately make the marsh unstable, hence less resilient at the landscape scale. This is because the formation of erosion gullies around dense clumps of vegetation restricted marsh lateral expansion, preventing the merging of neighbouring patches. This formation of erosion gullies leads to a patchy distribution of the vegetation and ultimately prevents marsh expansion into larger-scale cover (Fig. 5.1) (van Wesenbeeck et al., 2008). Therefore, although I observed that dense, biomass-rich vegetation increased marsh resilience at the regional and national scales (Chapter 4), such benefits of plant biomass and density were not always observed at the tussock scale (Fig. 5.1). My work in Chapter 2 demonstrates that mechanisms occurring at the smallest scales have the potential to shape the bigger-scale dynamics such as marsh down-shore extent or response to disturbance, which I observed across the UK (Fig. 5.1).

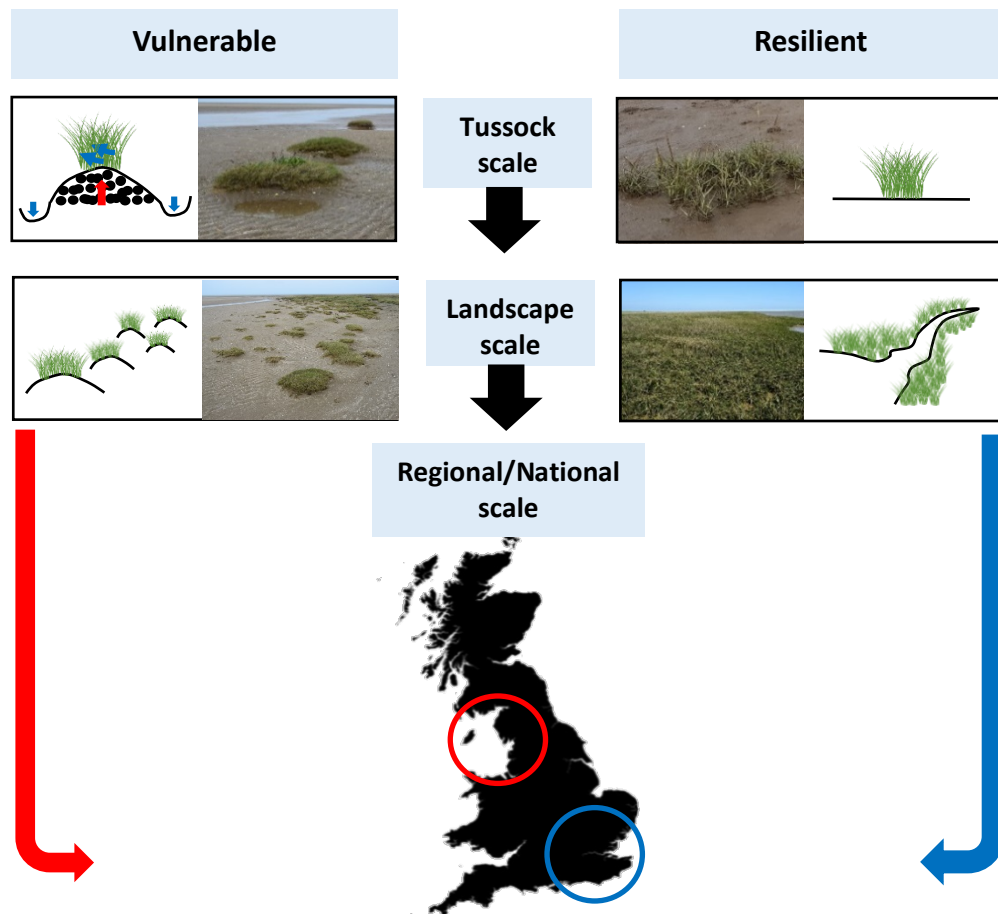


Fig 5.1. Flow diagram showing how tussock-scale resilience (small-scale) can lead to larger-scale (regional and national) patterns of resilience.

5.2 Temporal scales of resilience

My thesis illustrates that the assessment of salt marsh resilience is dependent on the scale at which we view it. Ignoring the scale-dependence of any given observation could, therefore, lead to misrepresentation of the overall resilience of the system (Wang et al., 2017). My findings agree with those of Ladd et al., (in review – a paper that I co-authored), who found that observations of temporal change in the cover of a single marsh within an estuary can provide false representation of overall marsh resilience at the estuarine scale. Marshes can erode in response to channel shifts, which may happen periodically (Pringle et al., 1995; Cox et al., 2003). Ladd et al., (in review) analysed 75 years of aerial photographs and found that when a marsh on one side of an estuary eroded as the tidal channel moved towards it, a marsh on the opposite side expanded in the absence of the erosive force of the

channel. Despite differences (i.e. erosion on one side, expansion on the other), the net area of marsh remained fairly stable at an estuarine scale, implying high resilience at a large-scale (Ladd et al., in review). My thesis is predominantly focused on resilience in the context of spatial scales, yet this example also illustrates the importance of assessing resilience over longer time-scales.

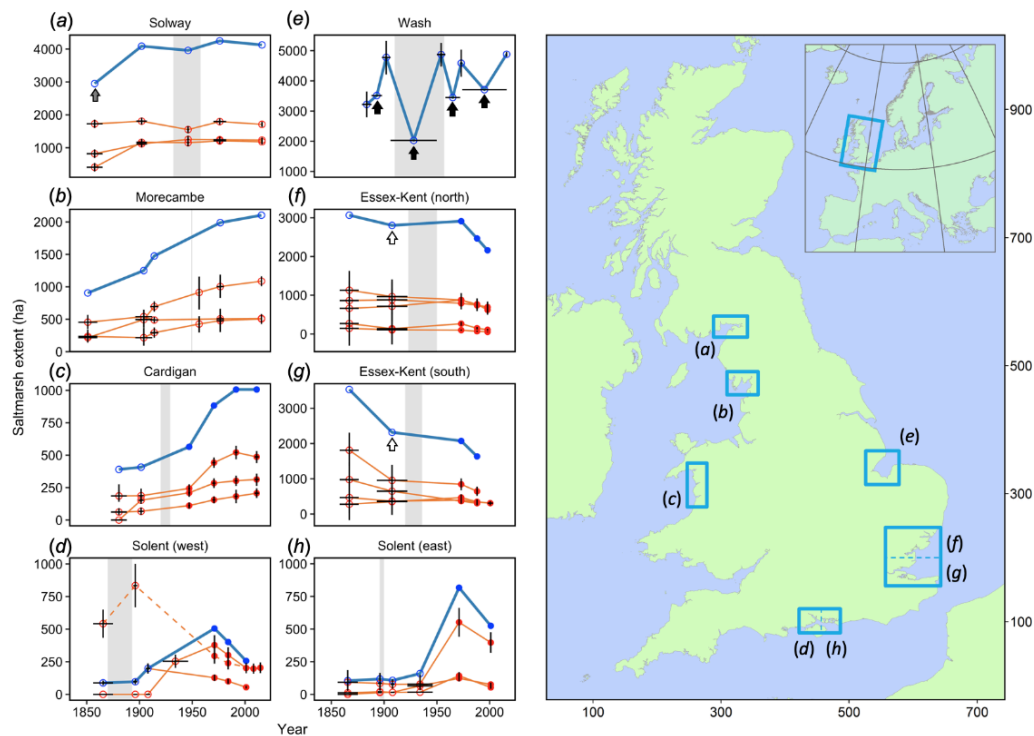


Fig 5.2. Change in estuarine-scale marsh extent across the UK; (a) Solway (south-west Scotland), (b) Morecambe Bay (north-west England), (c) Sarnau (west Wales), (d-h) Solent (south England) and (g-f) Kent (south-east England). Regional- (blue line) and estuarine-scale (orange line) change in aerial extents of salt marshes between 1856 and 2016 were detected from photographs (filled circles) and maps (hollow circles). Arrows indicate occurrences of embankments (solid arrow), canalisation (grey arrow) or the collapse of sea walls after storms (hollow arrow). Grey shading indicates *Spartina* spp. colonisation in each region. Vertical error bars indicate 95% confidence intervals in marsh area extent. Horizontal lines indicate the dates over which surveys of marsh extent were carried out. Essex-Kent and Solent regions have been subdivided for ease of presentation. Regional-scale marsh change (blue line) only includes marsh extent measures for all estuary in a given region and year. Marsh change in Southampton estuary (panel d: dashed line) was excluded from the regional scale marsh change line due to paucity of contiguous cover in saltmarsh extent across multiple years. Figure taken from Ladd et al. (in review), a paper that I co-authored.

An important conclusion from the Ladd et al., (in review) study, and one that is relevant to the findings of my research, is that these patterns in marsh expansion and retreat would not have been possible to detect without considering both the spatial and temporal scales of the observation. In the same way as only observing one marsh on one side of the estuary might misrepresent the overall resilience at a spatial scale, the findings of Ladd et al., (in review) also suggest that short-term studies might misrepresent the overall resilience over longer time scales. The relevance of considering temporal as well as spatial scales is presently discussed.

My experiments show salt marshes on the south-east coast of the UK are more disturbance-resilient (Chapter 4) than marshes on the north-west coast and protrude further down-shore (Chapter 3). This seems contradictory of known patterns of salt marsh decline in the south-east and marsh expansion in the north-west (Fig. 5.2) (Ladd et al., in review; Horton et al., 2018). Ladd et al., (in review) showed that sediment supply and sea level rise explained long-term trends of marsh resilience across the UK. In reality, there is no contradiction; it merely illustrates that a system may decline if it is located in a larger-scale stress context, even if the same system has disturbance-resilience traits that allows it to recover from small-scale disturbances in the short term, as the following describes. The intrinsic properties (e.g. sediment grain size and vegetation biomass) of north-west coast marshes give less erosion resistance and slower vegetation recovery in the short-term (findings of Chapters 3 and 4), but they might still be more stable in the long-term because the external drivers (e.g. sea level rise and sediment supply) are conducive to long-term resilience (Fig. 5.2- 3) (Ladd et al., in review). Therefore, despite marshes on the south coast displaying enhanced resilience over the short-term, they are least likely to recover over the longer term because the external drivers are less favourable to marsh growth (Fig. 5.2- 3). In south-east marshes, it may take a very long time for the marsh to accrete to a sufficient height for the vegetation to re-establish after an erosional period (for example as a result of landward retreat). This is because the marsh platform does not receive enough sediment, and the rate of sea level rise might exceed the vertical rate of sediment accretion (Ladd et al., in review). These findings once again introduce the question of scale, this time about the appropriate time scales over which

ecosystem resilience should be observed in order to make accurate long-term predictions of ecosystem persistence. This is why I conclude that marshes can be resilient over the short-term but vulnerable over the long-term (Fig. 5.3).

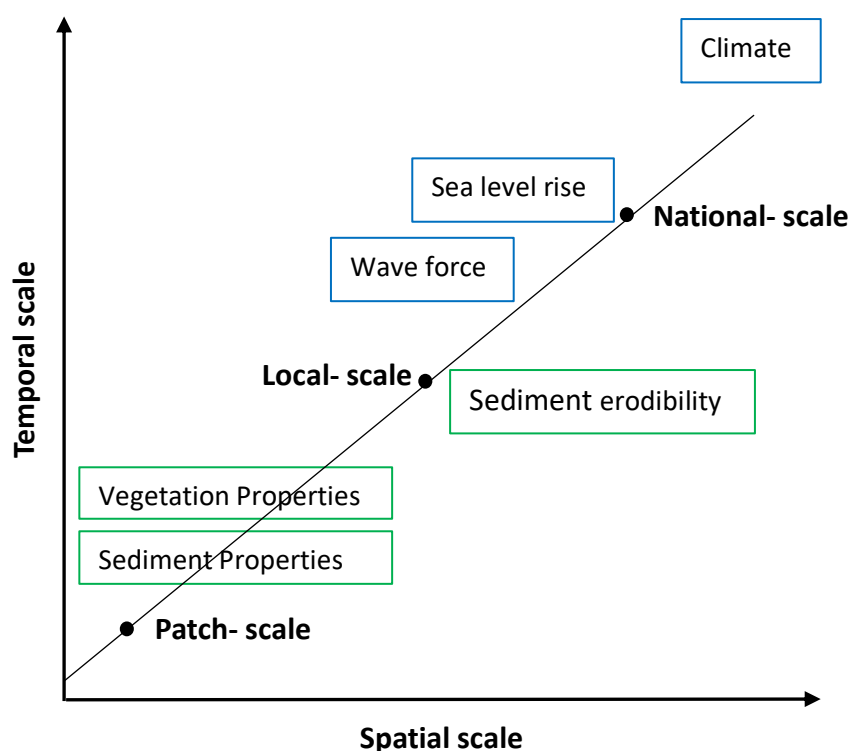


Fig 5.3. Schematic representation of the interactions between temporal and spatial scales on the drivers and traits of salt marsh resilience. Large-scale drivers (in blue boxes) explain longer-term patterns of resilience at national scales, whilst smaller-scale marsh traits (in green boxes) explain short-term resilience of marshes at localised scales.

5.3. Implications for salt marsh management

Environmental managers seek to conserve ‘the most resilient systems’ because they are most likely to continue delivering important ecosystem services into the future (Gedan, 2009). However, assessing whether an ecosystem is resilient or not is a difficult task in practice, the complexities of which I have investigated throughout the chapters in this thesis. This thesis presents an opportunity to highlight some important considerations for managers when determining ecosystem resilience in the future.

Understanding what determines whether a salt marsh expands or erodes is a priority for environmental managers, because changes in the position of the seaward marsh edge impact on the delivery of ecosystem services (Bouma et al., 2016; Willemsen et al., 2018). Despite the importance of understanding the processes responsible for regulating marsh positions in the tidal frame, few studies have investigated the mechanisms that regulate changes in lateral extents (i.e. expansion and retreat) (Bouma et al., 2016; Willemsen et al., 2018; Ladd et al., in review). I have added important knowledge to this research gap by identifying mechanisms and marsh traits that boost resilience, which could be applied by environmental managers to assess ecosystem resilience and inform conservation and restoration.

Marshes that reside lower down the shore, a potential outcome of enhanced resilience and seaward expansion, have a greater capacity to act as important nursery grounds for fish species than marshes that occur at higher elevations on the shore (Kneib, 1997). This has implications for management because the nursery value of salt marshes is likely to vary between geographical regions, depending on a number of factors including the position of the marsh in the tidal frame (Taylor, 2005). Marshes that support juvenile fish species (e.g. herring and seabass) might be prioritised for conservation and therefore the persistence of the lower extent of the marsh is of importance to management. In addition, marshes lower down the shore might also offer more effective flood protection, which could reduce the costs associated with maintaining man-made sea defence structures (Möller et al., 2014). It has been shown that having a bigger marsh in front of a sea defence can offer substantial cost savings for environmental managers because they can attenuate waves over longer distances, lessening their impact on the coast (Möller et al., 2014). Identification of traits that enable marshes to resist erosional forces and persist in the tidal frame has the capacity to improve management decisions to enable marshes to continue provisioning important ecosystem services such as coastal flood protection.

This thesis demonstrates how ecosystem resilience depends greatly on the scale employed by studies. There is a need for environmental managers to have a robust interpretation of the relevant scales for evaluating marsh resilience (Haslett et al. 2010). There has been a tendency for monitoring strategies to focus on single marsh sites and monitor them over short time frames (Pye & French, 1993; Phelan et al., 2011; Macgregor & van Dijk, 2014; French et al., 2016). My research predicts issues with upscaling such small-scale patterns to characterise trends over larger spatial and temporal scales, because resilience varies contextually at larger-scales, and that it is possible to isolate the important drivers of lateral marsh change (Ladd et al., in review) from the drivers of resilience (Chapters 3 and 4). Thus, while short-term resilience is reduced in marshes on the north-west coast of the UK, due to for instance coarse sediment characteristics in those marshes and recovery being slower (Chapters 3 and 4), their long-term resilience is enhanced, mainly due to having a rich supply of sediment (Ladd et al., in review). This shows that, if the appropriate scales are not considered, environmental managers risk misidentifying the key drivers of resilience, and ultimately mistaking short-term changes from long-term trends. My findings about the importance of scales emphasises the need to monitor and identify the causes of erosion and therefore the most appropriate management action before intervention occurs.

Marshes are valued for important services (e.g. coastal flood protection and carbon sequestration), but their delivery of these services depends on spatial and temporal scales. At different spatial scales, marshes may only provide important coastal flood protection if they are dissipating waves in front of a town on that particular side of an estuary. Whilst, over temporal scales, we have learnt that marshes are dynamic and undertake switches from expansion to retreat at their lower edges, which means a potential loss of the important ecosystem services they provide as a result of extended periods of landward retreat. Therefore, a marsh might offer an important service now (e.g. carbon sequestration), but its dynamic nature means that the services can also change which is something that is not currently accounted for in salt marsh management.

Misidentification of the appropriate scales may have led to the failure of several restoration projects for coastal ecosystems and salt marshes in the past (Silliman et al., 2015). Environmental managers often reconcile marsh loss/degradation by planting patches of pioneer species on the mudflat to boost marsh establishment and growth (Mitsch & Jorgensen, 2004). In Chapter 2 I showed that vegetation density, which is an important variable taken into consideration in restoration planting designs, interacts with wave forcing to have varying effects on marsh patch expansion. Dense patches of pioneer vegetation facilitated sediment build-up and plant survival under conditions of high wave forcing, whilst under conditions of low wave forcing, individual plants within dense patches competed against each other for resources (e.g. space, light and nutrients), which led to overall plant mortality and loss of resilience. This finding demonstrates how the same vegetation density can change from having a positive to a negative effect across a gradient in wave forcing, and therefore shows the importance of considering interactions (in this instance of plant density with wave forcing), in restoration planting designs. The ideal configuration of a trait for boosting marsh growth should be tailored to the environmental conditions, which are site specific.

Chapters 3 and 4 also indicate that biotic and abiotic properties, such as vegetation type and sediment characteristics can be applied in some salt marsh restoration designs (Wang et al., 2017). Specific plants with dense root systems have been shown to enhance the stability of salt marsh edges (Chapter 3) (Wang et al., 2017). Such local species can be transplanted to collapsed areas with high erodibility to reinforce the marsh edge (Wang et al., 2017). In Neotropical forest restoration designs, patches of vegetation are grown in a muddy substrate ahead of re-planting to ensure that the plants persist when relocated to the site (Poorter et al., 2016).

This thesis has found that salt marsh resilience is influenced by large-scale climatic variables including latitudinally-driven differences in annual temperature and wind-wave forcing. Both of these large-scale climatic variables are expected to be influenced by climate change over short- and long-terms, further complicating predictions of marsh resilience to erosion along global coastlines. The

present thesis found that higher annual temperatures had overall positive effects on salt marsh resilience by increasing plant metabolic rates and above-ground vegetation biomass at the sites (findings of Chapter 4). Yet, there is evidence to suggest that increasing global temperatures as a result of climate change will have overall negative effects on salt marsh resilience (REFERENCE). Warming temperatures are contributing to increasing sea levels via the melting of ice-caps in Polar Regions (REFERENCES). This large-scale climatic phenomenon is already taking effect on global coastlines, as in the UK alone southern regions experience up to X mm of sea level rise and in northern regions up to X mm each year. Two of the main threats to salt marshes as a result of rising sea levels are drowning as a result of excessive tidal inundation and increased wind-wave activity (REFERENCES). In addition to the indirect effects of warming temperatures on salt marshes, some direct consequences are already being reported in the literature including habitat encroachment as increasing temperatures will cause mangroves, which are the dominant vegetated wetland in sub-tropical regions, to extend northward at the expense of salt marsh habitat.

As well as the long-term drivers of salt marsh loss, such as rising sea levels and temperatures, as a result of climate change, marshes may also endure a higher frequency and severity of extreme weather events. As discussed at the beginning of this thesis, the UK alone was struck by a higher number of extreme weather events in the past years, which could be the result of a changing climate. Such extreme events bring with them short-term changes in temperature and hydrological conditions, which have the potential to affect marsh resilience over both short- and long-terms. An increasing frequency and severity of drought events has already been reported in the literature in south-eastern USA marshes, and significant die back of salt marsh plants as a consequence (Angelini et al. 2016). Other extreme events known to threaten marshes include storms, which induce erosional impacts at their edges lasting up to several days. This thesis showed that marsh resilience is most at risk under higher levels of wind-wave forcing (measured by maximum wave height), and therefore an increasing frequency and severity of storm events may threaten marsh resilience over longer- as well as shorter time scales the responses of marshes to further extreme events. Increased wind-wave forcing

(measured by maximum wave height), which we showed to negatively influence marsh resilience, may also be expected to increase as a result of increasing sea levels and extreme weather events.

I showed that these patterns of marsh resilience were influenced by regional differences in temperature, wind-wave forcing and sea level rise. Climate change and associated extreme weather events may be expected to influence marshes at regional scales. Marshes in southern regions of the UK are currently and forecasted to experience the highest rates of sea level rise, whilst marshes in northern regions experience the greatest wave forcing and may be expected to experience more frequent and severe weather events. Extreme ocean waves in the central North Sea arise due to intense extratropical cyclone wind from either the cold conveyor belt (northerly-wind events) or the warm conveyor belt (southerly-wind events). The largest wave heights are associated with northerly-wind events which provide a larger fetch to the central North Sea to aid wave growth.

This thesis provides an insight into the responses of salt marshes to factors that may be further influenced by climate change and associated extreme weather events. This thesis shows that salt marshes are most at risk from factors that are likely to be affected by climate change, further complicating the prediction of their resilience along global coastlines. Furthermore, the effects of changes in climate will affect salt marshes over multiple temporal and spatial scales, further complicating our ability to predict marsh resilience into the future.

5.4 Limitations and future directions of the research

Understanding what makes an ecosystem resilient requires comparative data sets that span both space and time. The temporal scales of this thesis might not be long enough to make accurate assessments of the longer-term patterns of resilience, thus introducing a limitation. For example, in Chapter 2, I only observed pioneer patches of vegetation over twelve months, which may not have been long enough to observe the full development of marsh patches, for instance whether or not neighbouring patches would, ultimately, merge together. In addition, in Chapter 4, vegetation recovery was

observed over two growing seasons only, so I might not have captured the full recovery of the vegetation. Some marshes might take longer to recover from disturbance, whilst others can recover over shorter periods, but this was not taken into consideration in my Chapter 4 experiment. Therefore, a direction for future research would be to investigate the drivers and traits of resilience over longer temporal, as well as larger spatial scales.

My findings in this dissertation, in combination with the findings of Ladd et al., (in review), suggest that marshes can be resilient over the small- scale and short-term, but vulnerable in the large-scale and long-term. This has important implications for interpreting and managing salt marsh resilience, as these contradicting trends over various scales may lead to misidentification of the causes of erosion and hence the overall health of the system. One direction is for future studies to investigate salt marsh resilience over long temporal as well as spatial scales. This study focused on twenty salt marshes across the UK. While this number of sites and the geographical range is considerably greater than in most salt marsh studies, the spatial constraints of the study has implications for the interpretation of the overall findings. With a greater number of sites over more global regions I might be better equipped to unravel the effect of some of the latitude-confounded drivers, including mean annual temperature and inundation duration, which influenced the results of Chapter 4.

Several studies highlight the importance of single bio-physical traits, such as sediment or vegetation properties that influence ecosystem functioning, for marsh resilience (Feagin et al., 2009; Angelini & Silliman, 2012; Willemsen et al., 2018). Here I have shown that an important resilience trait in one marsh may not provide the same positive effects in another marsh. For example, in Chapter 2, I showed that dense patches of vegetation boosted the survival of individual plants in wave-exposed settings; yet, in wave-sheltered sites plants competed with each other for resources which caused high mortality. Similarly, below-ground root density was important for provisioning erosion resistance in sandy erosion-prone marshes, but it did not provide the same resistance in the more resistant muddy marshes in Chapter 3. A direction for future research would therefore be to further investigate how

resilience traits change, and hence interact, across environmental gradients (e.g. temperature and wave forcing), to understand where and when switches between positive and negative effects on ecosystem resilience are likely to occur. This may be especially important in light of the forecasted changes to climatic conditions. With consorted effort across different biological and environmental contexts, we will, ultimately, be able to predict which marshes are likely to recover following disturbance, and why that is, for the benefit of global salt marsh management.

I aimed to collect as much contextual data as possible from the salt marsh sites around the UK which might help to explain potential differences in marsh resilience. I deployed pressure sensors and sediment bed level dynamics sensors (SED's) at all of the sites, but I experienced some technical problems which meant that I did not retrieve water pressure data from all of the sites. These shortcomings meant that I had an incomplete gradient of these contextual variables (wave forcing and mudflat sediment dynamics) across the UK. I also deployed temperature loggers at the sites to retrieve temperature measurements, but due to long delays between visiting the study sites around the UK the majority of the loggers were lost in the field before downloading the data. This meant that I had to retrieve the temperature measurements from local weather stations instead. These issues with the instrumentation illustrate some of the limitations of large-scale studies. Although suspended sediment concentration and sea level rise are both major drivers of salt marsh resilience (Ladd et al., in review), my short-term observations would not have allowed for any significant impact on the results, and therefore they were not measured.

5.5 Conclusions

This research set out to better understand the mechanisms of resilience in salt marshes, and to investigate how these might vary across gradients in environmental and climatic conditions to affect long-term marsh stability. I have demonstrated that assessing the mechanisms of resilience is a highly complex process, which requires study of multiple scales of interactions between a number of resilience traits and drivers. This level of complexity makes predicting how marshes are going to

respond to new climate regimes a daunting exercise. I emphasise that marsh resilience is specific to the temporal and spatial scales at which we observe it. It is also context-dependent, varying with large-scale climatic and environmental gradients, as well as with variation in regional-scale conditions (e.g. geomorphology, hydrodynamic forces, etc.). Climate-change will alter environmental conditions, such as temperature, sea level rise and storminess, into the future and act at all scales of resilience considered in this thesis, to challenge the long-term stability of ecosystems. In a time of climatic uncertainty, we are addressing a pressing need to understand what increases the vulnerability of salt marshes to disturbance. Only by exploring the drivers and traits of resilience across different scales and contexts will we be able to gain useful insights into understanding the mechanisms of resilience in salt marshes, and to usefully apply this information to make predictions about the continued persistence of marshes. I hope that this dissertation has contributed towards that ultimate goal.

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