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How to create a saltmarsh: Understanding the roles of topography, redox and nutrient dynamics

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Abstract

The restoration of saltmarsh is critical given the importance of the habitat and the degradation and losses it faces. However, success of saltmarsh restoration has been limited, particularly in replacing plant communities, despite like-for-like replacement being a legal requirement. Previous research found elevation in the tidal frame and sediment redox potential are important drivers of vegetation communities, and are different between restored and natural marshes. However, elevation and sediment redox potential together are insufficient to explain differences in plant communities. Topographic features are thought to alter redox potential-elevation relationships, though its role in plant communities is not currently known. Nutrient concentrations can also impact vegetation, however we lack evidence as to the typical concentrations in natural saltmarsh or restored sites, and how close these are to detrimental levels. This thesis explores these environmental properties in restored and natural saltmarshes, and how they may interact to drive plant communities.

Results indicated that nutrients were highly variable both spatially and temporally. In contrast to expectations, there was a negligible effect of former land-use on surface soil development in a newly developing marsh. Instead of land-use, a combination of sedimentation and elevation appears to be the strongest predictor of nutrient properties, thus a better understanding of incoming sediment and elevation changes may lead to improved predictions of likely soil development. The results from nutrient analysis also indicated that globally saltmarshes are typically Phosphate enriched and thus the management of N input at natural saltmarshes should be avoided.

Restored marshes have different topographic characteristics (flatter, wetter and more often concave). A lack of topography existed on both site and local scales, resulting in more homogenous plant communities (again at, sites and local-scales). Natural plant diversity was driven by elevation, local topography and redox, whereas on MR sites it was almost entirely driven by redox potential. The results show that more topographic manipulation is required to aid community convergence with natural diversity, and thus replicate natural conditions in restored saltmarshes.

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1 Introduction: Saltmarsh ecology and restoration success

1.1 Saltmarsh ecology

Saltmarsh is a habitat defined by the presence of halophytic (salt tolerant) vegetation and alluvial deposition, which is periodically inundated by tidal waters (Allen, 2000). Sites that fulfil these criteria are often prograding, occurring primarily within sheltered embayments and other areas protected from tidal energy (waves and strong currents) (Allen, 2000; Shao, 2014).

Although nature has an inherent value (Ehrlich and Ehrlich, 1992), there is growing trend in assigning ecological and / or monetary values to habitats for the services they provide, known as ecosystem services (Costanza *et al.*, 1997; Naidoo *et al.*, 2008). The values placed on ecosystems are often used as tools for policy and decision makers, e.g. when choosing to restore habitats. As a collection of plants, physical processes and topographic features, saltmarshes deliver many valuable ecosystem services (Barbier *et al.*, 2011). The delivery of these services is often linked directly to the type of vegetation present, but also to the topographic niches and other features the site contains (Costa *et al.*, 1994; Pennings *et al.*, 2009; Möller *et al.*, 2014). For example, high ground can be used as breeding grounds for wading birds, complex networks of creeks provide nursery grounds for fish, and clusters of taller vegetation offer wave protection and shelter. Therefore, within the context of biodiversity-ecosystem functioning theory (Soliveres *et al.*, 2016), a diverse saltmarsh in both physical form and biota will have the highest value. It is important to recognise that vegetation dominates the value provided by saltmarsh as it is the fundamental component of the habitat; without encouraging vegetation the marsh will not deliver the same level of ecosystem services.

One of the primary and most quantified values of saltmarsh is as a sea defence (King and Lester, 1995; Barbier *et al.*, 2011). Plants cause friction which reduces the energy of waves, with nearly 30% of wave energy dissipated by a 100m stretch of healthy saltmarsh (Möller *et al.*, 2014). This attenuation means that, in places, saltmarsh outperforms many built structures in defending from tidal energies, whilst also offering a two to five fold monetary saving (Narayan *et al.*, 2016). This saving comes from the significant costs involved in heightening walls (c. £8 million per kilometre), and maintenance that can cost

£3,560 km^{-1} y^{-1} in the UK. Consequently, saltmarshes present an excellent option for sustainable and cost-effective barriers to storm events that are robust to erosion.

Further to this, the annual growth of vegetation and sedimentation leads to the slow burial of Carbon synthesized from CO_2. This process traps Carbon in saltmarsh sediments leading to improved primary productivity and further Carbon storage. The value of coastal Carbon storage is significant, saltmarsh bury nearly 55 times more Carbon per year, per unit area, than tropical rainforests, with global averages of 87.2 ± 9.6 Tg C per year, although they only occupy just 1% of the global land surface area (Duarte, Middelburg and Caraco, 2005; McLeod *et al.*, 2011). However, it is worth noting that this process and value is entirely reliant on the continued preservation of those locked soils, and erosion will lead to release of formally trapped Carbon (and other chemicals) back into the water course.

Saltmarshes are globally threatened; they have already suffered global historic losses of ~50% of habitat area due to anthropogenic pressures (Barbier *et al.*, 2011). Reclamation has been the biggest cause of loss, and in some regions of the world land claim is continuing (Tian *et al.*, 2016). Further to this, alterations to global processes, such as climate change and sea level rise, can result in either direct loss through erosion or alterations to the ecosystem services delivered by saltmarshes (Gray and Mogg, 2001; van der Wal and Pye, 2004). Global mean sea level is predicted to rise by between 0.2 and 1m by 2100 (Church *et al.*, 2013) and has recently been accelerating (Hay *et al.*, 2015). Coastal habitats are becoming trapped between these rising sea levels and static sea defences, in a process known as coastal squeeze (Morris *et al.*, 2004), which prevents the natural inland retreat of the habitat. This results in the steepening of the foreshore, reducing the horizontal extent of intertidal habitat (van der Wal and Pye, 2004; Firth *et al.*, 2014). The consequence of this steepening is perhaps felt strongest in the upper intertidal and transition zones, inhabited by upper saltmarsh plant communities and rare coastal invertebrates, as these zones are naturally small in area and coastal squeeze may threaten their existence (Burd, 1989; UK BAP, 2008).

Eutrophication (increased nutrient availability) of the world's coastlines is a growing and significant environmental, economic and social concern (Cloern, 2001; Verhoeven *et al.*, 2006). Chronic eutrophication in saltmarsh soils decreases root mass and increases sediment surface fractures (Feagin *et al.*, 2009; Turner, 2011; Deegan *et al.*, 2012). Root growth in the pioneer zone however can also be increased under enriched conditions (Johnson *et al.*, 2016). This suggests the consequences of enrichment are location specific within the marsh. With nutrient enrichment leading to increased erodibility, only an increase in elevation (from accretion) can compensate for lost substrate. Although the consequences of nutrient enrichment are well studied, interpreting nutrient data is difficult because nutrients are highly stochastic both in time and space (Magalhães, Bordalo and Wiebe, 2002; Pott *et al.*, 2014; Smith, Jarvie and Bowes, 2017). Moreover most of our current knowledge stems from nutrient addition experiments with very high concentrations rather than from the marshes themselves, meaning ‘natural’ baseline conditions are poorly quantified.

In addition to sea level rise and eutrophication, the effects of climate change associated with changes in CO_2 concentration, temperature, precipitation, and atmospheric regimes, pose threats to saltmarsh. A full review of the effects of these on coastal habitats in the UK is provided by (Mossman *et al.*, 2015), a publication I co-authored during my PhD studies.

Adaptations of saltmarsh plants

The halophytic plants that inhabit saltmarshes are adapted to survive the stresses of regular saline inundation (Rozema *et al.*, 1985), but their tolerance to these conditions vary, leading to the zonation of plant communities regularly observed on saltmarshes. Plants have evolved a range of adaptations to high salinity environments, including specialist glands and modified transportation pathways to facilitate the loss of salt from leaves or roots, and retention of water, sugars and solutes (Colmer and Flowers, 2008; Flowers and Colmer, 2015). Despite developing these adaptations, most saltmarsh species can grow in non-saline conditions (they are not obligate halophytes), although many are restricted to saline conditions because they lack competitive ability in terrestrial conditions with low salinity (Janousek and Mayo, 2013). Table 1-1 summarises the key adaptations of halophytes to salt and flooding stress.

Table 1-1 Summary of key halophyte adaptations to salinity and flooding

Adaptation	*Advantage*	*Reference*
Salinity (stress)		
Succulent leaves	Water retention	**[1]**
Salt exclusion (glands)	Reduced Na^+ in leaves	**[2, 3]**
Compartmentation	Osmotic regulation	**[4, 5]**
Reduced stoma	Substitute Na^+ for K^+	**[6]**
Flooding duration		
Root aerenchyma	Enhanced O_2 movement	**[7]**
Long roots	Fresh water adventurousness	**[8]**
Shallow roots	Aerobic soils	**[9]**

Reference Key: [1] (Konnerup *et al.*, 2015), [2] (Munns and Tester, 2008; Nedjimi, 2014), [3] (Nedjimi, 2014), [4] (Alhdad *et al.*, 2013), [5] (Slama *et al.*, 2015), [6] (Robinson *et al.*, 1997), [7] (Justin and Armstrong, 1987), [8] (Naidoo and Mundree, 1993), [9] (Colmer and Flowers, 2008).

Saltmarsh plants also require adaptions to the stresses of prolonged inundation. Some species have modified transportation pathways to enable more efficient flow of gasses between the emergent and submerged parts of the plant during inundation, whilst others alter the local oxygenation of soil, which reduces the pressure of prolonged deoxygenation (Clapham, Pearsall and Richards, 1942; Goodman *et al.*, 1969; Gray and Scott, 1977). Table 1-2 summarises the specific adaptations of nine saltmarsh plant species common in the UK.

Table 1-2 Summary of adaptations to saline conditions and regular flooding of nine of the most abundant saltmarsh plant species in the UK (Mossman, Davy and Grant, 2012). Succu. = succulent leaves, Comp. = compartments, Redu. Stoma = Reduced Stoma, Aeren. = Aerenchyma.

Species	*Salt adaptations*				*Flooding adaptations*			***Ref.***
	Succu. leaves	Salt exclusion	Comp.	Redu. Stoma	Aeren	Long roots	Shallow roots	
Aster tripolium	x		X			X		**[1]**
Puccinellia maritima	x	X	X	X		x	X	**[2]**
Spartina anglica		X	X			x		**[3]**
Salicornia europaea agg.	x		X	X	x		X	**[4]**
Triglochin maritima	x			x		x		**[5]**
Atriplex portulacoides	x					x		**[6]**
Limonium vulgare	x	X				x		**[7]**
Armeria maritima	x	X	X			x		**[8]**
Sarcocornia perennis	x		X	x		X		**[9]**

Reference Key: [1] (Clapham, Pearsall and Richards, 1942), [2] (Gray and Scott, 1977), [3] (Goodman *et al.*, 1969), [4] (Davy, Bishop and Costa, 2001), [5] (Davy and Bishop, 1991), [6] (Chapman, 1950), [7] (Boorman, 1967), [8] (Woodell and Dale, 1993), [9] (Davy *et al.*, 2006)

1.1.1 Formation of saltmarsh

The formation of saltmarsh is conditional upon the stabilization of freshly deposited marine sediment. This fresh sediment is stabilised by plant colonisation, and the net result is a gradual increase in surface elevation, through a process known as accretion. This ‘process’ of accretion is a combination of contain organic matter and mineral sediment. Saltmarsh formation can only occur where both suspended sediment is present within the water column, and the tidal energy is low enough to allow settlement, for example in embayments, estuaries and other sheltered regions (Allen, 2000).

In the formation of a new saltmarsh, the seabed is initially submerged. With continued accretion the surface slowly rises, eventually exposing sediment on a more regular basis. When this surface sediment reaches an elevation close to the local level of mean high-water neap (MHWN) tides, pioneer saltmarsh vegetation, such as *Puccinellia maritima*, *Spartina* ssp. and *Salicornia* ssp., begin to colonise (Davy, 2000). These early-colonizing plants further slow the flow of tidal waters containing sediment, facilitating additional accretion and contributing organic matter to the sediment via trapped algae caught on plant structures, and the decay of the plants themselves (Chapman, 1959; Zhou *et al.*, 2006). These processes raise the marsh surface in the tidal frame, ameliorating the environmental conditions and allowing later successional species, which are less tolerant of tidal inundation, to colonise. This process, known as ‘facilitated succession’, is well described in the literature, with examples of *Spartina* spp. trapping sediment and thus allowing *Puccinellia maritima* to colonise (Huckle, Marrs and Potter, 2002), or *Spartina* spp. facilitating *Sarcocornia perennis* (Castellanos, Figueroa and Davy, 1994).

As accretion continues, diverse communities develop in the mid-marsh elevations. Here, some species are associated with topographic niches such as creek banks (Chapman, 1950), and others in more waterlogged conditions around pools (e.g. *Triglochin maritima*) (Chapman, 1959; Davy, 2000). The final steps in accretion are typically slow, represented by the narrowing grey band in Figure 1-1. In the highest elevational zone, saline-intolerant species can out-compete halophytes. Although elevation is clearly important, the balance of nutrient inputs, salinity, interspecific competition and drainage also impact plant zonation (Silvestri, Defina and Marani, 2005; Davy *et al.*, 2011).

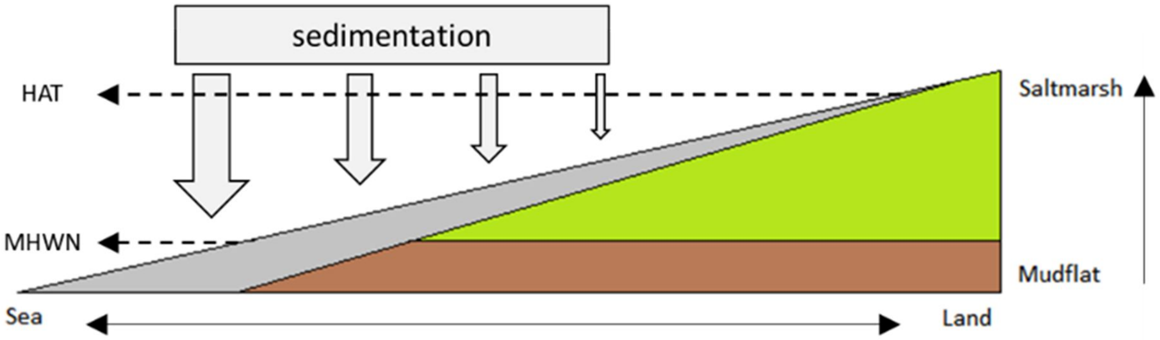

Figure 1-1 Schematic cross-section of the process of sediment accumulation (grey wedge) during saltmarsh development. Greater accumulation is seen nearer the sea, facilitated by plant colonisation. (HAT = Highest astronomical tide, MHWN = Mean high water neap).

1.1.2 Environmental drivers of plant zonation

1.1.2.1 Elevation & topography

Elevation in the tidal frame determines the frequency and duration of tidal flooding (hydroperiod), and is the major driver of saltmarsh plant distribution (Davy *et al.*, 2011). Its role was recognised by early ecologists (Carey and Oliver, 1918; Oliver, 1925; Chapman, 1959) and, more recently, researchers have utilised modern technology to increase the precision and scale of elevation sampling (Collin, Long and Archambault, 2012). Elevation is an important driver because saltmarsh species vary in their tolerance to the stresses of flooding, resulting in a zoned pattern where zones are closely associated with elevation in the tidal frame (Zedler *et al.*, 1999; Davy *et al.*, 2011).

Elevation, and thus hydroperiod, also play an important role in driving other marsh gradients, such as salinity, waterlogging and accretion (Bockelmann *et al.*, 2002; Li *et al.*, 2013), many of which are correlated. This is not to say all alterations of elevation have a consistent effect on hydroperiod because proximity to features such as creeks or poorly draining topographic features (e.g. pools) will either exacerbate or reduce this effect. In addition, small changes (e.g. ± 15 cm) in elevation, often described as topography, are potentially a strong driver of plant community by influencing other environmental conditions. For example, a hummock as small as 10-20 cm will experience reduced flood inundation, decreases in both organic and mineral material input compared to the surrounding areas (Cahoon and Reed, 1995) and will drain more freely, resulting in a higher redox potential compared to the surrounding area, regardless of elevation (Mossman *et al*., in prep). Depressions tend to be waterlogged or accumulate fresh sediment, which reduces air spaces and therefore lowers redox potential (Varty and Zedler, 2008). Although seeming relatively small variations in surface elevation, these features represent a significant portion of the elevation range of a marsh. For example, natural marshes contained topographic variation c.20 cm over horizontal distances of 50 m (Brooks *et al.*, 2015), equating to ~ 20% of the entire elevation range present (Mossman, Davy and Grant, 2011).

While elevation *per se* is well established as a driver of plant communities, relative elevation (topography) is less well understood, nor is its implications to other environmental conditions, or the final effect on saltmarsh vegetation. Currently, the concept of 'topography' in saltmarsh literature often refers to differences in elevation between point measurements. More precisely however, topography is the type and arrangement of physical features of a surface taking the form of names and numbers describing physical features such as orientation (compass bearing), slope (angle) and location (e.g. high, low). These descriptions can be qualitative or quantitative and used to categorise or describe physical features such as humps, depressions and pannes.

It is important to recognise the critical role of topography in saltmarsh ecology as it may have long-term impacts in both its physical form and biological colonisation. Previous models of saltmarsh formation and ecology (e.g. Allen, 2000) have focussed on elevation as the primary driver, and do not include the importance of relative elevation (topography). However, I hypothesise that topography has important effects on plant communities and zonation, within a complex network of drivers. These interactions with topography however, have not been well studied. In Figure 1-2, I propose a model of the environmental influences on plant distribution. Figure 1-2, illustrates a *"trickle down"* effect of individual drivers on saltmarsh diversity and/or productivity based on key literature. However, this literature rarely investigates the interactions between environmental variables within this tier (blue boxes). Furthermore, these studies have rarely employed multiple environmental variables to describe saltmarsh zonation in field conditions, usually experimenting with artificial enrichment or manipulations to study impacts.

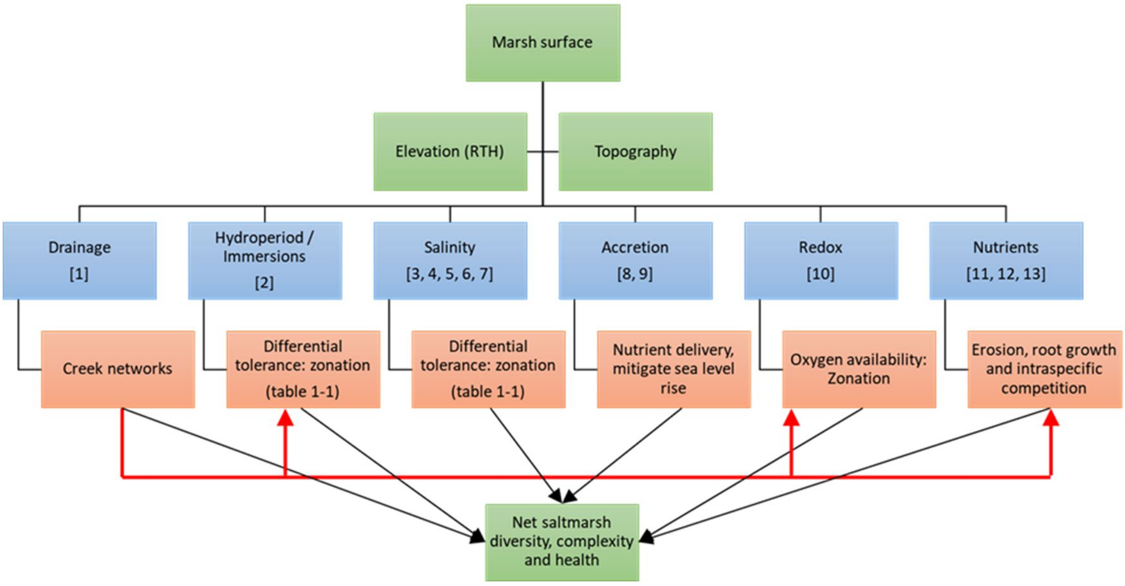

Figure 1-2 Trickle-down effect of topography and surface elevation on other environmental gradients and saltmarsh diversity. Key: RTH = relative tidal height. Primary drivers (green boxes), Secondary environmental conditions linked to elevation (blue boxes) and tertiary mechanisms or consequences of interlinked environmental variables (orange boxes). [1] (Wallace, Callaway and Zedler, 2005) [2] (Cahoon and Reed, 1995) [3] (Alhdad et al., 2013) [4] (Flowers and Colmer, 2008) [5] (Horton and Murray, 2007) [6] (Janousek and Mayo, 2013) [7] (Silvestri, Defina and Marani, 2005) [8] (Craft, 2007) [9] (de Groot et al., 2011) [10] (Davy et al., 2011) [11] (Burden et al., 2013) [12] (Emery, Ewanchuk and Bertness, 2001) [13] (Fox, Valiela and Kinney, 2012)

1.1.2.2 Waterlogging and redox potential

Waterlogging is one the key properties that results in differing plant communities, and ultimately results in anoxic conditions (thus low redox potential). This low redox potential in turn promotes anaerobic decomposing microbial communities, and the development of toxic species of Manganese, Iron and Sulphur that impede plant growth (Sánchez, Otero and Izco, 1998; Pezeshki, 2001; Pezeshki and DeLaune, 2012).

Redox is short for reducing-oxidising reactions and describes the status of electron transfer within chemical reactions. Electron transfer is a critical process in organic, inorganic and biochemical reactions. Possibly the most visual example of these reactions within soil and plant ecology are those that result in changes to the colour of soil. When deprived of oxygen, e.g. where soil pores are waterlogged or filled with very small sediment particles, oxidising reactions cannot occur leaving the soil a black colour (Figure 1-3 A). In the presence of oxygen however often soils take on a reddish hue created by the slow oxidation of metals (Figure 1-3 B), notably the dominant redox couple in wet soils of Iron to Iron oxide, a reddish mineral (Fiedler, Vepraskas and Richardson, 2007).

Plants are differentially tolerant of low redox potential and as a result, redox is a powerful determinant of plant zonation over the entire marsh surface. For example, *Puccinellia maritima* is tolerant of low redox potentials, which allows it to colonise areas at higher elevations than expected where low redox potentials are present (Davy *et al.*, 2011). In contrast, *Suaeda maritima* and *Atriplex portulacoides* are less tolerant of low redox, reducing conditions (Davy *et al.*, 2011).

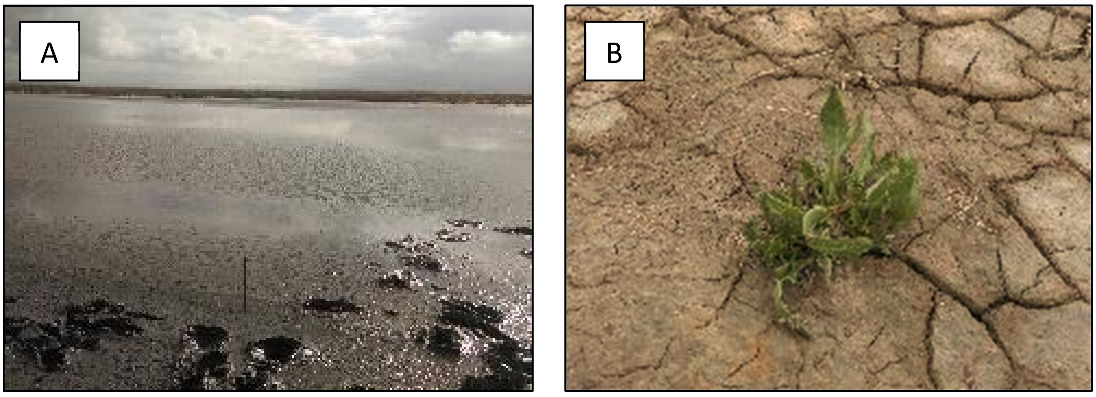

Figure 1-3 Photographs of reducing conditions in saltmarsh soil A black in colour (typical waterlogged anoxic, reducing soil, ~ -200 mV), and oxidation, reddish hue to soil often dryer (oxygenated soil, ~ +200 mV). Steart Managed realignment scheme in Somerset.

We currently know that redox potential is positively correlated with elevation in saltmarshes (Mossman, Davy and Grant, 2012). However, this relationship is imperfect (Davy *et al.*, 2011). This may be due to the roles of local microtopography, whereby on very small scales features may aid drainage on local scales or promote the accumulation of fine sediment in very shallow pannes, impinging Oxygen transfer. Figure 1-4 illustrates the topography of a typical marsh surface with topographic features, such as creeks and hillocks, and hypothesised redox conditions that are directly linked to drainage, topography and elevation combined. However, the relationships between topography, elevation and redox potential have not been clearly tested, and nor have the implications of these on vegetation colonisation.

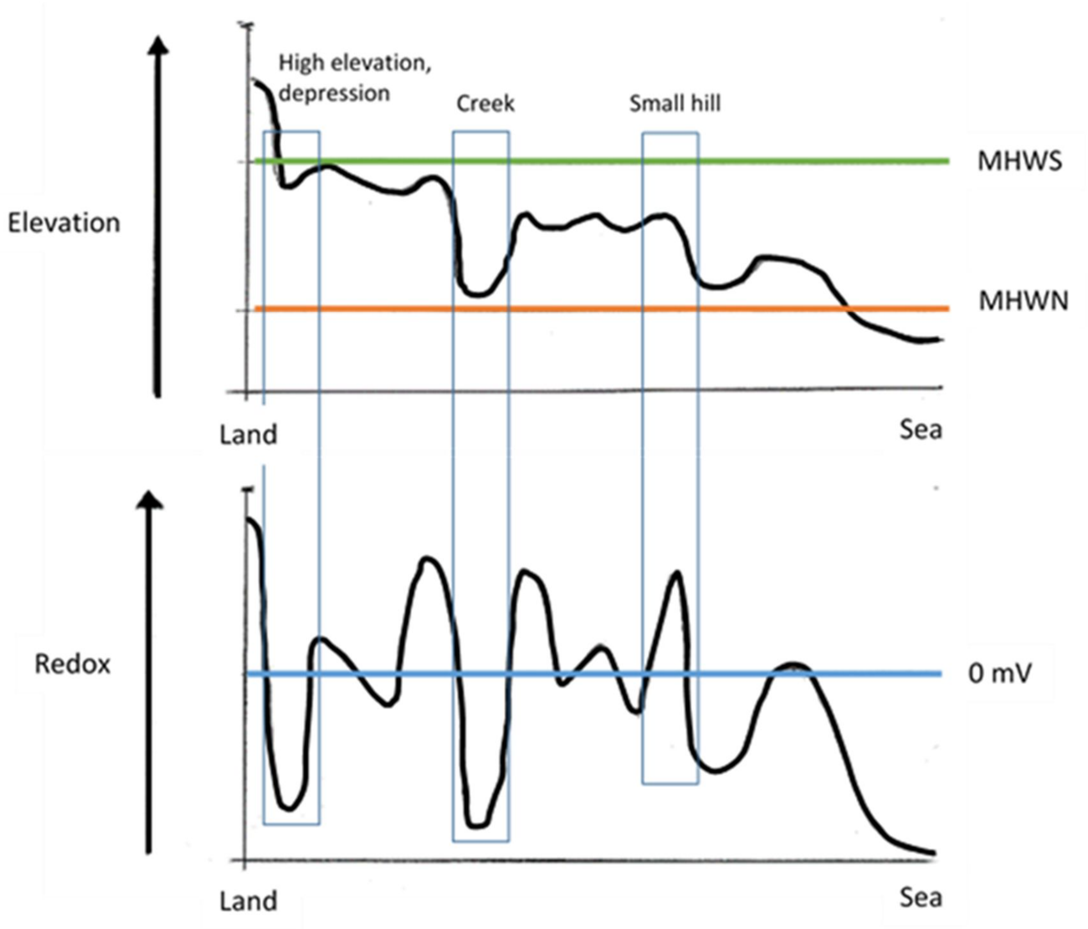

Figure 1-4 A theoretical interpretation of the relationship between topography, elevation, and redox potential.

1.1.2.3 Nutrients

Saltmarshes are thought to be nutrient-limited environments (Levine, Brewer and Bertness, 1998; De Schrijver *et al.*, 2011; Geatz *et al.*, 2013). The theory of nutrient limitation in saltmarshes is based on experimental studies that find increased above-ground biomass and shifts in community composition with enrichment of macronutrients such as Nitrogen (Boyer and Zedler, 1999). Nutrient enrichment can also lead to vertical expansion of elevational niches in some species (Emery, Ewanchuk and Bertness, 2001; Fox, Valiela and Kinney, 2012).

Nutrient enrichment in saltmarsh has been shown to lead to increases in late-successional species and dominance of grasses, such as *Elytrigia atherica*, thus reducing diversity;

increased nutrients appear to release these species from the salinity stress of the upper marsh (van Wijnen and Bakker, 1999). It is plausible that increased inundation caused by sea level rise may help to mitigate any potential shift towards upper marsh species driven by nutrient enrichment. The result of this being that communities shift back towards lower marsh species due to the increased inundation and salinity stress (Donnelly and Bertness, 2001). Redox potential plays an important and complex relationship with nutrient availability and can indicate important ratios of nutrients within the Nitrogen cycle, such as Nitrate and Ammonium. We currently have poor estimates of the current nutrient status within saltmarsh soils, and we do not fully understand the relationships with elevation, salinity and waterlogging, making predictions of nutrient concentrations and their roles in saltmarsh ecology extremely challenging.

1.1.2.4 Salinity

Salinity has an impact on zonation as plants have differential adaptations to this environmental pressure (Table 1-1 and Table 1-2). Salinity is often considered a function of elevation, with areas experiencing more frequent tidal inundation being more saline. However, correlations between salinity and elevation can be weak (Silvestri, Defina and Marani, (2005) because salinity is also driven by evaporation (Bertness and Ellison, 1987; Pennings, Grant and Bertness, 2005), and freshwater inputs. Thus there are temporal patterns, with salinity highest in the summer months when there is increased evapotranspiration and irregular tidal flushing; this temporal variability is greatest at mid to high elevations (de Leeuw, Olff and Bakker, 1990). Salinity is also highly spatially variable, with topographic features such as pannes having hypersaline conditions due to the absence of plant cover, which increases evaporation (Pennings and Callaway, 1992).

1.1.2.5 Interactions

The drivers of the natural zonation of saltmarshes described above. Are often considered in isolation and regarded as having direct effects on saltmarsh vegetation. However, I hypothesise a more complex set of interactions with both elevation and topography at its core (Figure 1-2). As a result, I suggest that all these drivers combined act as a ‘balance beam’ between typical communities (Figure 1-5). The beam suggests that the increase of any one block will tilt the competitive balance, in this case between pioneers and upper marsh species. Experimental studies referred to in the previous subsections have all shown that increases in each of these factors (boxes) tip the balance towards either of these two typical communities.

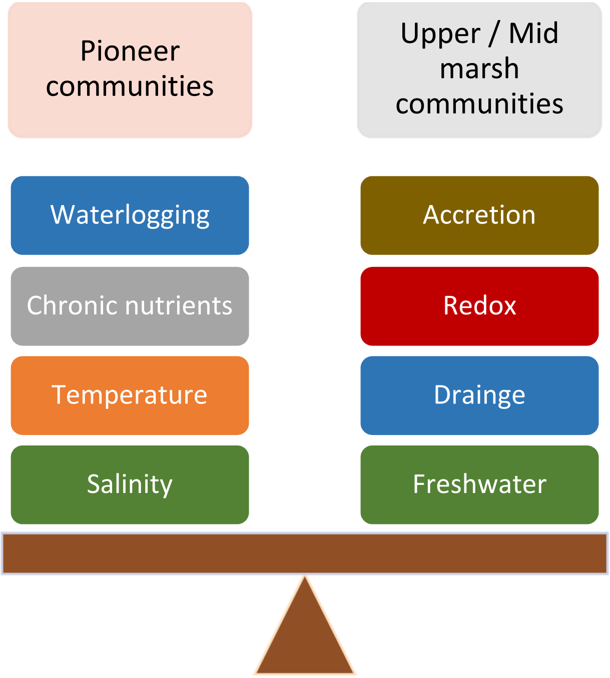

Figure 1-5 The ‘balance beam’ I hypothesise of ambient conditions and community abundance in a saltmarsh.

1.1.3 Further drivers of saltmarsh development

Although the focus of this thesis will be abiotic and physical properties of saltmarshes. The following section will recognise the important roles of plant-plant, animal-plant and microbial interactions that themselves may drive the abiotic and physical properties observed.

1.1.3.1 Soil-Microbial communities

Saltmarshes play and important role in global nutrient cycling acting as both a sinks and sources for various nutrients (Duarte, Freitas and Caçador, 2012; Shao, 2014). It is in this respect that soil microbes influence the form and function of a saltmarsh playing an important role in the bio-availability nutrients required for plant growth and within food web interactions (Hines *et al.*, 2006). Microbes can be divided in many ways though we will consider bacteria, actinomycetes, fungi, algae, protozoa and nematodes. These micro-organisms are abundant in soil and if a carbon source is present for energy and they produce useful bio-available nutrients though processes of decomposition, ammonification, nitrification and mineralisation that can be absorbed by plant roots.

In the case of saltmarshes, decomposers play an important role at early stages of succession prior to vegetation (Schrama, Berg and Olff, 2012). Microbes can also mitigate increased environmental pressure on plants that can result in a competitive advantage for specific species changing the plant community composition (Machado *et al.*, 2012). Interestingly, microbes also benefit from the presence of plants. Colonisation of plants can mediate the negative effect of detrimental chemicals that would otherwise slow the microbial denitrification processes (Almeida *et al.*, 2014). This symbiotic relationship demonstrates the complex nature of a stable saltmarsh where both microbial community and appropriate vegetation reinforce each other through a network of mediation and microbial facilitation. These findings suggests that pre-sampling of realignment soils may be important in tracking microbial and plant communities and also offer a novel method of monitoring the consequences of soil evolution regarding the restoration and management of saltmarshes (Caffrey *et al.*, 2007; Laudicina *et al.*, 2009; Duarte, Freitas and Caçador, 2012).

1.1.3.2 Grazing and food web interacts

It has been suggested that vegetation succession is only understood in the context of food web dynamics (Schrama, Berg and Olff, 2012). An implication of this in terms of MR is that only though the provision of complete and comparable food webs can an equivalent successional saltmarsh processes occur.

In Figure 1-6, we provide a visual representation of the potential divergence from a reference food web stemming from a divergence from the stable processes. Much of saltmarsh food web literature has a focus the consequences of pollution in altering food webs and their subsequent impacts upon the saltmarsh health and vegetation succession. One such example of this type of study in China that suggests the possible threats of non-native plants to increased bioavailability of metals in the water column of which the consequence is yet unknown (Quan *et al.*, 2007). The pace of change in saltmarsh food webs may not be instant due to enrichment, indeed the effect of enrichment may take multiple years to be fully revealed (Pascal and Fleeger, 2013). Grazing to can alter saltmarsh communities due to physical and chemical pressures that may lead to decreased vegetation health, increased soil exposure and alterations in the microbial communities (Ford *et al.*, 2013; Schrama *et al.*, 2013; van Klink *et al.*, 2015). The implication from studies around the world posed show that food web alterations are significant threat saltmarsh development processes. Indeed, the very provision of many ecosystem services we rely upon will suffer without an appreciation for the animal-plant, plant-plant and microbial interactions and functions within a complete food web. The alteration of migratory, seasonal blooms provides a unique insight into the interplay of terrestrial and marine systems and the possible threats posed to the marsh itself. This interplay is well summarised in an Australian study that depicts the load on saltmarsh, microbes and microalgae as primary producers in a complete food web (Laegdsgaard, 2006).

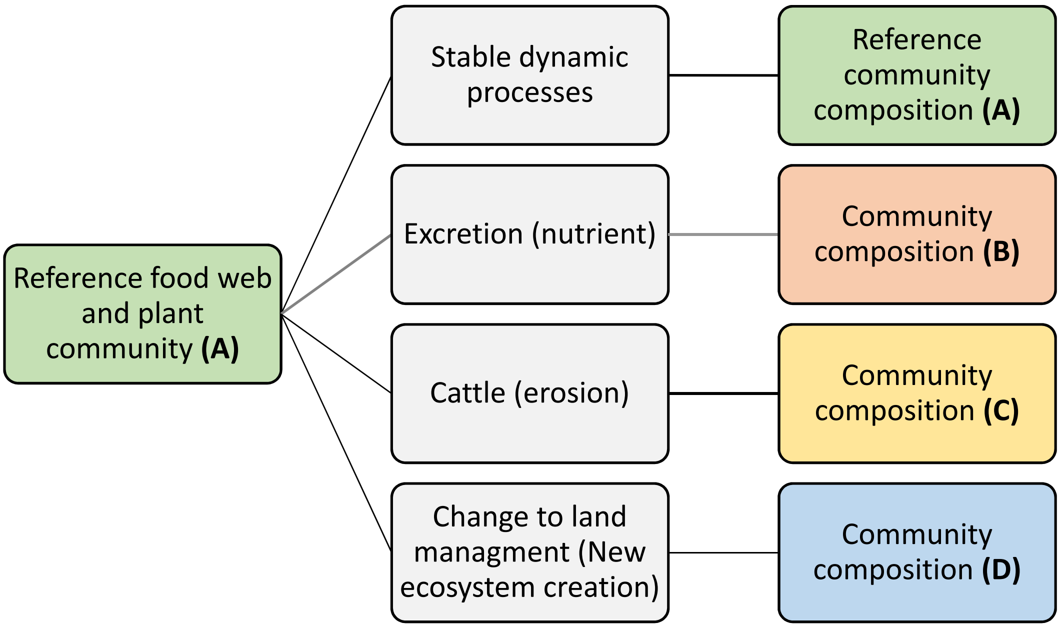

Figure 1-6 Given a reference food web and plant community (green A), we can hypothesis that alterations (grey) to the structure and food web will result in differing communities (red, yellow and blue B, C and D).

1.1.3.3 Nonlinear events and climate change

Outside of the biotic unstudied variables within thesis there is a further and possibly less linear driver of the status of saltmarshes. Climate, storminess and alterations to wave energy can impact saltmarshes. Firstly experimental work has suggested that higher temperatures could lead to an expansion of pioneer saltmarsh plants down into mudflats (Gray and Mogg, 2001), this would reduce the area of unvegetated sediment available for feeding birds (Durell *et al.*, 2006), a significant ecosystem service of considerable value (Barbier *et al.*, 2011). It is not only temperature shifts and the consequences of altering plant communities that are affected by climatological factors. Periodic formation and loss have been reviewed in the Thames estuary (van der Wal and Pye, 2004). In this review one of the primary drivers of period of loss is stated as likely prolonged periods of changes to wind and waves. This suggestion has gained further support in recent years where ‘normal’ weather patterns (i.e. prolonged periods of similar conditions) is can lead to more erosion of the saltmarsh than one off far stronger events (Leonardi, Ganju and Fagherazzi, 2015). In essence the current observed saltmarsh community is a product of the creation of spatial heterogeneity in physical properties with an added often unobserved factor of niche creation via heterogeneity in temporal environmental conditions known as ‘regeneration niches’ (Grubb, 1977).

1.2 Countering saltmarsh loss

Globally, there is a minimum estimate of ~ 55,000 km^2 of saltmarsh (Mcowen *et al.*, 2017), with large areas in temperate land masses such USA and China, but small islands with large coastlines also have significant area of saltmarsh. Despite their importance, global saltmarsh extent has been in steady decline with losses at a minimum of 1–2 % per year (Adam, 2002). Saltmarsh loss has historically been dominated by reclamation for various uses, including agriculture, urbanisation and port construction/development (Gedan, Silliman and Bertness, 2009). While in Europe the substantial land claim has now slowed, this is not the case in other regions losses to industry, housing or agriculture have been accelerating in recent years (Tian *et al.*, 2016; Mcowen *et al.*, 2017). In addition, many regions are showing a trend towards net erosion of marsh, likely due to climate change and eutrophication (Britsch and Dunbar, 1993; Morris *et al.*, 2004).

Saltmarshes have been offered protection in law in many countries and regions of the world (Broome, Seneca and Woodhouse, 1988), with recent legislation requiring compensatory habitat to be created to counter losses, e.g. the EU Habitats Directive (European Commission, 2007). The Habitats Directive requires replacement for all saltmarsh lost with compensatory habitat that has “equivalent biological characteristics”. These biological equivalent habitats must also be of “comparable proportions of habitats and species” to the saltmarsh negatively affected since 1992, and importantly, created prior to any future degradation or development. This places member states in a position that proactive restoration is the only method to meet the requirements of the legislation. The US Clean Water Act (ca. 1972) also requires no net loss of marsh extent across national or state scales, but provides flexibility in the location of compensatory habitat, as long as there is minimum ecosystem function locally (e.g. fish nursery and wave protection) (Copeland, 1999).

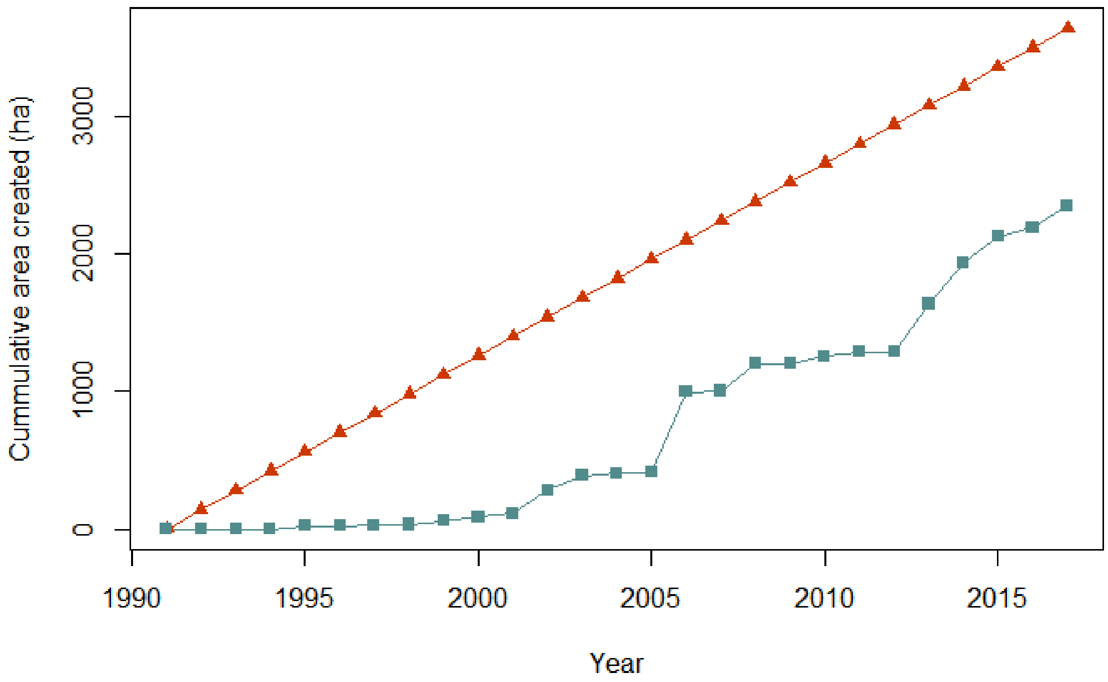

Figure 1-7 Cumulative total of the area of saltmarsh restored in the UK (slate grey squares) and the cumulative total of target area (140ha per year) (orange triangles).

If the UK government is to reach its expected legal targets as determined by the Habitats Directive, there is an ongoing need to create approximately 140 ha per year of biologically and functionally equivalent saltmarsh (Rupp-Armstrong and Nicholls, 2007). At the time of writing (2018), 53 saltmarsh creation schemes have been conducted, generating ~ 2,350 ha of intertidal habitat (ABPmer, 2018). This is some 1289ha behind the pace required to compensate for the current, and historical losses (see). The figure of 2,350 ha is also generous as it assumes that all the area flooded result in saltmarsh plant communities (rather than mudflat) or equally importantly, that the sites have equivalent biological and functional characteristics, (something rarely quantified in the literature). In recent years, some of the largest schemes have been completed, possibly showing the effectiveness of the EU legislation and growing appreciation for saltmarsh habitats, including the sites Steart, Medmerry and Wallasea Island (Phase 1), totalling 37% of all restored marsh created to date (ABPmer, 2018).

Attempts to establish or re-establish saltmarshes though restoration techniques have a relatively long history. Managed realignment (MR), or ‘de-embankment’, is the deliberate breaching of tidal blockades such as sea walls, embankments or levees allowing tidal waters to flood the selected land. This type of scheme often goes hand in hand with the construction of new sea walls inland creating a compartment of land allowed to be flooded. A similar method of creating marshes is called regulated tidal exchange (RTE). This method is much like MR with the exception that tidal inundation is controlled with a sluice gate. Success of RTE has been variable because it is difficult to establish an accurate simulation of flooding and sedimentation, leading to slow colonisation of plants (Masselink *et al.*, 2017). These engineered marshes created through MR and RTE very rarely embrace post-restoration intervention, relying on the initial design to fulfil all the conditions required for natural colonisation of plants. Planting and seeding are not carried out in the UK. Experimental, post-restoration topographic manipulation has been undertaken at one site, however these have not been monitored to evaluate the effects on the vegetation community. At other sites, topographic manipulation has more recently been incorporated into site design (e.g. Steart, Hesketh Out Marsh East and Wallesea), but we have limited understanding of the type, size and distribution of topographic features in natural or restored marshes, and so the money spent on these groundworks may not be as efficient as it could be.

1.2.1 Saltmarsh restoration success

Restored marshes do not have equivalent vegetation communities to the reference marshes they are expected to match, even after 50-100 years (Mossman, Davy and Grant, 2012). Equivalence is rare in the majority of European restoration schemes (Wolters, Garbutt and Bakker, 2005; Chang *et al.*, 2016), and in the US (Boyer and Zedler, 1999; Zedler and Callaway, 2000). Plant species richness is lower on restored saltmarshes, despite some sites being >50 years old (Garbutt and Wolters, 2008). In UK restored saltmarshes, some mid-marsh species (e.g. *Triglochin maritima*) are underrepresented regardless of time since restoration (1-131 years, (Mossman, Davy and Grant, 2012)). In contrast, other species were more common. For example, at the older realigned sites (25-131 years), *Atriplex portulacoides* and *Spartina anglica* were more abundant than expected.

The recreation of other ecosystem services and functions, such as Carbon storage or fish use, are also less successful (Colclough *et al.*, 2005; Burden *et al.*, 2013), and this may be due to the fact they are linked to vegetation burial (Carbon storage) and habitat complexity (fish use), reiterating the importance of equivalent vegetation. In terms of creating biologically equivalence for taxa other than plants, restoration sites are usually quickly colonised but again rarely reach the same overall structure as natural marshes. For example, birds can quickly colonise (Atkinson *et al.*, 2004), although habitat structure may not be suitable for all species (Zedler and Callaway, 1999). Benthic and terrestrial invertebrates also quickly colonise but community structure is different (Mazik *et al.*, 2010), possibly due to the role of below ground biomass (from plants growth) enhancing the colonisation potential of some invertebrates (Johnson *et al.*, 2018).

1.2.2 Possible drivers of biological divergence in restoration sites

There are a range of potential biotic and abiotic causes for the differences in vegetation communities between natural and restored saltmarshes. While restored sites may immediately provide a range of suitable environmental conditions for colonisation (Hughes, Fletcher and Hardy, 2009), differences remain. Here I discuss how these drivers occur, interact and result in the current communities we observe.

MR schemes tend to occur on areas that were formerly reclaimed from saltmarsh for agriculture, and which are therefore lower elevation than adjacent natural marshes due to the process of dewatering, compaction and relative sea level rise since the reclamation. The low initial elevation can result in substantial accretion for example, one site (Tollesbury, Essex, UK) there was a mean accretion ~14 cm over the site after five years (Garbutt *et al.*, 2006). A consequence of this substantial 14 cm of accretion may be reflected within the plant communities. This MR scheme was initially, and still being, dominated by pioneer species 19 years after restoration (pers. obs.). It is very likely that this may be due to the site remaining too low and excessive accretion causing seedling mortality (Bouma *et al.*, 2016).

Agricultural activities such as ploughing greatly alter the soil chemistry and structure (van Klink *et al.*, 2015; Spencer *et al.*, 2017), and increase salinity and waterlogging at plant rooting depth (Di Bella *et al.*, 2015). MR schemes are typically created on former arable land and so nutrient concentrations are thought to be initially high; indeed total inorganic nitrogen can be 2.5 times higher than adjacent agricultural land on a MR scheme, up to 15 years after flooding (Burden *et al.*, 2013). However, in other studies nitrogen levels in MR could also be were lower that adjacent arable land just four years after flooding (Langis, Zalejko and Zedler, 1991). Understanding the status of nutrient levels in restored saltmarshes is a challenge because there are limited examples in the literature and they are contradictory. Furthermore, many studies do not compare restored systems to reference sites, and there is no clear review of the nutrient status of natural marshes, a globally important ecosystem.

Agricultural activities, such as ploughing, also removes topography and flatten the surface. Indications from one MR site suggest that natural saltmarshes may be more varied in elevation than MRs, particularly at small scales e.g. 1-10 m, and natural marshes remain more varied than engineered efforts that we might expect to approximate natural surface texture (Brooks *et al.*, 2015). Reduced surface topography will lead to a uniform regime of inundation and uniform redox conditions. Natural marshes tend to be more oxic at the lower elevations, and have lower redox at the highest elevations in comparison to both MR and older accidently created saltmarsh (Mossman, Davy and Grant, 2012). We know that low redox potential is expected in local depressions and higher redox on well-drained mounds (Castellanos, Figueroa and Davy, 1994; Varty and Zedler, 2008), but these topographic features are likely to be less prevalent in both upper and lower areas of MR sites. Consequently, plant diversity across the elevation range of restored marshes maybe reduced due of the limitation of niche provision. Moderate and upper marsh species in particular, that are tolerant of waterlogging conditions are likely to see reduced availability of niches (Varty and Zedler, 2008). *Limonium vulgare*, *Triglochin maritima* and *Plantago maritima*,rare on restored saltmarshes of all ages (Mossman, Davy and Grant, 2012), this is because they occur at higher elevations and moderate redox potentials (Davy *et al.*, 2011; Sullivan *et al.*, 2017). *Atriplex portulacoides*, which is the potential dominant, shares the elevational niche of these species but is most abundant in the highest redox potentials – conditions more frequent on MR sites. There is however, very limited information on the comparative topography of natural and restored sites, or the consequences of these features on redox potential, or in conjunction with redox potential in understanding spatial distributions of saltmarsh vegetation (zonation).

Creek networks assist the drainage of saltmarsh, contributing to creating a range of environmental conditions and thus niches for species to inhabit. However, density and complexity of creeks is lower on MR compared to natural marshes (T. Smith, unpublished MSc thesis, Chirol *pers. comm.*). The creek design of MRs can lead to a more uniform flow of water across the sites (Ellis and Atherton, 2003), with consequences for drainage and niche availability for plants. Crooks *et al.*, (2002) showed drainage regimes in restored saltmarshes could result in significant alterations in plant communities, with the notable increases in abundance of *Puccinellia maritima* in undrained sites and *Atriplex portulacoides* in the drained.

A final possible source for disparity in species composition between restored and natural marshes may stem from the availability of seeds or propagules. Restored marsh seedbanks have lower seed counts, and lower probability of germination (Morzaria-Luna and Zedler, 2007). Saltmarsh propagules may be dispersed by birds (Soons *et al.*, 2016) or by the tide. Wolters, Garbutt and Bakker, (2005) suggest the process of seed movement into a realigned site is ‘step-wise’, with pioneer species having the most opportunities for dispersal as they are inundated more regularly and therefore accumulate on rising tides. This as a result, may increase their dominance in the early colonisation periods. To accompany this possible accumulation of pioneers, several mid marsh species, such as *Limonium vulgare* and *Triglochin maritima*, rare on restored sites, are known to have low seed viability (Davy and Bishop, 1991), reducing their colonising ability. While these studies may go some way to demonstrate that dispersal may be limiting to colonisation, it does not explain why some species remain rarer on restored marshes even after 100 years, despite being present on adjacent natural marshes. It can be hypothesised that some species require a prerequisite ‘window of opportunity’ either in terms of a suitable environmental niche or little competition to colonise (Hu *et al.*, 2015; Sullivan *et al.*, 2017).

1.3 Restoration ecology

The field of restoration ecology has undergone a significant period of growth in the past two decades, aiming to conserve, enhance and preserve biodiversity and ecosystems (Young, Petersen and Clary, 2005; Choi, 2007). Ultimately the goal of ecological restoration is to provide a means for long term repair / recovery of a community or ecosystem (Young, 2000; Davis and Slobodkin, 2004). As a result, a successful restoration project must be considered the timely production of equivalent habitat, in both form and function, when compared to that of a reference, benchmark or a historical baseline (Strange *et al.*, 2002; Boorman, 2003). Despite policy requiring equivalence, returning a system to a historical state is challenging (Palmer, Ambrose and Poff, 1997).

In order to actively improve restoration outcomes, we must have greater understanding of the balance between different stable states (e.g. communities), ecotones (e.g. halophyte to terrestrial) and transition zones (gradients), and of ecosystem functions and mechanisms (e.g. niche occupation, intraspecific competition, succession) (Young, Petersen and Clary, 2005). This information is often lacking in natural, baseline systems and so recreating these conditions through restoration is inherently challenging. There has been limited development of predictive models in restoration (Brudvig, 2017), which impedes our ability to foresee the effects of management decisions making changes risky to justify (Zedler, 2017).

1.4 Summary and key knowledge gaps

Little is known about the topographic diversity of natural or restored saltmarshes, or how this topography develops over time. Consequently, we do not understand how any effect of topography interacts with the relatively well-studied drivers of vegetation such as elevation and redox, or if it has a similar ability to drive communities on its own. Further to this, we currently do not know if topographic complexity is related to the spatial pattern of plant communities. We know MR sites fail to develop the same biological characteristics as natural counterparts but there is no information to describe how diversity manifests itself spatially in natural marshes, let alone on MR sites. Filling this significant gap in the literature may aid future restoration and highlight the importance of encouraging Beta diversity and its drivers to improve restoration of saltmarshes. As there are currently no appraisals of management interventions that have aimed to encourage diversity post restoration, we are yet to understand to consequences of management decisions or begin to assess their potential value. Despite their importance in the structure of vegetation communities, measurements of nutrient levels in restored saltmarshes are rare, and studies often lack a comparative natural system. Furthermore, our understanding of the baseline nutrient status of natural marshes is weak, making the study of temporal changes or restoration challenging.

1.5 Thesis outline and structure

In this thesis I characterise the relationships between elevation, topography, redox potential and sediment nutrient concentrations, and demonstrate how these relate to the distribution of plant communities on both natural and restored saltmarshes. I also investigate how environmental conditions develop over time on a newly restored site, testing for signatures of prior land use. Specifically, I aim to:

1) Characterise typical topographic structure of natural and MR saltmarshes and investigate differences between them.

2) Quantify the nutrient status of natural and restored saltmarshes, relating these concentrations to known levels of eutrophication.

3) Quantify the temporal changes in soils conditions following restoration of tidal flooding and investigate their evolution in relation to natural saltmarsh and permanent agricultural soils, examining the roles of former land-use and topography as potential drivers of any differences observed.

4) Determine the relationships between elevation, topography and redox potential, and the effects these have on vegetation diversity.

5) Investigate the potential for topographic manipulation as a management tool to improve vegetation diversity, thus increasing restoration success.

1.5.1 Chapter outlines

Chapter 2: Restored saltmarshes lack the topographic diversity found in natural habitat. Accepted for publication in Ecological Engineering

In this chapter I use LiDAR and GIS to quantify site-level topography across natural reference saltmarshes and restored sites of various ages. I also compare restored sites to coastal agricultural fields, which represent conditions prior to restoration. This allows the detection of transitions from pre-restoration agricultural conditions towards those in a natural habitat.

Chapter 3: Global analysis of the nutrient status of natural and restored saltmarshes

In this chapter I conduct a systematic review of global measurements of nutrient concentrations in natural and restored saltmarshes. I aim to assess the extent to which saltmarshes are nutrient enriched beyond levels at which erosion is known to occur and investigate if restored sites are more enriched due to their prior agricultural use.

Chapter 4: Temporal changes in soils conditions following restoration of tidal flooding in a new managed realignment scheme: signatures of time, space and land use

In this chapter I investigate the developing sediment characteristics of a newly flooded MR site. I sampled prior to flooding to create an initial baseline and then quarterly for 2.5 years to investigate temporal changes, and in four differing land uses to detect spatial variability and signatures of agricultural land use.

Chapter 5: Lack of local topography results in homogenous vegetation communities on restored saltmarshes

Here I investigate the differences in topography, redox and plant diversity between natural and MR saltmarshes. I examine the spatial arrangement of heterogeneity in the two types of saltmarshes, with additional analysis of recently constructed topographic manipulations designed to aid increased vegetation diversity.

Chapter 6: Discussion and management implications

In this final chapter, I consolidate the lessons learned in this project. I will start by discussing briefly the key findings regarding the roles of topography, redox and nutrients independently and together within natural and MR systems. I will make recommendations for further research discussing current barriers to my findings. I will conclude by discussing the management implications of my research within restoration science and the restoration of saltmarshes.

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2 Restored saltmarshes lack the topographic diversity found in natural habitat

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Abstract

Saltmarshes can be created to compensate for lost habitat by a process known as managed realignment (MR), where sea defences are deliberately breached to flood low-lying agricultural land. However, the vegetation that develops on MR sites is not equivalent to natural habitat. In natural sites, surface topography and creek networks are drivers of vegetation diversity, but their development on restored sites has not been well studied. We investigate the topographic characteristics of 19 MR areas, and compare these to nearby natural saltmarshes (representing desired conditions) and to coastal agricultural landscapes (representing conditions prior to MR). From high-resolution LiDAR data, we extracted values of elevation, six measures of surface topography (although two were later excluded due to colliniarity), and three measures of creek density. MR and natural marshes differed significantly in all surface topographic indices, with MR sites having lower rugosity and more concave features, with greater potential for water accumulation. MR sites also had significantly lower creek density. MRs and coastal agricultural landscapes were more similar, differing in only one topographic measure. Importantly, there was no relationship between age since restoration and any of the topographic variables, indicating that restored sites are not on a trajectory to become topographically similar to natural marshes. MR schemes need to consider actively constructing topographic heterogeneity; better mirroring natural sites in this way is likely to benefit the development of saltmarsh vegetation, and will also have implications for a range of ecosystem functions.

2.1 Introduction

Saltmarsh is a valuable intertidal ecosystem that provides habitat for rare species, as well as important ecosystem services such as water regulation, wave attenuation, and recreation (Barbier et al. 2011). Loss of saltmarsh, particularly due to agricultural reclamation, has been substantial, with less than 50% of the extent of historic habitat remaining worldwide (Adam 2002; Barbier et al. 2011). Although land claim still occurs, one of the major threats currently affecting saltmarsh is sea-level rise (Adam 2002; Hay et al. 2015; Nicholls et al. 1999), exacerbated by the construction of static, hard sea defences, which prevent the natural landward migration of marshes, so that marshes are trapped between sea defences and rising sea-levels. This coastal squeeze results in loss of saltmarsh (Morris et al. 2004).

New saltmarsh is being created to combat this loss of habitat (Callaway 2005; Zedler 2004), partially motivated by legislation requiring its replacement (e.g. European Commission 2007, USA Clean Water Act). Saltmarsh can be created through the process of managed realignment (MR), where sea defences are deliberately breached following the construction of new defences further inland, to allow tidal waters to flood the land between (French 2006). Low-lying, coastal agricultural landscapes provide a key location for the restoration of saltmarshes, because much of this was saltmarsh prior to land claim.

Saltmarsh plant and invertebrate species can quickly colonise newly established MR sites (Garbutt et al. 2006; Mazik et al. 2010; Wolters et al. 2005), but community composition and function are often different to that found on natural saltmarshes. For example, plant communities that develop on MR sites are not equivalent to those found on natural saltmarshes (Mossman et al. 2012a). Furthermore, the vegetation on sites established on agricultural land accidentally breached during storm surges remains different to that on natural marshes, even 100 years post flooding (Mossman et al. 2012a). These differences in plant assemblages reduce biogeochemical functions such as carbon storage (Moreno-Mateos et al. 2012) and are likely to have knock-on effects on other plant-influenced ecosystem functions such as wave attenuation (Möller and Spencer 2002; Rupprecht et al. 2017) and sediment erosion/ deposition dynamics (e.g. Ford et al. 2016), meaning that restored marshes are unlikely to satisfy legal requirements for biological and functional equivalency with natural marshes (Mossman et al. 2012a). Elevation (height above sea-level) is a key determinant of the vegetation communities that colonise restored sites because saltmarsh plants have clear elevational niches (Masselink et al. 2017; Sullivan et al. 2017; Zedler et al. 1999). Some restored sites were initially at low elevations because of relative sea-level rise and shrinkage of the land during the years of reclamation, and this may have limited vegetation colonisation (Garbutt et al. 2006).

Plant species also vary in their tolerance of poorly drained, waterlogged sediments (Davy et al. 2011; Huckle et al. 2002), with these conditions more frequent in some MR sites (Sullivan et al. 2017). However, the drivers underlying this increased waterlogging are poorly understood, although in some sites this appears to be due to poor drainage (Masselink et al. 2017). Local variation in surface elevation and shape, i.e. topography, can influence sediment drainage, with flat surfaces draining poorly. Increased topographic variation and complexity could increase the range in potential niches available and thus increase plant diversity (Kim et al. 2013; Moffett and Gorelick 2016; Morzaria-Luna et al. 2004), which could influence the provision of ecosystem services such as flood defence (Rupprecht et al. 2017). Furthermore, topographic features such as creeks are important to saltmarsh functioning, as they supply sediment and water across the marsh, and provide nursery habitat for juvenile fish (Cavraro et al. 2017; Desmond et al. 2000; Peterson and Turner 1994). Topography on natural saltmarshes can take many forms, such as hummocks, pans, creeks and levees (Figure 2-1; Goudie 2013). Land management during reclamation, such as ploughing, trampling and channelization of creeks, may reduce surface topography prior to restoration. For example, research at one MR site found reduced heterogeneity in surface elevation compared to natural marshes (Brooks et al. 2015). However, little is known about the topographic diversity of other restored marshes or how this topography develops over time.

We assess the surface elevation, topography, and creek network density and diversity of 19 MR areas, comparing these to natural saltmarsh and local agricultural reference sites. To do this, we use remote sensing (specifically, Light Detection And Ranging [LiDAR]) derived digital elevation models (DEMs), from which we calculate a range of topographic indices and creek network measures that describe the characteristics of the marsh surface. Using this data, we investigate the following questions: 1) Does topography differ between natural saltmarsh, restored saltmarsh (MR), and adjacent agricultural landscapes; 2) Does topography vary with age since restoration and with former land-cover; 3) Are any differences in topography between MR and natural saltmarshes consistent across the intertidal elevational range?

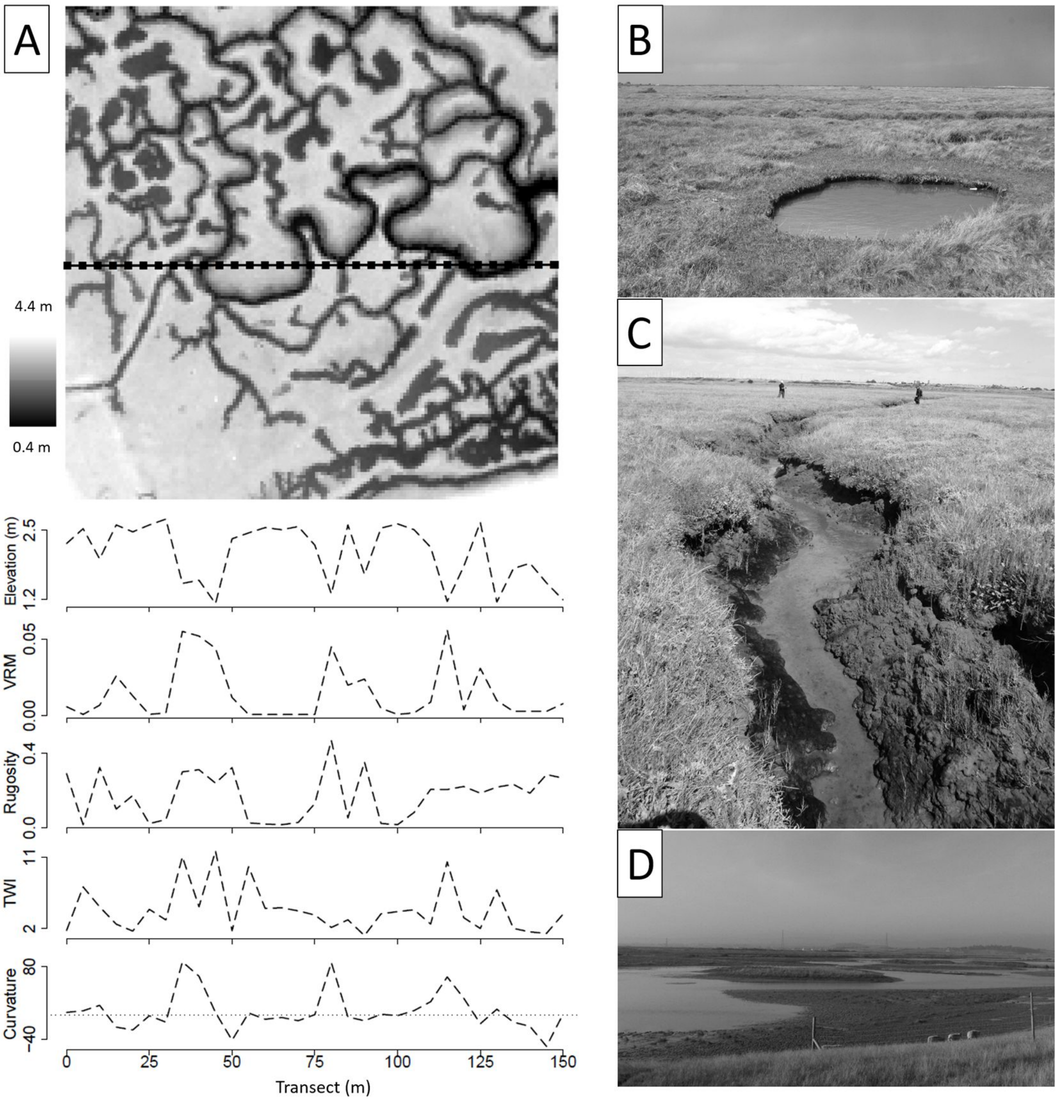

Figure 2-1 (A) A sample digital elevation model from Tollesbury (Essex) showing elevation (m ODN). Topographic variables have been illustrated along a seaward transect represented by a dashed line. The five plots below show measurements every 5 m along this transect. From top to bottom these are Elevation, vector rugosity measure (VRM), rugosity (s.d. elevation), topographic wetness index (TWI) and profile curvature. For profile curvature, the dotted line separates convex (-ve) and concave (+ve) scores. Photos illustrate (B) a concave salt pan with high TWI and low rugosity; (C) a creek with variable TWI, concave profile curvature and high rugosity; (D) a constructed hillock at a MR that has low TWI, higher rugosity and convex profile curvature.

2.2 Methods

2.2.1 Study sites

Seventeen MR sites, ranging from 4-23 years since the date of breach, were selected along the south and east coasts of the UK (Figure 2-2 and Table A2-1). Two of the MR sites were divided into two hydrologically distinct areas by sea walls or other landscape features, which resulted in a total of nineteen MR areas. MR sites were identified using the ABPmer online database (ABPmer Online Marine Registry 2014) and aerial photography, and later selected based on the availability of LiDAR data after restoration, as well as to ensure coverage of a range of geographic locations and site ages. Twelve natural saltmarshes and fourteen agricultural plots were sampled as reference sites, representing respectively the desired end-conditions and likely starting conditions of restored sites. Natural saltmarshes were selected to minimise the distance to MR sites (mean distance to MR site = 6.95 km) while ensuring that they were large enough for reference plots of similar size to MR sites to be created. In some areas of the UK, natural saltmarsh is currently undergoing substantial erosion (Cooper et al. 2001). This type of erosion is easily identified by interpretation of aerial photography due to substantial internal dissection and limited vegetation cover; these areas were not sampled. Sites affected by significant anthropogenic structures other than sea walls, such as slipways and groins, were also not selected. Areas of natural saltmarsh were often larger and lacked the clear boundaries of MR sites, which were enclosed by seawalls. In this study, we defined the extent of the sampled natural saltmarshes by using the mean shoreline length of the 19 MR areas. The extent of the marsh perpendicular to the shoreline was defined as the seaward edge of the vegetation, identified from aerial photography. Using these rules, a polygon was digitised within a GIS environment to establish site area of each natural marsh. The mean size of MR areas was 16.5 ha and natural saltmarsh was 18.2 ha. Agricultural reference areas were selected based on the criteria that sites should be as close as possible to MR areas (mean distance = 1.97 km), be adjacent to the coast/ estuarine system and be continuous fields (not surrounded by walls or roads as these can be problematic for the flow models used to construct some topographic metrics) that were large enough to create plots of similar size to MR areas (mean size of agricultural areas = 13.8 ha). MR is carried out on both arable and grazed land, so both were included as agricultural reference areas (topography was similar between arable and grazed reference areas, Fig. A1). Each estuarine complex containing a MR area had at least one natural reference (with the exception of the Clyst Estuary where no suitably sized natural reference marsh was available) and one agricultural reference area, ensuring that regional variation in variables such as tidal range and plant community composition were similarly represented in both MR sites and reference sites. Sampling multiple sites this way also enabled us to capture variation in reference conditions (Vélez-Martín et al. 2017).

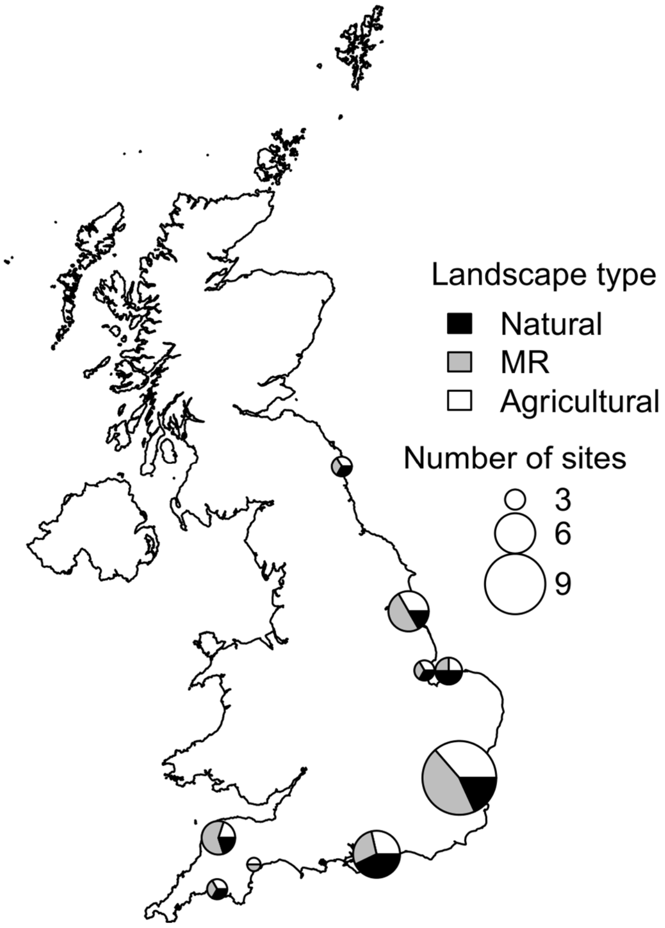

Figure 2-2 Location of study sites. Pie charts are positioned at the centroid of clusters of sites within 0.5 degrees of each other, and show the proportion of sites that were natural marshes, managed realignments (MR) and agriculture. The size of each pie chart is proportional to the number of sites sampled. Coordinates of each study site are given in Table A2-1.

Previous land cover of MR sites was identified using the land-cover datasets for 1990 and 2007 (Morton et al. 2011), enabling the comparison of topographic variation between different former land covers. Of the nineteen MR areas, we found eleven were formerly defined as dominated by grazing practises (mown or grazed turf, meadow and semi-natural swards) and eight as ‘arable’ use prior to breaching (arable and horticulture).

2.2.2 Quantifying topography

One-metre resolution LiDAR-derived DEM data were downloaded for all sites on 11th February 2016 from the free UK LiDAR resource (UK Government 2016). These were mosaicked into a continuous gridded raster surface (one for each site rather than a complete coastal DEM for England) in ArcGIS © version 10.2 (ESRI 2013). The date of the LiDAR survey was noted during download in order to calculate the number of years since restoration that the LiDAR data were collected, i.e. the age of the restored site (Table A2-1). The stated vertical accuracy (root mean squared error) of the UK LiDAR dataset was between ± 5 cm and ± 15 cm, with values tending to be lower in more recent surveys (Environment Agency 2016). For each location area, a site boundary polygon was digitised. We then randomly selected 10% of the cells contained within each polygon as our sampling points using a (minimum) separation between points of 1.4 m to ensure no resampling of values. At each sampling point, six measures of topography (including measures of rugosity, curvature, slope and topographic wetness) and three measures of the creek network density and diversity were initially calculated and extracted, with measures selected for their ecological interest whilst also limiting redundancy between measures (Table 2-1, Figure 2-1).

Table 2-1 Description of topographic variables selected and their form and functional importance. Note that slope and total curvature were not included in subsequent statistical analyses as they were strongly correlated with other topographic variables.

DEM variable	*Topographic relevance*	*Ecological importance*
Elevation [1,2]	Flooding duration	Zonation / sea-level change mitigation
Slope (deg.) [3]	Drainage and niche	Soil hypoxia
Vector rugosity measure (VRM) [4, 5]	Micro topography	Metre scale niche detection
Rugosity (RUG) [4, 5]	Micro topography	Metre scale niche detection
Total curvature [6]	Creek detection	Creek development, drainage
Profile curvature [6]	Creek detection	Creek development, drainage
Topographic wetness index (TWI) [7]	Local soil moisture	Soil hypoxia independent of slope
Distance to creek [8, 9, 10]	Drainage	Bio/Chemical sediment transfer
Creek order [8]	Network complexity	Erosion and levee creation (plant niche)
Creek density [11]	Drainage	Vegetation configuration

Reference key: [1] (Bockelmann et al. 2002), [2] (Brooks et al. 2015), [3] (Hladik and Alber 2014), [4] (Collin et al. 2010), [5] (Sappington et al. 2007), [6] (Moore et al. 1991), [7] (Sörensen et al. 2006), [8] (French and Stoddart 1992), [9] (Christiansen et al. 2000), [10] (Sanderson et al. 2000), [11] (Moffett and Gorelick 2016)

We employed a 3 x 3 cell neighbourhood (3 m^2) with a moving-window to calculate six of the topographic variables. We did not use a larger window as this would artificially smooth the landscapes losing the impact of smallest features (Liu et al. 2015), such as small creeks often < 1m in width, thus reducing the biological relevance of values obtained (Grohmann et al. 2011). From this, two indices of local surface heterogeneity, commonly known as rugosity, were extracted. The first measure of rugosity (RUG) was obtained using the standard deviation of elevation in the local 3 x 3 window (Grohmann et al. 2011; Hobson 1972). The second was the vector rugosity measure (VRM), a 3-dimensional measure of rugosity, calculated as the summed magnitude of variation along x, y and z vectors producing a ruggedness value on a scale of 0 - 1, with 0 being flat and 1 equating to maximum ruggedness (Hobson 1972; Sappington et al. 2007).

$VRM = \frac{\sqrt{\left(\sum_{i=1}^{n} X_i\right)^2+\left(\sum_{i=1}^{n} Y_i\right)^2+\left(\sum_{i=1}^{n} Z_i\right)^2}}{\mathrm{n}}$, where X_i = sin(slope) x cos(aspect), Y_i = sin(slope) x sin(aspect) , Z_i = cos(slope) and n = cell neighbourhood. VRM has been shown to not be strongly correlated with other topographic variables, thereby helping to avoid collinearity (Sappington et al. 2007). The third index obtained using the 3 x 3 cell neighbourhood was the topographic wetness index (TWI). TWI is defined as the number of cells draining through each point in the context of the local slope, and calculated as TWI = ln (a / tan b) where a = local upslope area and b = local slope in radians. High TWI values indicate drainage depressions and the lowest values centred on the top of ridges (Beven and Kirkby 1979; Sörensen et al. 2006).

Inbuilt functions within ArcGIS were used to calculate surface slope and two measures of surface curvature. Slope is a useful topographic variable measuring in degrees the angle of maximum elevation change within a pre-defined window, in our case 3 x 3 cells. Curvature is also calculated at local-scale and can be derived in several ways. Here, we use curvature following the direction of maximum slope (profile curvature), and an aggregated curvature in all directions (total curvature) (Moore et al. 1991). Negative values of curvature indicate a convex feature, zero a planar surface and positive values a concave feature.

The elevation relative to Ordnance Datum Newlyn (ODN, approximately mean sea-level) was extracted from the DEMs. However, elevation relative to mean sea-level does not account for the variation in tidal amplitude between regions. In order to place the elevation relative to ODN in the context of the local tidal regime, we transformed elevation into relative tidal height (RTH) on a scale of 0 - 1, where 0 = mean high water neap tide level (MHWN) and 1 = mean high water spring tide level (MHWS). Data for MHWN and MHWS levels were obtained from local port data and those published in Mossman et al. (2012b).

To describe the creek networks, we calculated distance to nearest creek (measured from each sampled point) and two site-scale measures, total creek density and the density of different creek orders. Creek metrics were not calculated for agricultural sites due to the lack of functional comparability with marsh creek networks. To delineate creeks from a DEM, we used flow accumulation threshold set at 1000 cells, as this value resulted in the most reliable delineation of creeks (i.e. without including relic creeks and salt pans). Flow accumulation-based networks can be subject to erroneous creeks in flat areas, so we used semi-automated methodology to increase accuracy (Lang et al. 2012; Liu et al.

2015), as a result aerial photography and satalite imagery were used to post-process the flow accumulation model as they have been shown to be effective at identifing creek networks (Goudie 2013; Moffett and Gorelick 2016). The creek networks were classified according to Strahler (1957) stream order, with the smallest (source) creeks assigned to first order, and order increments with each downstream intersection. In each site, lengths of all creeks were summed and the total creek density calculated. Creeks were split into the relevant stream order category and the density of each order of creek per site calculated.

Figure 2-1 visualises how the surface topographic measures relate to DEM and gives examples of topographic features *in situ*. Figure 2-1B shows a salt pan, which would have a positive profile curvature value, indicating it is a concave feature, and a high value for the topographic wetness index. Figure 2-1C shows a small creek and Figure 2-1D shows a constructed hillock on a MR site, a convex feature with negative profile curvature and low topographic wetness index.

2.2.3 Statistical analysis

Topographic variables were calculated from the DEMs in the R environment (R Development Core Team 2012) using the packages ‘raster’ (Hijmans 2015), ‘rgdal’ (Bivand et al. 2016) and ‘rgeos’ (Bivand and Rundel 2016). Pearson’s product moment correlations were used to identify collinearity between topographic variables; total curvature was omitted due to strong correlation with profile curvature ($r = 0.92$), and local slope omitted due to correlations with rugosity (RUG, $r = 0.97$), vector rugosity (VRM) and profile curvature (both $r > 0.5$).

All variables were not normally distributed (Shapiro-Wilks, all $p > 0.05$), so non-parametric analyses were used where possible. Kruskal–Wallis (K-W) tests were used to identify significant differences in the total creek density and densities of each creek order between landscape types. Site averages for each topographic variable were calculated and these were compared between pasture and arable former land covers with Kruskal–Wallis tests. Spearman’s rank correlations were used to test for correlations between the surface topographic variables and site age, site size, 1st order creek density, total creek density, and distance to nearest creek of MR sites. Linear mixed-effects models (LMMs) were used to test for differences in topographic variables between the three landscape types (natural marsh, MR and agriculture), with site as a random effect, using the R packages ‘nlme’ (Pinheiro et al. 2009) and ‘multcomp’ (Hothorn et al. 2008). Although these assume normality, they are robust to violations of this assumption when sample sizes are large (e.g. Arnau et al. 2013), as is the case with this analysis where tens to hundreds of thousands of data points were used in each analysis. LMMs were used to test whether differences in topography between natural and MR marshes varied across their elevation range, using the R package ‘lme4’ (Bates et al. 2015). To do this, we constructed a LMM with landscape type, relative tidal height and their interaction as fixed effects, and site as a random effect. We assessed the significance of this interaction term by comparing it to a nested model lacking the interaction term using a likelihood-ratio test. Likewise, we tested whether landscape type had a significant additive effect on topography while controlling for the effect of relative tidal height, by comparing a LMM with landscape type and relative tidal height as fixed effects with the nested model only containing relative tidal height as a fixed effect. Finally, we use LOWESS regressions to visualise relationships between topography and elevation in natural and MR marshes. All data were used to calculate LOWESS relationships, but data visualised are between relative tidal heights of -0.5 and 1.5 (97.8 % data) for clarity (total RTH range = -2.54 to 5.23). Confidence intervals around these relationships were calculated by taking 1000 resamples of the data with replacement.

2.3 Results

2.3.1 Comparison of topography between landscape types

All topographic measures, extracted at the randomly located sample points, differed between natural saltmarsh and MR landscape types, except for distance to the nearest creek and relative tidal height (RTH) (Figure 2-3). Both measures of rugosity were significantly lower on MR sites (VRM: $z = -3.49$, $p = 0.001$; RUG: $z = -2.40$, $p = 0.043$) and MR sites had significantly higher values of topographic wetness index (TWI: $z = 2.50$, $p = 0.032$), indicating they are flatter and have a greater potential for water accumulation. Profile curvature differed significantly between natural marsh and MR landscape types (Profile curvature: $z = 3.899$, $p < 0.00.1$), with MR being concave on average (mean ± s.e, 0.154 ± 0.107) and natural marshes convex (-0.264 ± 0.081) in the direction of the maximum slope. Total creek density was significantly lower in MR marshes (Table 2-2, $\chi^2 = 4.62$, $p = 0.03$). This difference was greatest for the smallest creeks (1st order), although differences were not statistically significant for any individual creek order ($p = 0.51$ for 1st order creeks, $p >= 0.257$ for other creek orders). Topographic wetness index and profile curvature values for the agricultural landscape were between those recorded for MR and natural landscapes respectively (Figure 2-3). VRM and RUG were both significantly different between MR and agricultural landscapes, with MR sites having higher rugosity (VRM: $z = -6.23$, $p < 0.001$; RUG $z = -2.64$, $p = 0.022$).

Rugosity was positively correlated with total creek density ($r_s = 0.67$, $p = 0.001$) and density of the 1st order (smallest) creeks ($r_s = 0.74$, $p < 0.001$), but negatively correlated with distance to nearest creek ($r_s = -0.66$, $p = 0.001$). The density of 1st order creeks was negatively correlated with topographic wetness (TWI $r_s = -0.47$, $p = 0.033$), suggesting these smaller creeks must also play a role in reducing up-slope catchments and flat areas.

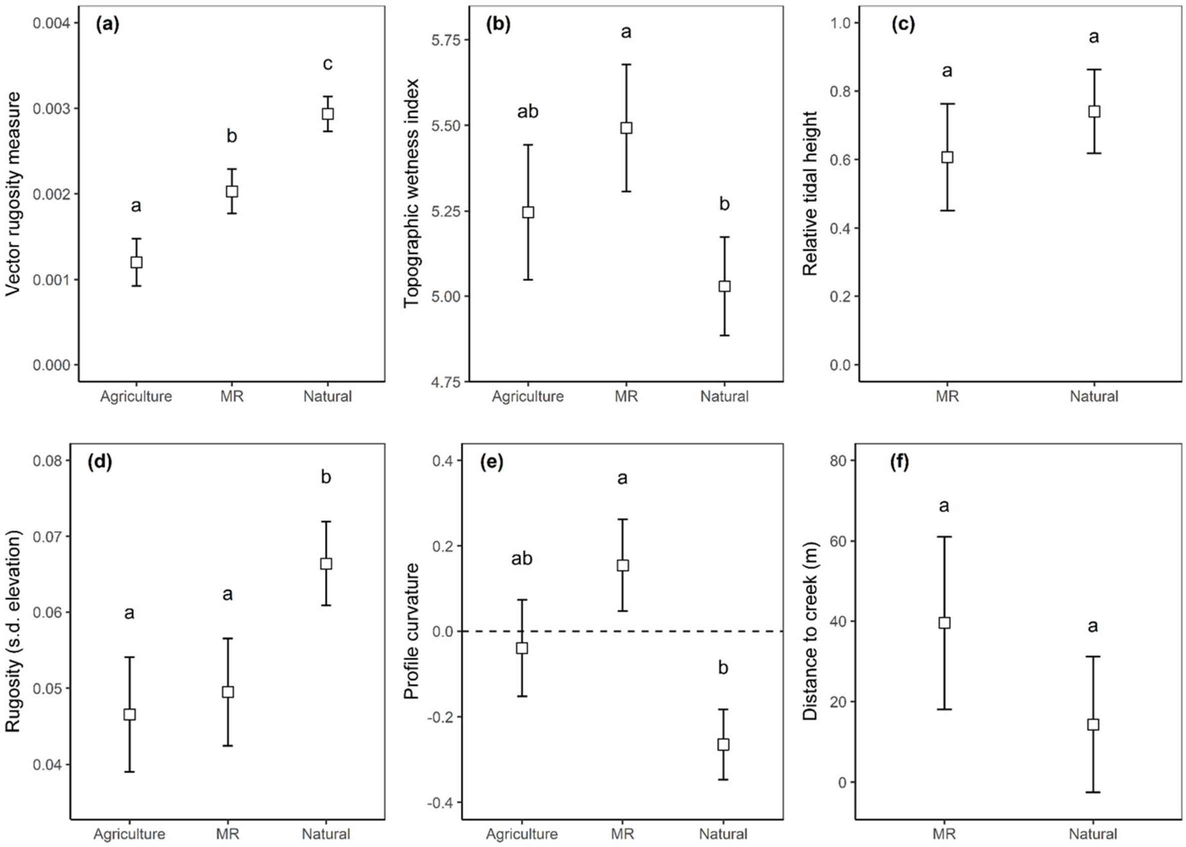

Figure 2-3 Mean (± SE) calculated via a GLMM of six topographic indices: (a) Vector rugosity measure, (b) Rugosity (s.d. elevation), (c) Topographic wetness index, (d) Profile curvature the dotted horizontal line in this graph represents a switch from convex (-ve) and concave (+ve) scores, (e) Relative tidal height and (f) Distance to nearest creek. Letters indicate significant differences (p < 0.05) between the landscape types.

Table 2-2 Mean (± standard deviation) density of creek orders (m.ha-1) for the natural marsh and managed realignment

Density of creeks	*Natural marsh (n = 12)*	*Managed realignment (n = 19)*	χ^2	*p*
1st order	127.26 ± 33.33	96.54 ± 42.98	3.78	0.051
2nd order	63.14 ± 21.17	65.43 ± 39.37	0.25	0.611
3rd order	35.07 ± 20.56	27.84 ± 21.17	1.28	0.257
4th order	18.55 ± 19.21	11.45 ± 6.45	0.03	0.855
Total density	233.21 ± 55.81	182.18 ± 71.31	4.62	0.030

One MR site contained a 5th order creek at a density of 1.62 m ha^{-1} omitted from table due to lack of comparison

2.3.2 Does topography differ with age since restoration and former land cover?

The age (time since restoration) and area of MR sites were not significantly correlated with any topographic variable (Figure 2-4; Table A2-3). Some individual restored sites overlapped with natural marshes in their characteristics, but there was no trend over time in these characteristics (Figure 2-4). There were no significant differences in any topographic variables between pasture and arable land covers prior to restoration (Kruskal-Wallis, all *p* > 0.05; Table A2-4).

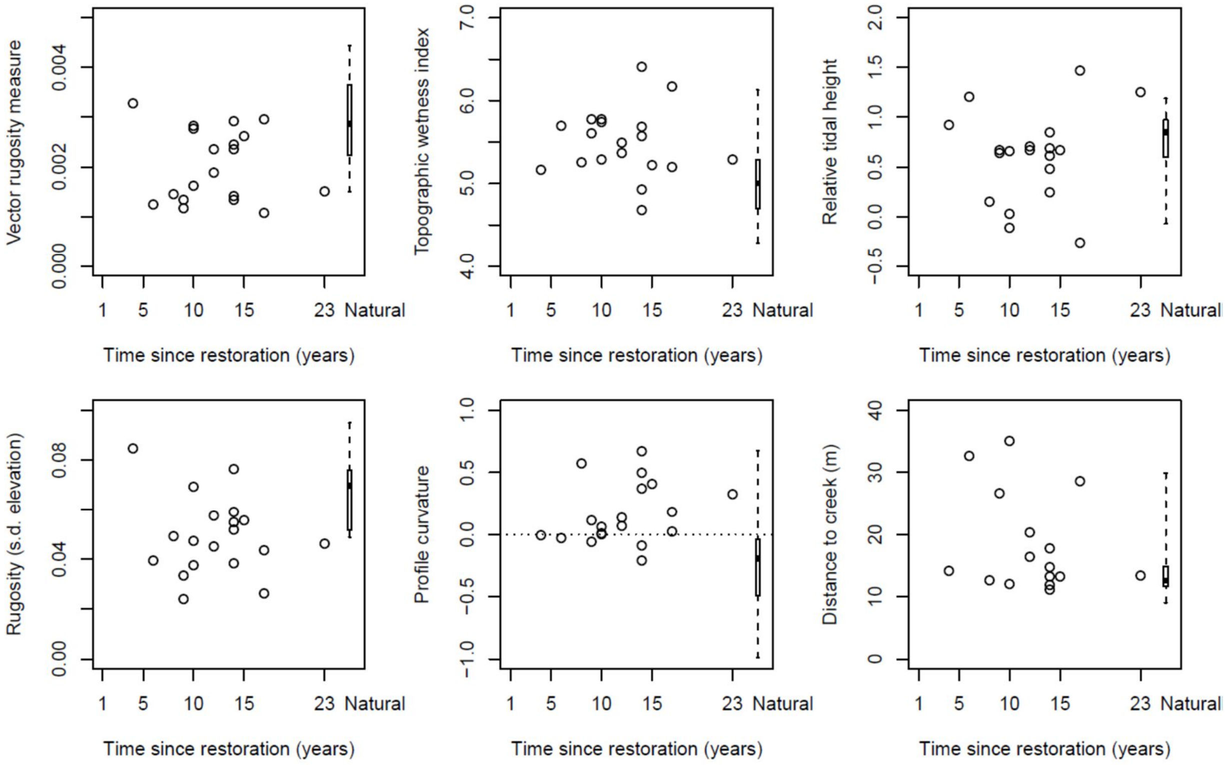

Figure 2-4 MR site means plotted against time since restoration in years for each of the six topographic indices: (a) Vector rugosity measure, (b) Rugosity (s.d. elevation), (c) Topographic wetness index, (d) Profile curvature the dotted horizontal line in this graph represents a switch from convex (-ve) and concave (+ve) scores, (e) Relative tidal height and (f) Distance to nearest creek. No relationships were statistically significant.

2.3.3 Consistency of topographic differences across elevations

There was a statistically significant interaction between landscape type and elevation for all topographic variables (Table 2-3). At RTH below zero, MR were flatter (demonstrated by lower VRM and RUG) than natural marshes and with substantially greater potential for water accumulation (higher TWI) (Figure 2-5). At these elevations, both natural and MR landscapes were dominated by concave features, with MR being less concave. Furthermore, distance to the nearest creek was the same in both landscapes, but as elevation increased there was divergence between the landscape types, and distance to the nearest creek was substantially greater in MRs than natural marshes above 0.5 RTH. Both rugosity measures were higher in natural than MR marshes between 0 and 1 RTH, but became similar at higher elevations. Between 0 and 0.5 natural marshes were dominated by convex features, whilst MR sites remain dominated by concave features. MR briefly become less concave than natural marshes above 0.5 RTH, but above 1.0 RTH MR became strongly concave compared to natural marshes that were moderately concave. MR showed higher potential for water accumulation than natural marshes, except between RTHs of 0.75 and 1.2.

Table 2-3 Effect of landscape type (restored or natural saltmarsh) and elevation above sea level (relative tidal height RTH) on topographic variables. This is examined as an interaction with relative tidal height, and as an additive term controlling for relative tidal height. The significance of each term was assessed using likelihood ratio tests between a LME model containing the term and a nested model without the term.

DEM variable	Interaction between landscape and RTH		Additive effect of landscape	
	χ^2	*p*	χ^2	*p*
Vector rugosity measure	13364	< 0.001	5.593	0.018
Rugosity (s.d. elevation)	10795	< 0.001	7.551	0.005
Topographic wetness index	1481	< 0.001	0.812	0.367
Profile curvature	10564	< 0.001	0.300	0.584
Distance to creek	615.96	< 0.001	1.552	0.212

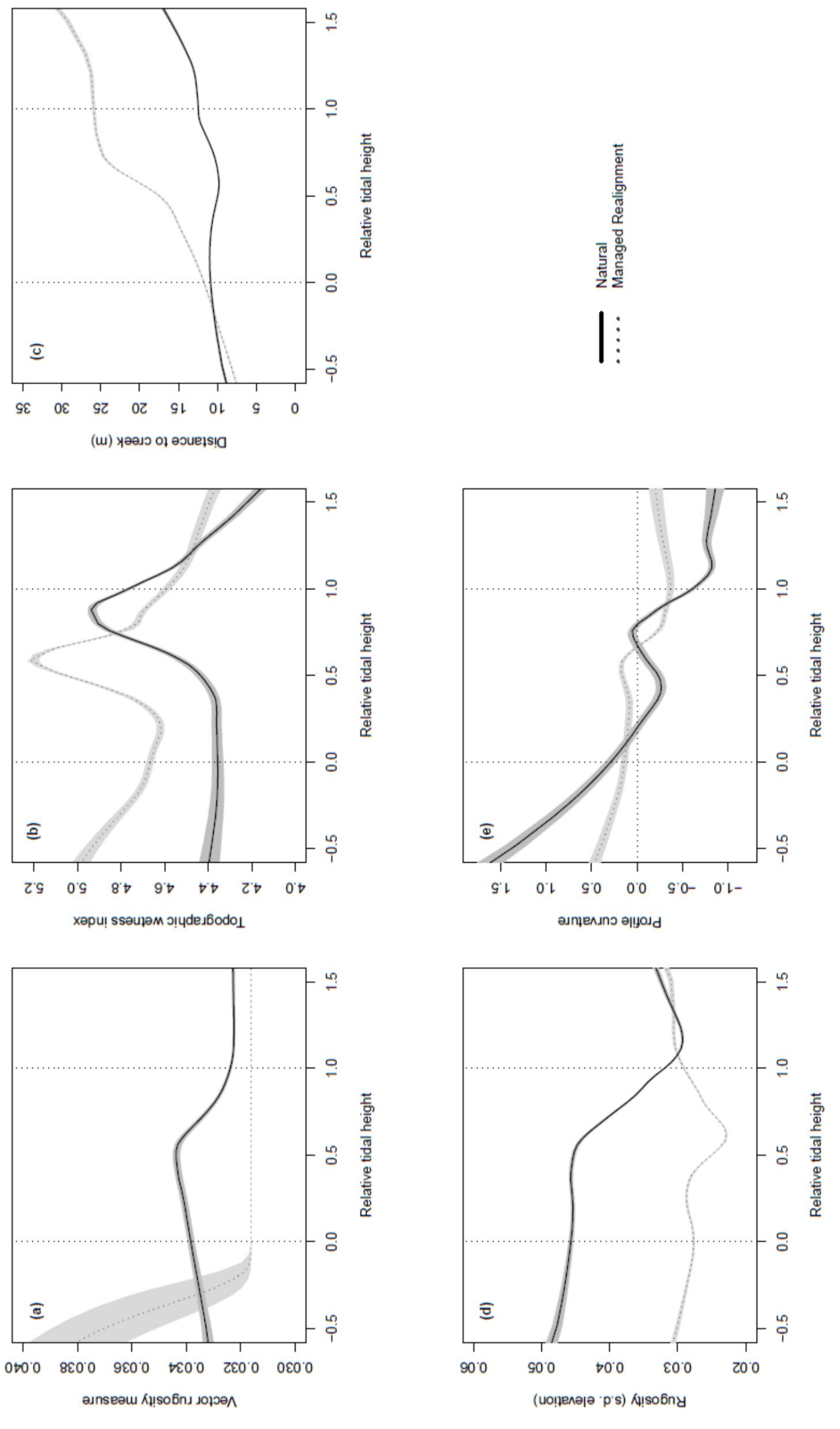

Figure 2-5 Relationships (Lowess regressions) between elevation and topographic variables for natural and restored (MR) landscapes. (a) Vector rugosity measure, (b) Rugosity (s.d. elevation), (c) Topographic wetness index, (d) Profile curvature the dotted horizontal line in this graph represents a switch from convex (-ve) to concave (+ve) scores, (e) Relative tidal height and (f) Distance to nearest creek. The elevations at which saltmarsh plants typically occur, 0 and 1 relative tidal height, are marked.

2.4 Discussion

2.4.1 Topography on restored saltmarsh

Saltmarshes restored through managed realignment differ in their topography to natural marshes, and are more similar to the agricultural landscapes they originate from. Compared to natural marshes, they have an enhanced potential for water accumulation (higher topographic wetness index) and lower densities of creeks. Importantly, there was no relationship between age of the restoration and any of the topographic variables. This indicates that, although some individual restored sites overlapped with natural marshes in their characteristics, overall, restored sites are not on a trajectory to become topographically similar to natural marshes over time. We note that, despite the absence of a linear trend, marsh development may exhibit non-linear dynamics (van Belzen et al. 2017); for example, large-disturbance events could alter trajectories of topographic development The lack of convergence of topography in our dataset is notable as it is mirrored in some other physical, chemical and biological components of restored saltmarshes such as vegetation establishment (Mossman et al. 2012a) and soil edaphic conditions (Hazelden and Boorman 2001); indeed, topography may act as a driver for these variables (Varty and Zedler 2008).

Previous studies have found restored marshes to be lower in the tidal frame, on average, than natural marshes (e.g. Garbutt et al. 2006). In contrast, we found that elevation did not differ between restored and natural marshes. However, all measures of topography varied with elevation and these relationships differed between the landscape types. At low elevations, MRs were dominated by local depressions (e.g. those surrounding the hillock in Figure 2-1D) that often take the form of permanent pools of water or poorly drained areas (indicated by high topographic wetness index), in contrast to natural marshes. This could explain the previous observation that, at low elevations, sediment redox potentials are lower in MR sites than at equivalent elevations on natural marshes (Mossman et al. 2012a). This is because drainage, in addition to tidal inundation, has substantial influence on sediment aeration (and hence redox potential (Armstrong et al. 1985)), and depressions and concave features retain water at low tide, resulting in lower redox potentials at the sediment surface (Varty and Zedler 2008).

2.4.2 Implications for vegetation development and ecosystem functioning

Elevation in the tidal frame and redox potential are the major determinants of the niches of saltmarsh plants (Davy et al. 2011). Our finding that restored marshes are flatter will equate to fewer elevational niches being available, and could lead to more homogenous vegetation observed on MR marshes (Collin et al. 2010). Even very small variations in elevation at restored sites resulted in differing vegetation communities (Ivajnšič et al. 2016). This is likely due to changes in immersion time (Masselink et al. 2017), known to impact plant mortality (Hanley et al. 2017). The concave-dominated environments of restored landscapes will generate poorly-drained conditions expected to be suitable for pioneer species, such as *Spartina anglica* and *Salicornia* spp. (Sullivan et al. 2017). Indeed, these species dominate restored marshes (Masselink et al. 2017; Mossman et al. 2012a; Zedler et al. 1999).

In contrast, we find that at elevations typically suitable for mid and upper marsh plants (e.g. RTH 0.75 -1.0), natural marshes have a higher potential for water accumulation than restored marshes, with an increase in concave features. These landscape features between RTHs of 0.75 and 1 can increase vegetation diversity by excluding dominant upper-marsh species, allowing plant species more tolerant of harsh conditions to colonise gaps (Sullivan et al. 2017; Varty and Zedler 2008). The absence of such environmental features at this elevation range on restored marshes may be limiting the establishment and persistence of waterlogging-tolerant mid and upper marsh species, such as *Triglochin maritima* (Fogel et al. 2004), that are rare or absent on restored marshes (Mossman et al. 2012a).

Plant species richness is higher in the areas immediately around creeks (Sanderson et al. 2000), presumably due to the resulting modifications of the abiotic environment, which gives a greater diversity of resulting niches. Our finding that restored landscapes have lower creek densities will therefore have consequences for saltmarsh vegetation. Moreover, creek networks are essential to the use of saltmarshes by fish and crustaceans, including commercially important species (Callaway 2005; Crinall and Hindell 2004; Peterson and Turner 1994). The lower creek density of restored marshes is therefore likely to reduce their ecosystem function as fish nursery grounds (Desmond et al. 2000).

Topographic heterogeneity is likely to influence ecosystem functioning both directly, and indirectly by affecting plant diversity and community composition (Callaway 2005). Diverse plant communities can enhance sediment stability (Ford et al. 2016) and may increase aboveground biomass production (Doherty et al. 2011), both of which would increase carbon storage. Furthermore, plant species differ in the extent to which they attenuate or withstand wave energy (Rupprecht et al. 2017), so diverse assemblages may enhance flood protection. Topography may also have direct effects on ecosystem functioning. Waterlogging associated with concave topography influences carbon cycling by microbes (Li et al. 2010), while these anoxic sediments are important locations for methane production (Oremland et al. 1982). Finally, wave energy is better dissipated by convex marsh profiles than concave ones (Hu *et al.* 2015), while the greater rugosity of natural marshes is also likely to increase wave attenuation (Moeller et al. 1996). It is important to note that while these likely differences in functioning would mean that ecosystem service provision by restored marshes is less than by natural marshes, restored marshes will still provide important ecosystem services relative to agricultural land (MacDonald et al. 2017).

2.4.3 Developing topographic heterogeneity on restored saltmarshes

There are a number of potential explanations for variation in topographic diversity between saltmarsh landscape types. We found no difference in the topography between sites that were arable or pasture prior to restoration. However, other research has found signals from pre-restoration land cover in poor surface drainage and changes to sediment structure, such as the formation of an impermeable layer (aquaclude) (Spencer et al. 2008; Spencer et al. 2017). This impermeable layer is an effective barrier to erosion, preventing the scouring required for creek formation (Chen et al. 2012), thereby potentially reducing creek density. This could limit the development of other topographic features in restored landscapes to the depth of newly deposited sediment. Furthermore, high sedimentation rates, as observed in many restored marsh landscapes (Garbutt et al. 2006; Mazik et al. 2010), may fill any existing depressions (Elschot and Bakker 2016) resulting in a smoothing of the marsh topography. In natural marsh landscapes, the patterns of topography are defined by the accretion of sediment at low elevations very early in marsh development (Elschot and Bakker 2016). Restored landscapes that are not at suitably low elevations at the time of flooding may miss this window of opportunity for topographic development. Furthermore, limited tidal exchange (e.g. single breaches, regulated tidal exchanges) may impair creek development by reducing scour and sediment accretion (Masselink et al. 2017).

We have shown that topographic differences can be detected from LiDAR-derived digital elevation models across multiple restoration sites, which provides us with the opportunity to use space-for-time substitution to learn lessons from former MR schemes and guide the design of future restored landscapes. Our results suggest that the construction of additional topographic features will be needed to create marshes that are more similar to natural sites, since these features do not develop over time at MR sites. The creation of small creeks and hillocks are likely to be most useful in improving outcomes for vegetation development, as hillocks are likely to be preserved despite high sedimentation and networks of small creeks will increase drainage within sites. Recently constructed managed realignments have included the creation of these topographic features, e.g. hillocks at Steart Marshes, UK (Figure 2-1D), and at Hesketh Out Marsh East, UK, small sinuous creeks with bank incisions to promote secondary formation and raised infill areas on the marsh to promote topographic variation (R. Shirres, *pers. comm.*). The functioning and longevity of these features should be monitored.

2.4.4 Conclusions

We find that within the time scales studied, restored saltmarshes are not on a trajectory to develop topography or creek densities equivalent to those of natural landscapes, and remain similar to the agricultural areas they originate from. These differences have implications for vegetation development and other aspects of restored marsh functioning, such as provision of fisheries habitat. Creation of more topographic features, including hillocks and small creeks, prior to restoration appears to be necessary to ensure restored saltmarshes develop topographic heterogeneity.

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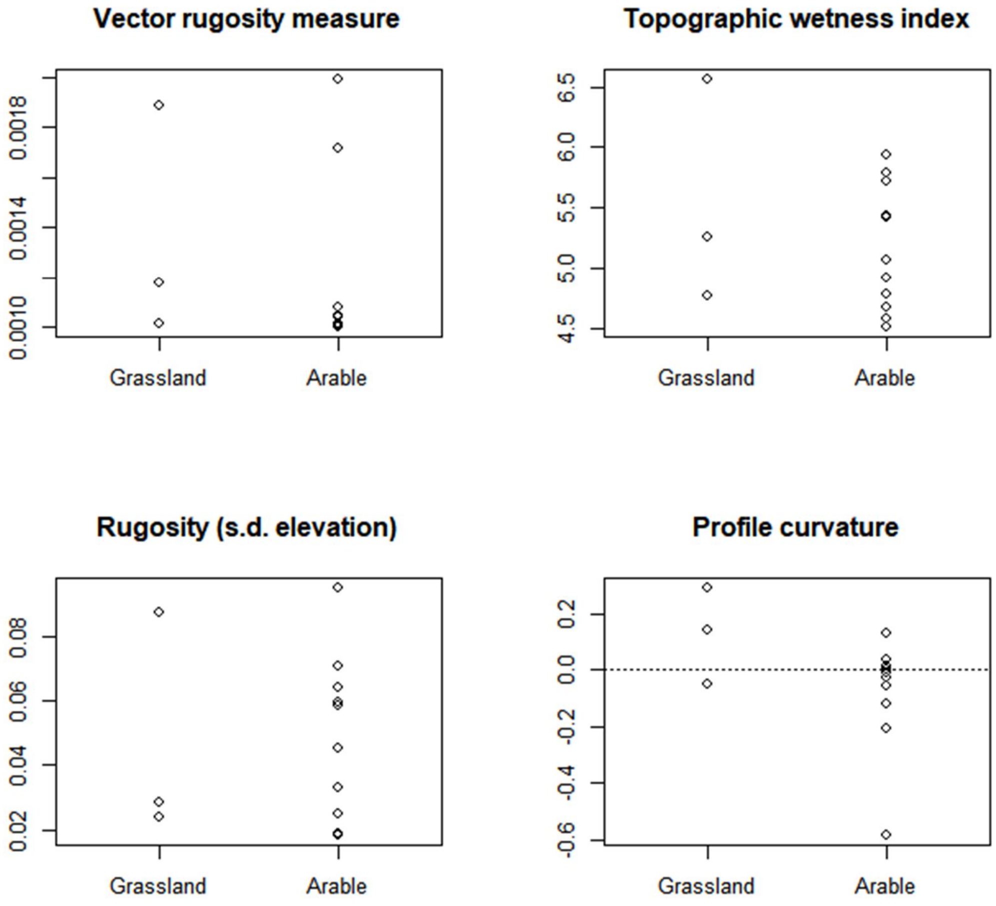
2.6 Appendices


Vector rugosity measure

Topographic wetness index

Rugosity (s.d. elevation)

Profile curvature

Figure A2-1. Comparison of topography between grassland and arable agricultural reference sites. Each point shows the mean per site.

Table A2-1. Description of study sites from natural saltmarsh (N), restored saltmarsh (managed realignment (MR) and agricultural (F) landscape types, with site width (m), seaward extent (m) and resulting area (ha). For restored sites, the year of restoration through the breaching of the sea wall and resulting reinstatement of tidal inundation, and the age of the site (years since restoration) at time of most recent LiDAR sample (Age), are given.

Location	*Estuary*	*Type*	*Width*	*Seaward extent*	*Size*	*Date of breach*	*Age*	*Lat*	*Long*
Alnmouth	Aln	F	191	334	6.2			55.3984	-1.6115
Alnmouth 1	Aln	MR	180	187	4.3	2006	6	55.3911	-1.6222
Alnmouth 2	Aln	MR	136	46	0.4	2008	4	55.3953	-1.6146
Alnmouth	Aln	N	251	171	2.6			55.394	-1.6138
Chowder Ness	Humber	F	355	481	10.5			53.6891	-0.4847
Welwick	Humber	F	1068	520	63.4			53.6484	-0.0005
Chowder Ness	Humber	MR	557	279	9.5	2006	9	53.6916	-0.4815
Paull Holme	Humber	MR	2541	246	79	2003	12	53.7086	-0.2187
Welwick	Humber	MR	1247	531	50.5	2006	9	53.6471	0.0095
Paull Holme	Humber	N	1673	238	30.1			53.6795	-0.1713
Brancaster	Norfolk	F	268	256	6.8			52.9653	0.6555
Brancaster	Norfolk	MR	320	240	6.1	2002	12	52.9722	0.6314
Brancaster	Norfolk	N	342	893	27.3			52.9682	0.5955
Holme	Norfolk	N	216	413	7.3			52.9716	0.564
Freiston	The Wash	F	388	434	15.6			53.0109	0.1424
Freiston	The Wash	MR	1380	503	65.6	2002	10	52.9646	0.0923
Freiston	The Wash	N	618	526	29.5			52.9735	0.1065
Abbotts Hall	Blackwater	F	471	377	15.2			51.7838	0.8332
Northey Island	Blackwater	F	233	213	4.6			51.7208	0.714
Orplands	Blackwater	F	332	350	11.4			51.7167	0.8636
Tollesbury	Blackwater	F	411	444	14.3			51.766	0.8341
Abbotts Hall	Blackwater	MR	843	257	22.5	2002	10	51.7846	0.8455
Northey Island	Blackwater	MR	203	53	1	1991	23	51.719	0.7148
Orplands A	Blackwater	MR	577	259	10.2	1995	14	51.7197	0.8676
Orplands B	Blackwater	MR	1066	271	14.3	1995	14	51.7223	0.8728
Tollesbury	Blackwater	MR	582	390	18.3	1995	17	51.7673	0.8402
Dengie	nr Blackwater	N	738	505	35.4			51.6881	0.9398
Sheppy	Thames*	N	647	359	21.2			51.3632	0.8715
West Itchenor	Chichester	F	370	171	5.3			50.8061	-0.8736
Wittering	Chichester	F	437	465	18.4			50.7879	-0.8989
Chalkdock	Chichester	MR	293	48	1.2	2000	14	50.8072	-0.8775
Thornham	Chichester	MR	295	193	5.4	1997	17	50.8332	-0.9149
Chichester	Chichester	N	391	126	3.9			50.7893	-0.9000
East Head Spit	Chichester	N	411	348	7.1			50.7841	-0.9113
West Thorney	Chichester	N	933	257	22.4			50.8163	-0.9006
Goosemoor	Clyst	F	268	111	2.6			52.9735	0.1065
Goosemoor	Clyst	MR	260	263	5.5	2004	8	50.6819	-3.4535
St. Germans	Plym/ Lynher	F	468	186	8.4			50.3843	-4.2821
Saltram	Plym/ Lynher	MR	248	275	5.6	2003	10	50.3848	-4.0857

St. Germans	Plym/ Lynher	N	344	205	11.3			50.3881	-4.283
Landcross	Torridge	F	313	188	4.1			50.9876	-4.1905
Annery Kiln	Torridge	MR	586	155	7	2000	15	50.9872	-4.1948
Pillmouth A	Torridge	MR	306	136	2.9	2001	14	50.9979	-4.1802
Pillmouth B	Torridge	MR	373	149	4	2001	14	50.9928	-4.1832
Bideford	Torridge	N	1400	100	13.5			51.0069	-4.2031

* reference for Blackwater due to shortage of non-eroding natural sites

Table A2-2. Summary of mean values (± standard error) of topographic variables for the three saltmarsh landscape types. Superscripts indicate significant (p-value < 0.05) based upon the GLMMs.

Topographic variables	*Natural marsh n =212210*	*MR n =314493*	*Agriculture n = 187457*	*Site effect*
Vector rugosity measure	0.003 ± 0.000 ^{a}	0.001 ± 0.000 ^{b}	0.001 ± 0.000 ^{c}	0.000 ± 0.005
Rugosity (s.d elevation)	0.066 ± 0.005 ^{a}	0.050 ± 0.007 ^{b}	0.047 ± 0.007 ^{b}	0.019 ± 0.065
Topographic wetness index	5.029 ± 0.144 ^{a}	5.492 ± 0.184 ^{b}	5.246 ± 0.197 ^{ab}	0.500 ± 2.482
Profile curvature	-0.264 ± 0.081 ^{a}	0.155 ± 0.107 ^{b}	-0.039 ± 0.112 ^{ab}	0.260 ± 11.399
Relative tidal height	0.740 ± 0.122 ^{a}	0.607 ± 0.155 ^{a}	n.a.	0.422 ± 0.338
Distance to creek	14.316 ± 16.811 ^{a}	39.591 ± 21.476 ^{a}	n.a.	58.239 ± 46.360

Table A2-3. Spearman rank correlation coefficients from managed realignment sites (n = 19) between variables of topography and the site measures of restoration age, seaward extent, site area and measures of creek density.

Remote sensing variables	*Site drivers of topography*					
	Age	Seaward extent	Area	Site creek density	1st order creek density	Distance to creek
Vector rugosity measure	-0.045	0.061	0.257	0.350	0.415	-0.173
Rugosity (s.d. of elevation)	-0.012	-0.333	-0.070	0.672 **	0.742 ***	-0.668 **
Topographic wetness index	-0.060	0.024	-0.154	-0.350	-0.476 *	0.391
Profile curvature	0.269	-0.122	-0.129	0.413	0.330	-0.354

*** *p < 0.001,* ** *p < 0.01,* * *p < 0.05*

Table A4. Mean (± standard deviation) of topographic variables from managed realignment sites that were pasture or arable prior to restoration as saltmarsh.

Remote sensing variables	*Grazing (n = 11)*	*Arable (n = 8)*	χ^2	*p*
Vector rugosity measure	0.001 ± 0.000	0.002 ± 0.000	1.534	0.215
Rugosity (s.d. of elevation)	0.049 ± 0.015	0.049 ± 0.017	0.000	1.000
Topographic wetness index	5.614 ± 0.397	5.323 ± 0.387	1.336	0.247
Profile curvature	0.229 ± 0.272	0.066 ± 0.171	0.981	0.321
Relative tidal height	0.774 ± 0.440	0.377 ± 0.383	3.606	0.057
Distance to creek	19.770 ± 11.488	62.837 ± 111.131	1.336	0.247

Table A5. Parameters of LME models of each topographic variable as a function of RTH, landscape type and their interaction.

DEM variable	*Fixed effects*					
	RTH	s.e.	Natural	s.e.	MR : RTH	s.e.
Vector rugosity measure (VRM)	-0.008	0.000	-0.006	0.001	0.006	0.000
Rugosity (s.d. elevation) (RUG)	-0.096	0.000	-0.071	0.010	0.069	0.000
Topographic wetness index (TWI)	-2.030	0.020	-0.355	0.339	0.900	0.023
Profile curvature	-16.774	0.010	-9.109	1.522	11.970	0.115
Distance to creek	10.120	0.378	20.054	22.864	10.810	0.435

3 Global analysis of the nutrient status of natural and restored saltmarshes

Abstract

Eutrophication is a serious global issue in both marine and terrestrial environments. Coastal habitats, such as saltmarshes, are known to be impacted by nutrient enrichment in several ways, including changes in plant communities and erosion of habitat. However, the status of nutrients in saltmarshes is not known, yet restoration and creation of naturalistic marshes is both expected and required by law. It is therefore important to acknowledge the current levels in natural marshes to understand the nutrient levels present in restoration schemes. Here we provide the first attempt to analyse and synthesise global nutrient concentrations in saltmarshes. We use a systematic literature review, supplemented with our own field observations, to investigate: 1) the status of the literature; 2) typical values present in natural saltmarshes and how these compare to levels known to impact marsh health and, finally, 3) the differences between natural saltmarshes and those restored or created from agricultural land. We found that there was not a clear picture of the nutrient status of natural saltmarshes. Variation in nutrient concentrations within and between sites was high (several orders of magnitude). In addition, a very large number of analytical methods have been utilised all with their own limitations and implications for interpretations. Not only this but troubles with interpretation is compounded within the literature by numerous units presented. We report a significant regional bias in global measurements, with no or extremely limited data from the southern hemisphere, despite some areas having substantial saltmarsh area. We also find temporal studies of nutrients are also rare, thus little evidence currently exists to define seasonality or the characterisation of soil development in all types of saltmarshes. Restored marshes had nutrient concentrations similar to natural sites, with the exception of typically lower Phosphate levels, indicating a limited signature of prior land use. We find consistent evidence in our field sampling and the literature to suggest many natural saltmarshes were Phosphate enriched, although the N:P ratios were usually lower than the threshold seen in experiments to cause erosion. In conclusion, we strongly support increased data sharing and availability of nutrient data and a drive towards more consistency in analytical methods and units.

3.1 Introduction

Eutrophication is well recognised as a serious global environmental, economic and social concern (Cloern, 2001; Verhoeven *et al.*, 2006). The issue is wide spread, In the US for example, 65% of estuaries are considered highly eutrophic (Bricker *et al.*, 2008). Saltmarsh is often considered to be an effective sink of water-borne nutrients and other pollution (Barbier *et al.*, 2011), and so, it has been suggested saltmarsh may help mitigate eutrophication. Although this may be the case for short term events nutrient enrichment can have significant negative impacts on saltmarshes through erosion and changes to plant communities, and so there is an extremely serious and often understated implication of viewing saltmarsh as a nutrient sink.

One mechanism whereby increases in soil nutrient concentrations causes saltmarsh erosion is due to preferential above ground biomass production by saltmarsh plants, with corresponding decreases in root production, in turn reducing soil stability (Deegan *et al.*, 2012). It is not just loss via reduced stability but increased nutrient concentrations can also result in either more late-successional (and upper marsh) species such as *Elytrigia atherica* (van Wijnen and Bakker, 1999), or lower marsh species such as *Spartina* ssp. (Levine, Brewer and Bertness, 1998). These two community shifts combined could result in the constraint of the diverse mid-marsh to smaller areas. It is plausible that this extending range of upper and lower communities may be a consequence of mid marsh plants performing poorly in enriched conditions (van Wijnen and Bakker, 1999). The loss of the diverse communities in the mid marsh may contribute to saltmarsh loss as diverse communities appear less susceptible to erosion (Ford *et al.*, 2016).

In recent decades, significant effort has been made to restore valuable saltmarsh habitat (Cui *et al.*, 2009; ABPmer, 2018). However, efforts to compensate for lost saltmarsh are yet to result in equivalent plant communities (Mossman, Davy and Grant, 2012). Vegetation communities in MR differ from natural marshes in a manner consistent with the effects of nutrient enrichment as they contain less plants typical of the mid-diverse marsh. As many restored marshes are typically created on former arable or other agricultural land we might expect elevated nutrient concentrations resulting from this former land use as a reason for reduced diversity in place. In addition, new saltmarshes are thought to accumulate more nutrients than established marsh (Craft, 1996). However, the nutrient status of restored systems has rarely been studied, and where it has, studies often lack a natural reference site for comparison or much reference to other literature.

There is currently a limited overview of natural or ambient nutrient conditions on saltmarshes, or whether these are impacted by eutrophication or not. Not only this but we also lack a global perspective of how eutrophic water may differ in its impacts on differing geological and species settings present in global saltmarsh distributions. One approach used to estimate the eutrophication status of the estuary or coastal water, can result from the interpretation of short-lived acute events and observations of biological events, such as algal blooms (Diaz, Selman and Chique, 2011). However, this may not translate well to the study of saltmarsh habitat because the elevation gradient means areas of the saltmarsh are flooded by this coastal water differentially, with some parts only receiving coastal water inputs once a year. If saltmarsh is a sink of nutrients, the current nutrient levels in the soil may not necessarily be well correlated with the acute levels in the estuary. Instead therefore we must turn to the literature to obtain a better appreciation of what ambient conditions maybe. However, much of our current understand from literature stems from the study of acute enrichment from pollution incidents such as (Mucha *et al.*, 2013) or experimental additions as per (Levine, Brewer and Bertness, 1998). To our knowledge only one study has thus far has developed a realistic and grounded experimental addition based on field observations of sites as identified as ‘not-impacted’ and ‘impacted’ by eutrophication due to visual evidence. The use of a treatment mirroring nutrient concentrations of a eutrophic site at currently ’non-impacted’ saltmarsh shows that such enriched experiment produces significant shifts from below to above ground plant biomass and consequent erosion of the marsh (Deegan *et al.*, 2012). Although there is room for this experiment to be repeated in multiple continents it is reasonable to assume these levels cause an impact as many saltmarshes species stem from the same genus and thus likely similarly impacted by enrichment.

Here we provide a systematic review of published concentrations of soil-available forms of Nitrogen and Phosphorous from natural saltmarshes. We use values from Deegan *et al.* (2012), to place our study in the context of ‘un-impacted’ and habitat-altering nutrient levels. We extend our review to review the current nutrient levels of created saltmarshes looking at a range of soil properties including Nitrogen and Phosphorous using the natural levels in each study as a baseline for the local created marshes to test for differences between these two systems in terms of soil nutrition. We hypothesise that restored saltmarshes will be comparatively nutrient enriched due to their prior agricultural land use. This study provides the first overview of the nutrient status of multiple natural and restored saltmarshes, the methods used by scientists and provides an early indication and guide to future the understanding nutrient driven consequences in saltmarsh habitat.

3.2 Methods

3.2.1 Literature search

A systematic literature review was conducted using the methods outlined in Pickering and Byrne, (2014). The systematic literature search was designed to identify original research that measured nutrient concentrations in saltmarsh. The search was performed in the electronic database Web of Science using the term: (tidal OR salt OR coastal) AND (marsh) AND (nutrient* OR nitrate OR nitrite OR ammonium OR phosphate) AND (sediment OR soil OR mud). This search returned 1298 papers on the 1st November 2017. An additional eight sources were obtained from Google Scholar and unpublished manuscripts (accredited in acknowledgements), resulting in 1304 sources after duplicates were removed.

3.2.2 Extraction of data for analysis

To ensure we only included articles appropriate to our aim, two levels of screening were utilised. The first level of screening used abstracts to ensure the paper 1) had a focus on saline saltmarshes (rather than tidal freshwater), with evidence of salinity from direct measurements or the presence of halophytic communities; 2) measurements of one or more of Nitrogen or Phosphorous concentrations, importantly under unaltered conditions i.e. not those from experimental manipulation studies or the monitoring of discrete, often acute, events as these are unlikely to represent the baseline conditions and; 3) measurements presented were taken from saltmarsh soil. If the paper met these criteria, then full text articles were obtained. Then the second level of screening was conducted.

The full text papers were excluded from the study if any of the following statements were true; 1) no data presented; 2) not primary source of the data; 3) inappropriate depth of samples (we required samples from a depth of 10cm ± 5cm, as this is commonly referred to as the rhizosphere (Caetano *et al.*, 2008). We recorded the numbers of studies excluded according to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Statement (Moher *et al.*, 2009) seen in Figure 3-1.

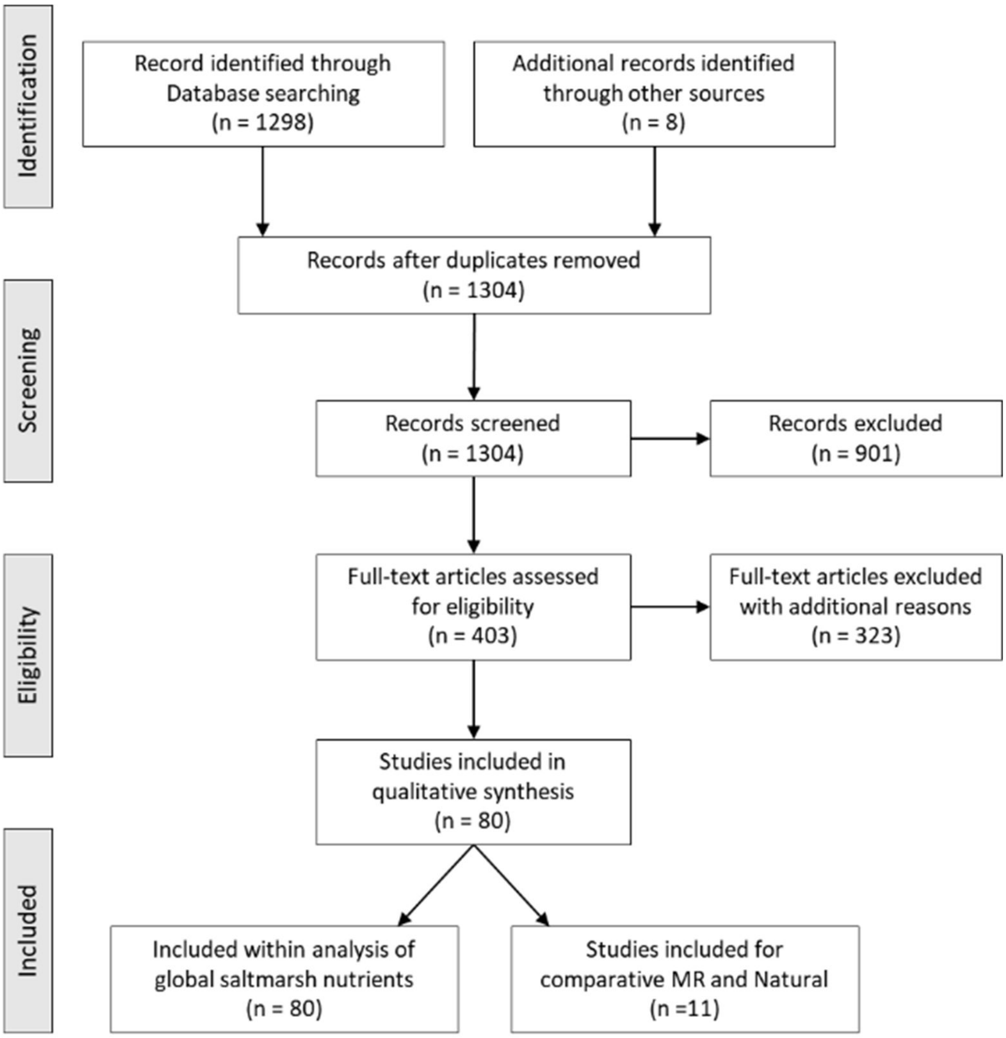


Figure 3-1 PRISMA literature search flow diagram.

From each paper, the concentrations of soluble forms of N and P (SN and SP) were extracted, including Ammonium, Nitrate, Nitrite and Phosphate. We also obtained the total mineral forms of N and P (TN and TP). To complement this data, we included other ecologically important variables measured in these papers, including Carbon (as organic

(OC) and total (TC)), water content, bulk density and redox potential. This resulted in a collated dataset of a total of 11 soil variables. Where numerical values of the soil properties were not stated in the paper, values were extracted from graphs using WebPlotDigitizer v3.9 (Rohatgi, 2015).

To our database of soil measurements, we added meta-data for each study including the location (country, estuary/river, study site), laboratory techniques, analytical equipment, the units of measurement, and the sampling strategy used (spatial / temporal / both). Once all the studies were collected, we defined 13 broad geographic regions (BGRs) to better visualise and interpret the data. Here we divided the USA into six coastal watersheds as defined by EPA (EPA, 2017). Studies from China were distributed within three water bodies, Bohai Sea, Yellow Sea and the East China Sea. Finally, Europe was divided in two regions, 'Northern Europe' including studies at latitudes higher than the Bay of Biscay, and the 'Southern Europe' at lower latitudes than this. Studies from with India and Argentina were not divided due to close proximities of the study sites.

3.2.3 Allowing comparison of concentrations between studies

In order to compare nutrient levels between studies, we converted readily unifiable units such as gravimetric (e.g. g/kg, mg/g and µg/g), volumetric (e.g. ml/L and µl/ml) and Molarity based units (e.g. mM and µM) to the most prevalent unit of each type.

Of the 80 studies that contained suitable data (

Figure 3-1), 11 of these contained data from both restored and natural systems. These papers used a variety of units, methods and sampling designs and so we calculated ratios of natural to restored concentrations. Within each paper, this ratio was calculated from measurements of that occurred on both marsh types at either the same time or within the same treatment (e.g. elevation). This normalised the data on a per paper basis, allowing all the papers to be included in the comparison on natural and restored systems. To compare soil redox potential a ratio cannot be used as negative values result such as -300 mV and + 300 mV would result in rations of 1 or -1. As a result, the difference between natural and MR was obtained via subtraction rather than a ratio, with values of

0 indicating no difference. This resulted in a total of 43 observations across 11 papers for the local ratio between natural and restored marshes.

As enriched waters can detrimentally effect saltmarsh, we compare concentrations obtained from the literature to those of Deegan *et al.*, (2012), where 4.65 ppm and 0.47 ppm for Nitrate and Phosphate respectively, indicate erosion-inducing levels, and 0.31 ppm and 0.09 ppm indicate unimpacted, reference conditions. Additionally, we add a further reference level of Phosphate of 37 mg/kg as this is deemed to represent nutrient enriched conditions in terrestrial grasslands (Brearley pers. comm.). In addition to the importance of actual concentrations of nutrients, the ratio of N:P is known to impact plant growth (Ryther and Dunstan, 1971). We therefore calculated the ratio of available N and P from our collated literature and compare these to that of Deegan *et al.* (2012). We also categorised the nutrient status of the closest estuary to the sampling sites in our database using Diaz, Selman and Chique, (2011) (eutrophic, hypoxic and improved), then compared the nutrient concentrations between these estuary categories.

3.2.4 Study sites and soil sampling

We selected three sites along the east coast of the UK where there was both a natural and MR scheme immediately adjacent and of similar ages (Tollesbury: 51.7671 N; 0.8378 E, 21 years since restoration, Orplands: 51.7191 N; 0.8631 E, 21 years since restoration and Freiston 52.9623 N; 0.0898 E, 14 years since restoration). All sites had no current grazing by livestock and were not experiencing widespread erosion. This resulted in three natural plots and three MR plots. In order to quantify the typical environmental conditions, we established a fractal sampling scheme, similar to that of (Brooks *et al.*, 2015). In each area, we set up one 50 x 50 m grid, with sampling points at every 10 m (n=36). At each sampling point the redox potential was measured with a Campbell Scientific calibrated ORP Probe (-700 to +1100 mV) at a depth of 5-8 cm, and until the reading stabilised (~ 5 mins). Where the substrate was too dry for insertion of the probe, a proxy value of 300 mV was used to represent the most aerated values in the dataset. Prior to field work, the probe was calibrated with Zobells solution. Approximately 30 g of soil was taken from ~5-8 cm depth at all sampling points, placed into a sealed polythene bag and stored at 4°C as soon as possible. The soil samples were homogenised for two minutes, and two 5 g subsamples were taken from each to measure soil water content (gravimetric weight loss at 105°C) and organic matter (percentage loss on ignition at 550°C), (Allen, 1989; Rowell, 1994). Using a 3 g subsample of soil we measured the water extractable nutrients in the form of the ions and cations of Ammonium, Nitrate and Phosphate. All concentrations were determined by agitating a 1:10 mixture of soil and deionised water for 1 hour in an orbital shaker, followed by centrifuging and 0.2 µm filtration. Then the samples were quantification using ion chromatography (Dionex ICS-5000).

3.2.5 Statistical analysis

All statistical analyses were conducted using R version 1.1.414 (R Development Core Team, 2011). To investigate differences between restored and natural marshes in nutrient concentrations collated from the literature, we tested if the distribution of ratios was different to 1, where 1 would indicate equivalent concentrations and <1 higher in restored marshes. As we could not calculate a ratio for redox potential, the difference in redox were tested against 0. We used single sample t-test or Wilcoxon signed rank test depending on normality (tested using Shapiro–Wilk’s tests).

3.3 Results

3.3.1 Distribution of studies

Globally, there was a strong bias in research towards the northern hemisphere, and the Atlantic on both the US and European coasts (Table 3-1). Despite substantial saltmarsh area, there was no data available from Australasia and Africa and only a single study in South America (Figure 3-2). Although there were 30 sites studied in both northern and southern Europe, there was an under-representation of repeated visits and measurements from the Baltic and Mediterranean Seas. There was also very limited opportunity to assess nutrient concentrations in the same area, since very few papers (18%) repeated sampling at the same sites as previous literature, with the majority of these being in China (Table 3-1).

Table 3-1 Distribution of saltmarshes studied, and the number of sites revisited within further studies.

Broad geographic region (BGR)	*Marshes studied*	*Sites revisited between studies*
USA (North Atlantic)	7	1
USA (Mid. Atlantic)	6	0
USA (South Atlantic)	22	4
USA (Gulf of Mexico)	6	0
USA (Pacific Northwest)	2	0
USA (California)	1	1
Europe (Northern)	30	1
Europe (Southern)	9	3
China (Bohai Sea)	8	5
China (Yellow Sea)	13	5
China (East China Sea)	2	0
India	13	1
Argentina	1	0
Total	***120***	***21***

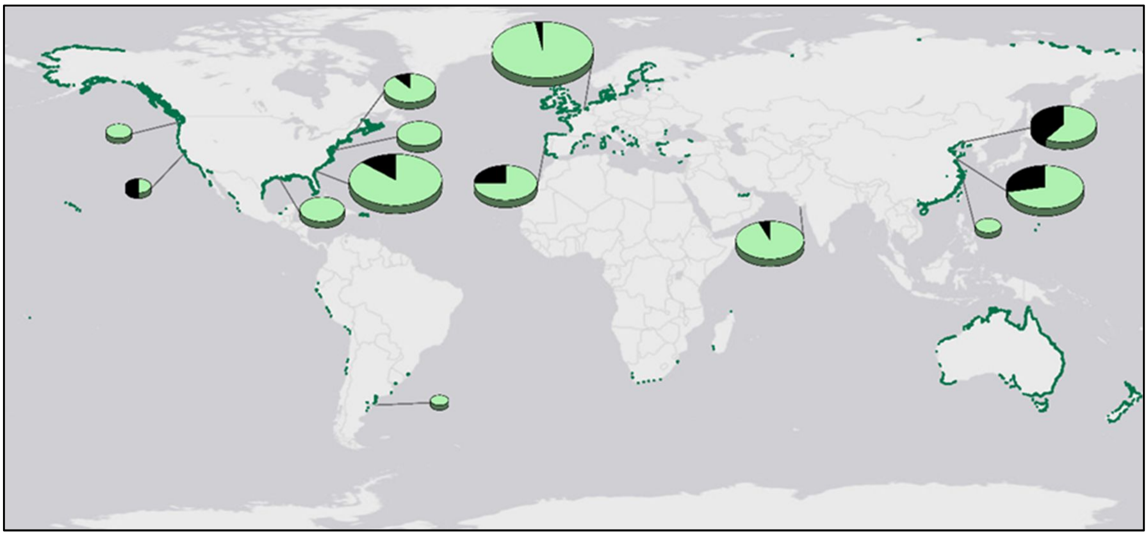


Figure 3-2 Global distribution of studies (n = 120) investigating nutrient concentrations in salt marshes overlaid up on the global distribution of saltmarshes (Mcowen et al., 2017).

3.3.2 Sampling designs used

The majority (73%) of the papers had the primary focus on spatial differences between or within saltmarshes, i.e. all samples were collected at a single point in time (Table 3-2). Examples of this spatial sampling include investigation of differences between management treatments, estuaries or consequences of elevations along the saltmarsh. There were 15 studies focused on changes in concentrations over time and 12 using both time and space to investigate saltmarsh nutrient dynamics.

Table 3-2 The distribution of papers studying nutrient concentrations divided by sampling strategy.

Sampling strategy	***Observations***	***Papers ****
Spatial	386	58
Temporal	84	15
Spatial / Temporal	247	12

* Note: The total 'papers' here is 85, as five of the studies contain data from multiple study designs e.g. the inclusion of a single sampling time point prior to principle investigation of the study.

3.3.3 Methods used in quantification

The methods and units used to quantify nutrient concentrations in the soil were highly variable, likely due to equipment availability at differing institutions. Forms of Nitrogen were the most commonly studied nutrients, with 65 % of papers studying a Nitrogen species compared to 48 % Phosphate (Table 3-3).

As tidal water is variable and key component of the saltmarsh soil composition, it is important to acknowledge this variable moisture when presenting results. The authors in the collated studies used various methods to standardise their results for the soil water component, such as normalising for moisture (mg/kg^{-1} of fresh or dry soil), or volumetrically, using soil bulk density as mg/cm^{3} or mg/ml. Most of these methods compensated for water content using various temperature and durations taking weight ratios from before and after adding yet more methodological divergence. These various methods make the normalisation values extracted extremely complex and the interpretation between studies almost impossible. Indeed, we find a minimum of eight unique units for any given form of N or P. In the extreme cases, as for the soluble forms of Nitrogen and Phosphorous the literature contained 11 units each (Table 3-3).

Table 3-3 The numbers of units, analytical methods and laboratory techniques used for quantifying the soluble forms of Nitrogen (Ammonium, Nitrate and Nitrite) and Phosphorous (Phosphate) and the total mineral forms (total Nitrogen and Phosphate). Additionally, the units and number of observations associated with these various analytical methods are provided as the final two columns on the right. (Key: Comb. = combustion, Unspec. = Unspecified, Obs. = observations).

Nutrient	***Extractant used***					
	Acids	*Water*	*Comb.*	*Unspec.*	*Units*	*Obs.*
*Soluble Nitrogen **	21	3	1	24	11	533
Total Nitrogen	14		33	8	10	319
Phosphate	14	6		18	11	298
Total Phosphorous			1	9	8	212

* Soluble Nitrogen includes (Ammonium, Nitrate and Nitrate)

As the majority of the studies investigated the soluble forms of Nitrogen (not least because there are three of them here), the laboratory preparation and analytical methods were dominated by variation in quantifying these Nitrogen forms. The most common of these methods were the use of various acids, but the concentrations of these acids and the equipment used were inconsistent. We found extraction by water the second most common method, followed by alternative methods such as soil probes and combustion. A full list of these extractants, methods and units are provided in Appendix 3-1, section 3.9.

3.4 Results - nutrient status of saltmarshes

Using the thresholds set out in Deegan *et al.*, (2012) to indicate ‘unimpacted’ and ‘impacted’ conditions, we plotted all the comparable data from units that are equivalent to ppm, namely mg/kg usually from solid soil extracts, and mg/l. We found that most of global marshes exceed levels of Phosphate shown to be detrimental to soil stability. In terms of Nitrate, much of evidence suggests elevated levels above that of an unimpacted threshold but current rarely exceeds the erosion-inducing level (Figure 3-3). However, the N:P ratio in most studies was below that of the impacted treatment in Deegan *et al.* (2012), and where the Phosphate concentration was the highest (red), the N:P ratio was typically below 1 (Figure 3-4). Nitrate can have an impact independent of the ratio with P, but its impacts are exacerbated to its maximal effect towards likely erosion forming conditions where N is both high (red) and the N:P ratio is > 1:10. Nitrate concentrations were typical lower than Phosphate, but still often above the levels of erosion-forming treatments (Figure 3-3). Plotting the concentrations of Nitrate within the N:P (Figure 3-4), we see that the majority of the highest Nitrate levels (red) are typically beneath the green horizontal dashed line ‘not impacted’.

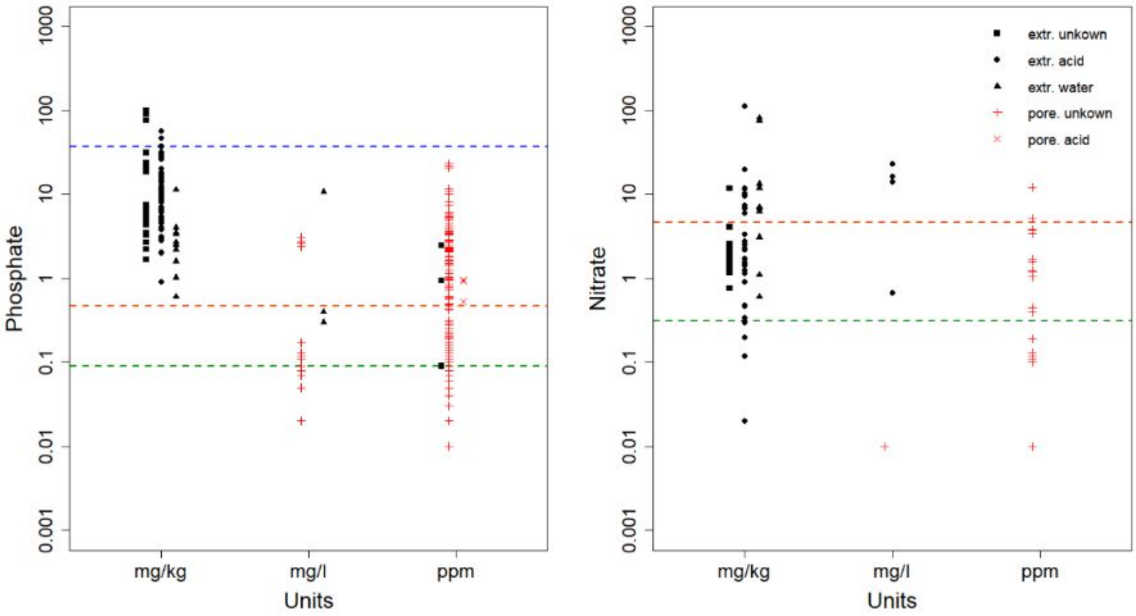


Figure 3-3 Nutrient concentrations in saltmarsh sediments (extractable (extr.) and porewater (pore)). Only units comparable to ppm were plotted. Symbols denote the analytical techniques used to measure the concentrations. Dashed lines indicate the 'impacted' (orange) and green the 'unimpacted' nutrient concentrations from (Deegan et al., 2012). Blue horizontal line indicates levels present in enriched terrestrial grasslands.

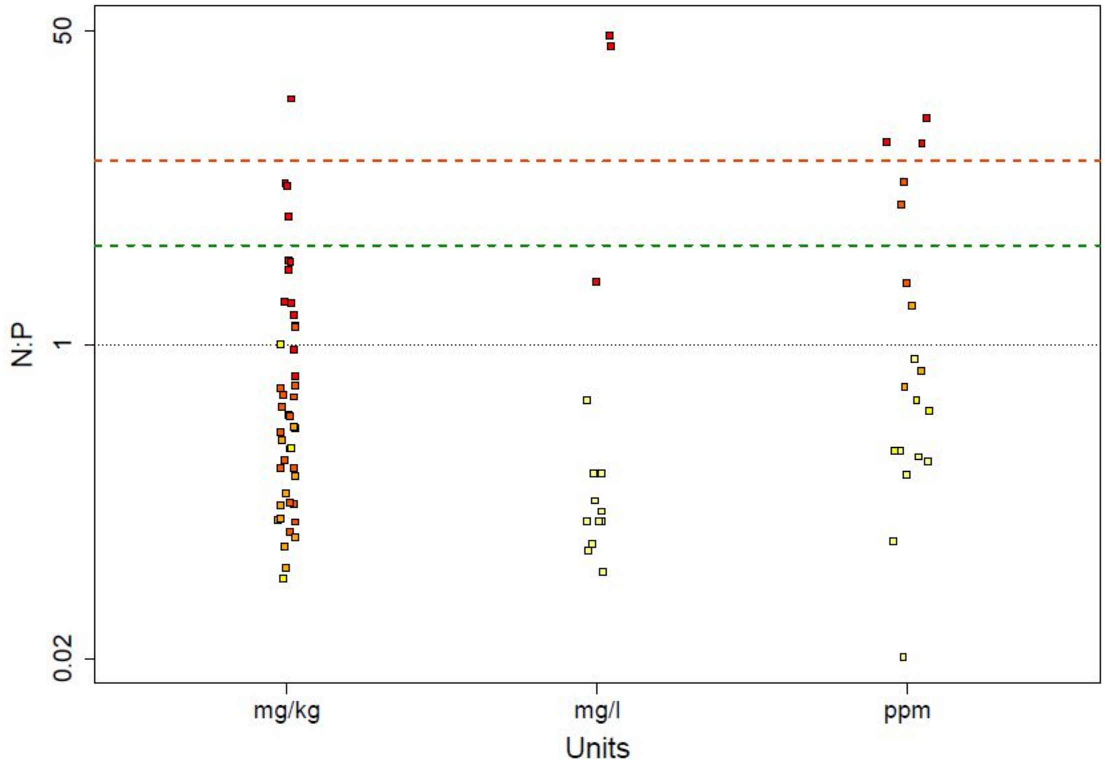


Figure 3-4 N:P ratios (Nitrate to Phosphate) in saltmarsh sediments. Only comparable units to ppm are plotted. Squares are coloured on a heat-ramp from yellow (low) to red (high) based upon the Nitrate (right hand plot) concentrations. The heat ramp is based on five categories separating data at 0.2, 0.4, 0.6, 0.8 quartiles. Dashed lines indicate the 'impacted' (orange) and green the 'unimpacted' N:P ratios from (Deegan et al., 2012).

3.4.1 Natural and restored comparisons

Using the ratios of soil measurements in natural saltmarsh to restored saltmarsh, we found that water content, total Phosphorous and total Carbon were all significantly higher in natural marshes compared to restored marshes (Figure 3-5) and (Figure 3-6). Redox potential was also significantly different between the two marsh types, but the direction of the difference could not be obtained as we had to use the absolute difference between measurements.

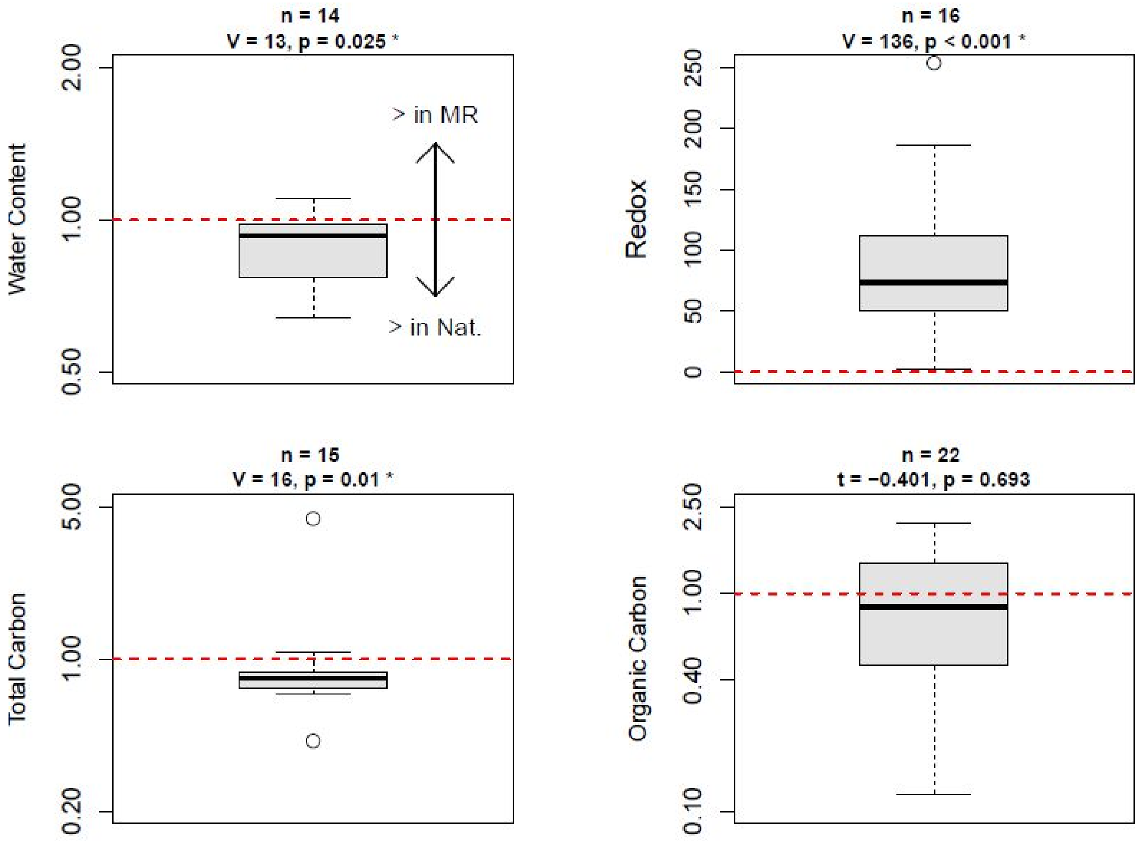


Figure 3-5 The ratios of soil conditions in natural to restored saltmarshes (water content, redox potential, total carbon (TC), organic Carbon. Median divides the box; box sides drawn at 25th and 75th quartiles; whiskers at 1.5 times the box width. The red dashed horizontal line in all plot represents a ratio/difference of zero, i.e. where the measurements are the same in both natural and restored marshes; values below this indicate higher levels on the natural marsh.

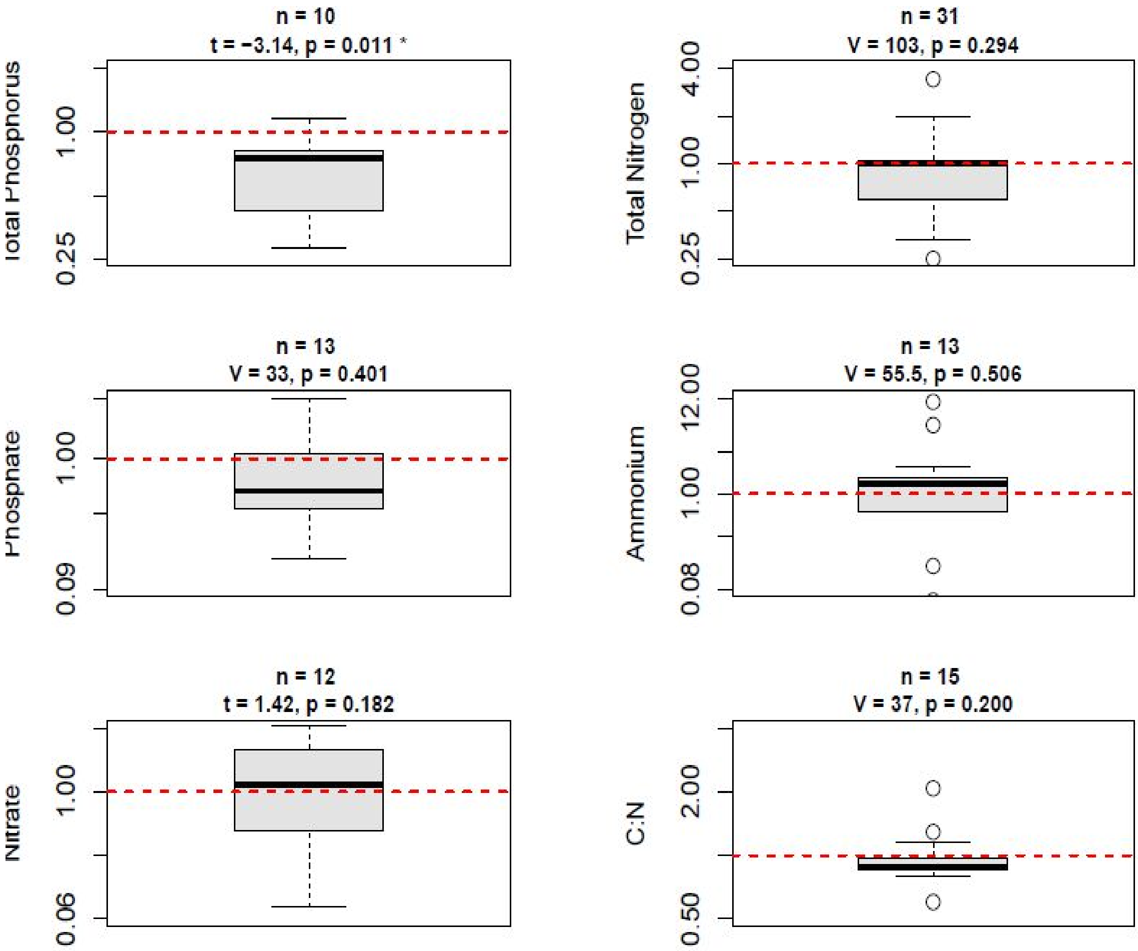


Figure 3-6 The ratios of soil conditions in natural to restored saltmarshes, total Phosphorous (TP), total Nitrogen (TN), Phosphate (SP), Soluble Nitrogen (Ammonium), Soluble Nitrogen (Nitrate) and C:N). Median divides the box; box sides drawn at 25th and 75th quartiles; whiskers at 1.5 times the box width. The red dashed horizontal line in all plot represents a ratio/difference of zero, i.e. where the measurements are the same in both natural and restored marshes; values below this indicate higher levels on the natural marsh.

3.5 Discussion

We aimed to establish the current levels of nutrients within natural saltmarsh to assess the potential eutrophication status. In doing so we have appraised the current state of the literature, finding inconsistences in the methods of nutrient quantification, reported units and spatial coverage of sampling. The consequences of these inconsistences make conclusions regarding the likely nutrient status of natural saltmarshes extremely challenging.

We find that nutrient concentrations vary greatly, with values ranging over four orders of magnitude, that may indicate some sampling bias and error in the literature. However even within the same location and study similar variation can be observed with nutrient concentrations ranged over 2-3 orders of magnitude. This variation may stem from several sources that include:

1. The eutrophication status of the estuary/coastal waters. Large numbers of these waterbodies are deemed to be eutrophic by Diaz, Selman and Chique, (2011) and so we would expect this to be reflected in the nutrient concentrations of the saltmarsh. However, when we compared the collated concentrations from the literature against their local estuary condition, we found no clear patterns (Appendix 3-2). There are a few possible reasons for this, including the proximity of the categorized estuary to sampling location, with some of these being over 30 km apart. Furthermore, the most recent update to the status maybe several years adrift and often stems from other biological observations or acute events that are often used to provide a eutrophic status, such as the presence of algal blooms.
2. Differential runoff and acute events, such as rainfall, between sites and sampling times. These are known to impact soil conditions within small time window (Pott *et al.*, 2014). This variation can be detected between individual tributaries of the same estuary that may reflect localized agricultural practices and urbanisation (Smith, Jarvie and Bowes, 2017).
3. The number of inundations per year a sampling point is exposed. This may be important because many estuarine and coastal waters are eutrophic and so the number of times a point is exposed to these enriched waters is likely to be reflected in the local nutrient concentrations. However, most studies do not present nutrient data

with matched elevation data in the context of local tidal regime and so the importance of this in our database cannot be quantified.

Concentrations of both Phosphate and Nitrate ranged from almost non-existent in the soil (<0.01 ppm equivalent) to levels that are extremely high (100 ppm equivalent) (Figure 3-3). In general, Phosphate concentrations tended to be higher than the level known to contribute to saltmarsh erosion (Deegan *et al.*, 2012). Nitrate was also regularly measured at levels above that of unimpacted marsh, but with fewer occurrences greater than the impacted level, suggesting marginally less Nitrate enrichment. In experimental enrichments, the addition of Phosphorous alone often does not increase the above ground biomass of plants, however Nitrogen addition on its own does, and the combination of both results in additional biomass above that of Nitrogen addition alone (Patrick and Delaune, 1976; Cargill and Jefferies, 1984; Sundareshwar, 2003). This requirement for a combination of nutrients to have an impact likely explains why the saltmarshes in this study remain despite the very high phosphate concentrations present. Thus, both the actual concentrations and the relative proportions of N and P are important. Typical N:P ratio in coastal waters is 15:1 (Ryther and Dunstan, 1971). Here we find that saltmarsh typically have lower N:P ratios than coastal water (15:1) and both the treatments present in Deegan *et al.*, (2012) (~10:1 and ~5:1). This would suggest a proportional lack of N compared the very high phosphate levels. Although this does not take in to account that increased N alone will impact the saltmarsh vegetation (Sundareshwar, 2003).

We found that the highest (> 80 percentile) Phosphate concentrations typically occur at the lowest N:P ratios (<1). Although this may seem intuitive, this reflects a serious threat to these saltmarshes because any increase in Nitrogen will drive the N:P towards that of Deegan *et al.*, (2012), known to result in erosion. These findings highlight two important management issues; first, many marshes are Phosphate-enriched and thus action is required to decrease Phosphate run-off, and secondly, further Nitrogen enrichment of saltmarsh soils will almost certainly lead to shifts in community or growth form (Smith and Schindler, 2009; Johnson *et al.*, 2016), and further erosion of existing saltmarsh (Deegan *et al.*, 2012).

Our understanding of the effects of realistic nutrient enrichment in saltmarshes remains limited. Experimental work, such as that of Deegan *et al.* (2012), has provided a first step in understanding of impact of this in the field. We strongly support continued effect-based research to establish context-dependent measurements of saltmarsh nutrient concentrations. We also suggest the use of both concentrations and ratios may lead to more informative characterisation of eutrophic status.

Consequences for saltmarsh restoration

We find that restored saltmarshes contain less Phosphate (and total Phosphorous) than natural marshes (Figure 3-5 and Figure 3-6), with some restored sites containing almost no Phosphate. In contrast, Nitrate and Ammonium levels on restored and natural marshes were not different. This indicates that restored marshes have higher N:P ratios, and thus although lower in total concentrations of nutrients (P), the N:P would be closer to those of Deegan *et al.*, (2012). While there may be potential negative impacts of the higher N:P ratio, our findings do not support our hypothesis that nutrient concentrations would be higher in restored sites due to their former agricultural land use. Although there may be other impacts of former land use, such as reduced sub-surface porosity (Spencer *et al.*, 2008, 2017).

One of the ecosystem services provided by saltmarshes is carbon storage under newly deposited sediment. Previous work suggests carbon storage in created marshes is not as effective as a natural marsh (Moreno-Mateos *et al.*, 2012; Burden *et al.*, 2013). Our synthesis of the literature finds that restored marshes tend to have less Carbon in their sediments (Figure 3-5). Restored sites are often low and thus have very rapid accretion rates, so the carbon may be less dense per unit of volume, not necessarily less carbon in total. Carbon measurements therefore need include sedimentation rates or bulk density in calculations. This finding has some practical restoration design implications as there tends to be more Carbon sequestration in the upper marsh (Burden *et al.*, 2013). Thus, creation of upper marsh could enhance carbon storage.

This work marks a first attempt to unite and synthesise the current knowledge of nutrient concentrations within natural and restored marshes. However, we are yet to develop a clear picture of these concentrations as much of the data are not comparable. We strongly support a systematic approach to the presentation of units in the literature, the methodologies used, and further encourage the open access to data with the additional provision of meta/contextual data to each measurement, such as elevation or current erosion levels.

3.6 Conclusions and recommendations

Nutrient concentrations in saltmarshes are highly variable, but with a tendency to be Phosphate enriched. The exception to this is in restored marshes where Phosphate concentration are low, this is in contradiction to our expectation of nutrient enrichment due to prior land use. This may suggest different management techniques are required to deal with nutrient related issues. Overall our understanding of nutrient levels is poor due to a lack of comparable methods and units and large geographic regions currently unstudied.

To address these key issues with interpretation of the variable and inconsistent status of the literature we conclude with four key recommendations and directions for future research in terms of nutrients on saltmarsh ecosystems.

1. The use of the same treatment concentrations as Deegan *et al.* (2012), to be used on multiple continents to assess inter species and geological setting impacts to ensure a global ‘enriched’ and damaging level of Phosphate and Nitrate be established.
2. A collaborative effort between professional bodies such as Natural England, Environmental Protection Agency (USA) alongside coastal researchers. This is important as saltmarsh is unlike all other soils due to its pre-existing and dynamic concentration of salts that already exceed or mirror the chemicals used in many extraction methods. The goal of this workshop would be to establish a readily repeatable method of extraction that is not dependent on apparatus available.
3. A collaborative effort between soil and coastal journal editors is required to establish an expected reporting standard such as ppm equivalent in the supplementary information or paper itself. We also strongly support the open access to raw data rather than visual representation of data as raw data will assist in statistical power and future data sharing.

4. The establishment of online, website repository for nutrient data in saltmarsh ecosystems to be started by this meta-analysis and freely available to the saltmarsh community to both added too and use freely in future manipulation studies.

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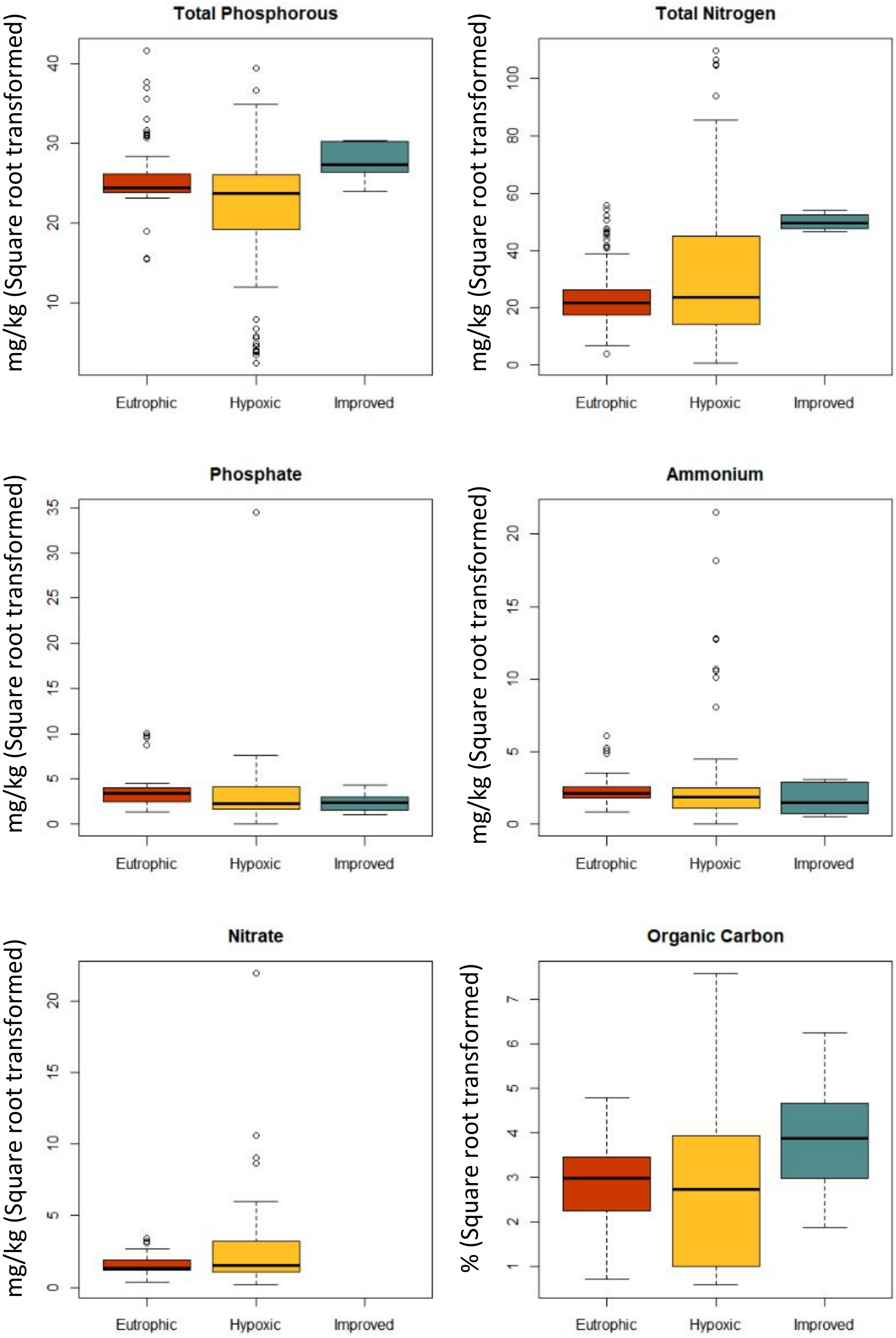
3.8 Appendix

Appendix 3-1 Tabulated analytical methods, equipment and extractants used in saltmarsh nutrient studies. (Key: Unspec. = Unspecified, conc. = concentration, ICP = Inductively couple plasma spectrometry, IC = Ion chromatography)

Analytical method		*Equipment Used*		*Extract*	
Colourimetric	71	Flow injection	21	KCl (Unspec. conc.)	18
Combustion	36	Spectrophotometry	8	Acid digest (Unspec.)	21
ICP	9	Elemental analysers	27	Water	9
IC	9	ICP	9	Olsen P	7
Field equipment	2	IC	9	2M KCl	3
Literature reference	10	Electrodes	2	1M HCl	3
Unspec. equipment	27			3.5M HCl	2
				Mehlich 3	2
				Morgan’s solution	2
				Bray-2	1
				Nessler’s	1
				0.5M K_2SO_4	1
				HCl (Unspec. conc.)	1

There several often-unmentioned analytic issues with the use of each sampling method for soil nutrient composition. The use of colourimetric devices measure the absorption of light on a specific wavelength and included such analytical equipment such as continuous flow analysis; segmented flow analysers; spectrophotometry and atomic absorption spectroscopy is common. However colourimetric determination requires precise mixing times, colour development and temperature between batches, which can be a sources of error (Allen, 1989; Rowell, 1994). Away from the individual nutrient quantification methods a broader array of ions, cations and elemental metals have been simultaneously measured using ion chromatography (IC) and inductively coupled plasma spectrometry (ICP). Reasons for wide ranging methods include lower detection limits, savings in labour, time and storage reagents, and no use of carcinogens in IC (Jackson, 2000; Miranda, Espey and Wink, 2001). Some downfalls to IC also exist, most notably, Chloride peaks can sometime obscure Nitrate on the chromatograph particularly when 2 mol^{-1} L KCl is used as an extractant.



Appendix 3-2 Comparison of the nutrient concentrations (total Phosphorous, total Nitrogen, Phosphate, Ammonium, Nitrate, and organic Carbon) in saltmarsh sediment and the status of the estuary (Eutrophic, red; Hypoxic, yellow; Improved, green). Median divides the box; box sides drawn at 25th and 75th quartiles; whiskers at 1.5 times the box width.

4 Nutrient, sedimentation and soil oxygenation dynamics in a newly inundated managed realignment scheme

Abstract

In September 2014, one the largest managed realignment (MR) schemes in the UK, Steart Marshes, was breached, creating 262 hectares of new intertidal habitat. The creation of new habitat in this manner can play an important role in future flood defence and aid governments to reach legal targets that require them to create compensatory habitat for that which has, and is being, lost. Despite obligations that this habitat must be similar to natural marshes, MR has thus far have failed to deliver the same plant communities as natural saltmarsh. Many restored saltmarshes, including Steart Marshes, are created on former agricultural land. Prior agricultural land use is known to impact the physical properties of the developing soils on restored marshes, such as porosity. Such prior land use might also be expected to lead to a legacy of high nutrient concentrations in the newly restored habitat. However, only limited research has investigated the development of soil nutrient concentrations following restoration, and this is limited to short time scales. As a result, our understanding of nutrients and other soils properties in a newly developing restored saltmarsh is lacking in both temporal and contextual detail.

Here we investigate the roles of former land use on the development of soil properties in Steart Marshes managed realignment over a 31-month period, starting immediately prior to flooding. We compare these soil properties to those on both agricultural and natural saltmarsh reference sites. We found that, although land use initially may have an impact on some nutrient concentrations, this is quickly lost due to stark changes caused by the reinstatement of tidal flooding. Soil properties were highly variable between sampling periods, with strong seasonality especially in summer, but there was no clear chronological pattern in the soil properties, an indication of no directional development. However, we did find that there was a relationship between elevation of the quadrats including the change due to recent sedimentation and soil properties. This is likely because of former land use being lost underneath high rates of sedimentation.

The signature of former land use on the surface soil chemical composition is rapidly lost and replaced by the roles of seasonality and changing elevation as a function of sedimentation. The impacts of seasonality have the greatest impact on dissimilarity from the natural marsh once restoration of tidal flooding is established. Smoothing these seasonal disparities in soil conditions therefore should equate to a more natural variation in nutrient concentration. This could be achieved via the added drainage in winter months or the encouragement of vegetation in summer to assist the maintenance of soil moisture.

4.1 Introduction

Saltmarshes are valuable intertidal habitats providing a range of ecosystem services, such as wave attenuation and recreation (Barbier *et al.*, 2011). Saltmarsh has faced centuries of loss and damage due to land claim for agriculture, and is currently at risk from erosion driven by eutrophication (Cloern, 2001; Deegan *et al.*, 2012) and sea-level rise (Hay *et al.*, 2015). Since the early 1990s, legislation (e.g. Copeland, 1999; European Commission, 2007), has required the creation of new saltmarsh habitat, prior to the loss occurring. To achieve this, many countries have utilised a method called “managed realignment” (MR) or “de-embankment” to generate new habitat. During MR, existing sea defences are breached, usually proceeding the construction of new landward defences. This allows for the controlled tidal flooding of carefully selected packets of terrestrial, usually agricultural, land.

However, MR sites have failed to deliver the same plant communities, bird species and invertebrates (Zedler and Callaway, 1999; Mazik *et al.*, 2010; Mossman, Davy and Grant, 2012). The use of former agricultural land as a base for a new saltmarsh may influence the restoration success, as agriculture is known to result in changes in soil structure and chemistry, which can also prevent subsurface drainage and alter plant communities (Crooks *et al.*, 2002; Spencer *et al.*, 2011; van Klink *et al.*, 2015). The combination of compaction and reduced subsurface drainage may result in greater proportion of areas of waterlogging and lower redox potential. This in turn may lead to differences in plant communities, as species are differentially tolerant of anoxia (Colmer and Flowers, 2008; Sullivan *et al.*, 2017). The former agricultural use may also result in higher nutrient concentrations on restored sites. However, the legacy of potential soil enrichment has been little studied in saltmarsh restoration ecology. We also know that such changes in these nutrients can have significant impacts on the saltmarsh communities present (Levine, Brewer and Bertness, 1998). This may lead to a loss of diversity, which in turn can lead to reduced soil stability (Ford *et al.*, 2016). Indeed when these nutrients are present at levels considered moderate in terrestrial environments, this can lead directly to the erosion and loss of habitat we are aiming to restore or protect (Deegan *et al.*, 2012).

It is therefore very important to understand the conditions present in MR schemes, but very few papers have attempted to track the development of soil in restoration schemes. Blackwell, Hogan and Maltby, (2004) studied the short-term changes in soil conditions (e.g. Conductivity and Nitrate) immediately before and after restoration (total duration of the study was 6 months). They found that within the first four months of restoration there were no consistent patterns in Phosphate or Nitrate, but there was a large spike in Ammonium immediately following flooding. However, since this study was short term, it could not track this trajectory to see if it was a seasonal effect.

Despite the importance of nutrient and soil conditions within the colonisation of new saltmarshes, very little research has attempted to characterise the soil development as a using a wide range of soil chemistry and other properties, and temporal studies have rarely exceeded the first-year post restoration making our knowledge of temporal development extremely limited. As a result, there is a lack of understanding of how restored marshes develop, if they are nutrient enriched, and what drives the variation in these soil conditions such as elevation, land use or seasonality. Furthermore, there is limited understanding of the nutrient status of natural marshes (Chapter 3) and, as such, limited evidence against baseline conditions to compare the development of restored systems, reiterating the need for studies containing effective reference conditions. In this study we aim to assess the primary components of soil composition over a three-year period. We will review the trajectories of soil convergence or divergence within the developing MR site against natural and agricultural defences, discussing possible sources of dissimilarity between the habitats. Further to this, we will investigate the likely drivers of variation in important soil nutrients such as former land use, elevation and seasonality, discussing likely management implications.

4.2 Methods

4.2.1 Study site and sampling design

Steart marshes is situated at the mouth of the River Parrett, on the south bank of the Bristol Channel in Somerset, UK (51.191870 °N, -3.068518 °E). Tidal flooding was reinstated to the site in September 2014 via a single breach in the seawall. The new intertidal site covers 262 hectares, making it one of the largest MR in the UK. The site aims to providing enhanced flood risk management and aimed to generate intertidal saltmarsh and mudflat habitats (ABPmer, 2018).

Within Steart peninsula a total of 16 permanent quadrats were established. Twelve of these quadrats were within the MR site, stratified to capture the elevation range present within four different former land-uses. These land uses, arable (cereal or maize), pasture, grass ley and a disturbed plot with topographic manipulations that was formerly pasture, were identified from historical maps (Halcrow, unpublished report). To monitor reference conditions, one permanent quadrat was established on an adjacent agricultural field that remained pasture for the duration of the study. Finally, a further three quadrats were located on an adjacent natural saltmarsh (high, moderate and low marsh), identified by the presence of *Elytrigia atherica* (High), *Aster tripolium, Puccinellia maritima* and *Triglochin maritima* (mid marsh) and bare earth and *Salicornia spp*. (low marsh) respectively, (Figure 4-1 and descriptions in Appendix 4-3). Permanent quadrats were located a minimum of 50 m apart within land uses, except for the natural marsh where the elevation range present was confined to a small area, and as such samples were <5 m apart. All quadrats were revisited approximately every three months on a total of ten occasions (missing the winter of 2015) to track the development of the restored site through time. The ten survey visits were conducted between August 2014 (1 month prior to restoration, t = 0) and January 2017 (t = 31), all on neap tides.

Figure 4-1 Map of Steart marshes, showing the locations of sampling quadrats within the managed realignment site (Arable = light green, Disturbed = white, Grass ley = orange, Pasture = purple) and both the agricultural (yellow) and natural (blue) reference quadrats.

4.2.2 Soil and surface monitoring

Within each of the quadrats, soil redox potential was measured with a single reading at the central stake at approximately 8 cm below the surface using a VWR redox electrode, beginning at t = 10 months post restoration, when sufficient moisture allowed for the insertion of the probes to the appropriate soil depth. The measurement of redox potential was not possible at the agricultural reference as the surface was often too dry for proper application, and so, we used a proxy value of 300 mV to represent well aerated conditions. Approximately 50 g of soil was taken from the surface 8 cm at all quadrats on all sampling occasions and placed into a sealed polythene bag and stored at 4 °C as soon as possible. These samples were analysed for soil moisture, organic Carbon and additional eight soil nutrients (Chloride, Sulphate, Nitrate, Phosphate, Sodium, Ammonium, Potassium and Calcium) as per the methods outlined in Chapter 3. A further 0.5 g sample of dry soil was used to obtain the total Nitrogen % and Carbon % with a LECO TRUESPEC carbon and nitrogen analyser.

At 13 of the quadrats, we inserted a 1.5 m metal stake to the soil to a depth of 1 m (to avoid movement) to measure the sedimentation rate. Stakes were not inserted into the permanent agricultural reference quadrat or at the mid and low natural marsh sites. The location and the initial elevation of the stakes was measured relative to the UK national datum, Ordnance Datum Newlyn (ODN, based on mean sea level) using a RTK GPS (Trimble R10 GNSS, ± 1.5 cm vertical and ± 1 cm horizontal accuracy) at both the start of the study (hereafter 'initial elevation').

We measured the sedimentation between each visit, using the central stake at each quadrat. To this stake, we placed plate of 30 cm length containing ten holes spaced 2 cm apart onto a fixed washer approximately 6 cm down the central stake. We ensured a consistent sampling of sedimentation using a compass and reference points on the horizon to ensure consistent bearing and a spirit level for horizontal repeatability. Through the holes in the plate we lowered 50 cm pins obtaining ten measurements of elevation above the marsh surface using a ruler measuring the length of pin to the horizontal bar. Sedimentation baseline measurements were established at t = 4 as soon as possible after restoration, the use of a dGPS measurement upon deployment of these stakes abled us to derive an elevation measurement of the quadrats at each visit via the addition / subtraction of average sedimentation from the initial baseline elevation (hereafter 'current elevation').

4.2.3 Statistical analysis

All statistical analysis was conducted using R (R Development Core Team, 2011). Prior to analysis Shapiro–Wilk's tests were used to test for normality of the soil chemical concentrations and other environmental variables, finding only organic Carbon to be normally distributed. We plotted the temporal pattern of mean soil conditions using two-way interaction proceeded by analysis of variance models to test for significant drivers of variance in each of the nutrients though time, either: land-use (arable, disturbed, grass ley, pasture and saltmarsh); season (spring, summer, winter or autumn); elevation of the quadrat; or time since restoration in months. Alongside this, the mean sedimentation at the four land-uses and natural marsh for each visit was calculated and presented as both mean sedimentation since t = 0 and since previous visit, to identify trends and spikes in sedimentation.

Prior to ordination using Nonmetric Multidimensional Scaling (NMDS) using Euclidean distance and scaling to asses the similarity in quadrats through time, we tested for collinearity using Pearson correlation tests and removed highly correlated variables (threshold of $r^2 > 0.75$). This resulting in the removal of Sodium, Potassium, Calcium, and Elevation (current) from the subsequent NMDS. The NMDS were performed on sequential sampling visits for the uncorrelated soil physical and chemical properties to assess the differences in total soil conditions between the source land uses and elevations of the soils in natural and restored and agricultural soils. We further demonstrate the changes to soil conditions during the restoration process and natural temporal variance we use Procrustes test to assess correlation between time points. To test for significant differences in the soil conditions between our explanatory variables (former land use, time since restoration and elevation) we use a PERMANOVA within the ‘vegan’ package (Oksanen *et al.*, 2013). We finally used linear mixed-effects models (in the package ‘lmer.Test’ (Kuznetsova, Brockhoff and Christensen, 2017) to investigate the effect of land use and elevation on individual nutrients (Chloride, Sulphate, Nitrate, Phosphate, Ammonium, soil moisture, total Nitrogen, total Carbon and the C:N), accounting for site as a repeated measure.

4.3 Results

4.3.1 Seasonality and temporal signatures within land-uses.

Prior to restoration (t = 0) there were differences in soil chemical concentrations between the MR and natural sites (Appendix 4-1). Ammonium, Magnesium, Moisture, Chloride, Sulphate, and the C:N ratio were all higher on the natural saltmarsh than on the pre-restoration (t = 0) MR site. These significant differences are lost post restoration (Appendix 4-1). Following restoration of the site, there were peaks in all the soluble nutrients within both the MR and natural marsh. This is particularly noticeable from the first summer (t = 7) and first autumn (t = 10) after restoration Figure 4-1 and Figure 4-2. From the second winter (t = 13) onwards, conditions begin to stabilise and from after month 20, all the soluble nutrients are similar, in terms of actual values and levels of variation, in both the MR site and the natural saltmarsh. There was however, consistently lower redox potential within the MR compared to the natural marsh.

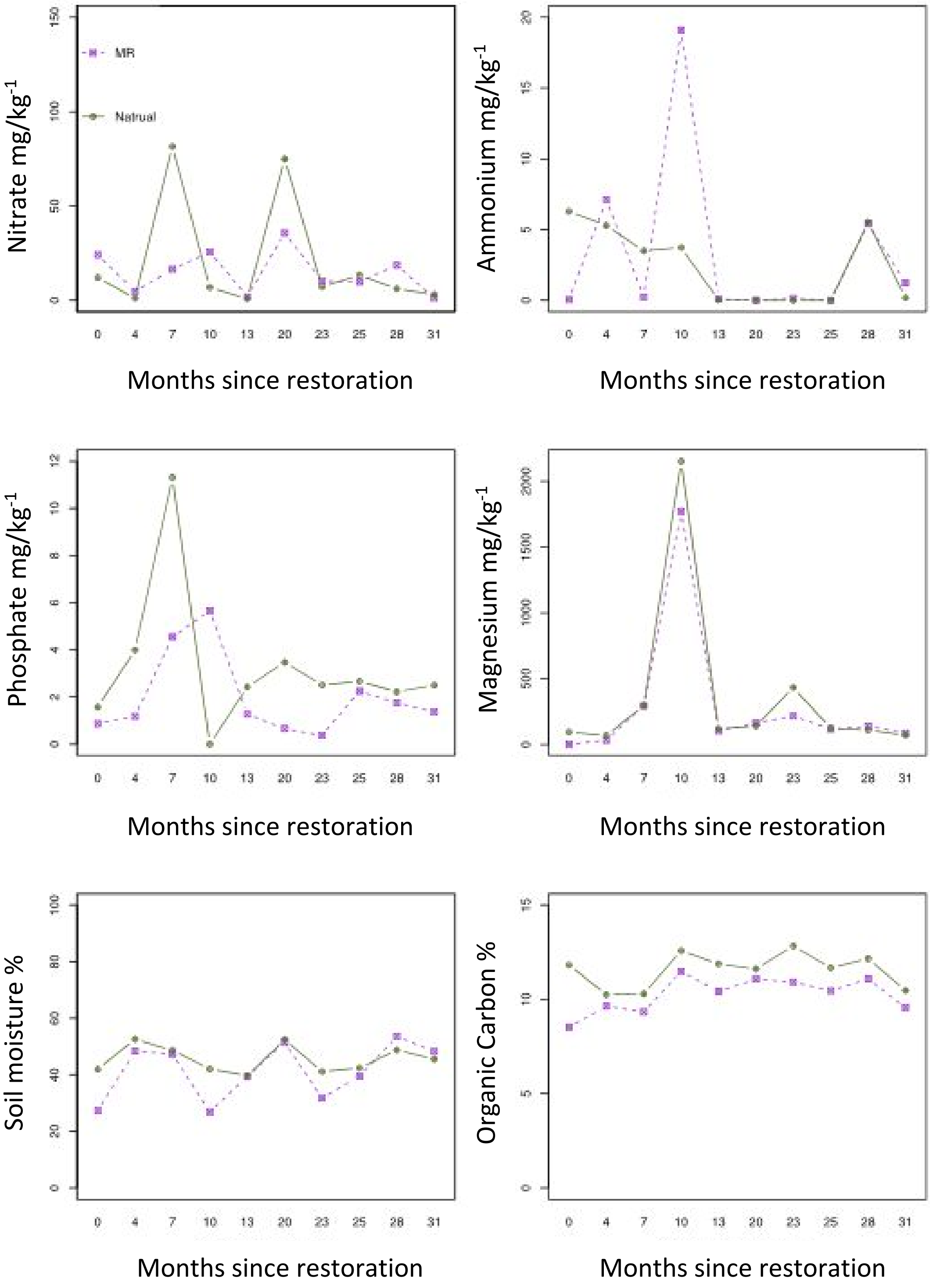


Figure 4-2 Mean for each sampling visit between the Natural saltmarsh (green) and MR site (purple dashed). Plot generated via interaction plots using two-way combinations of factors. Plots clockwise from top left: Nitrate, Ammonium, magnesium, Organic Carbon, Soil moisture and Phosphate.

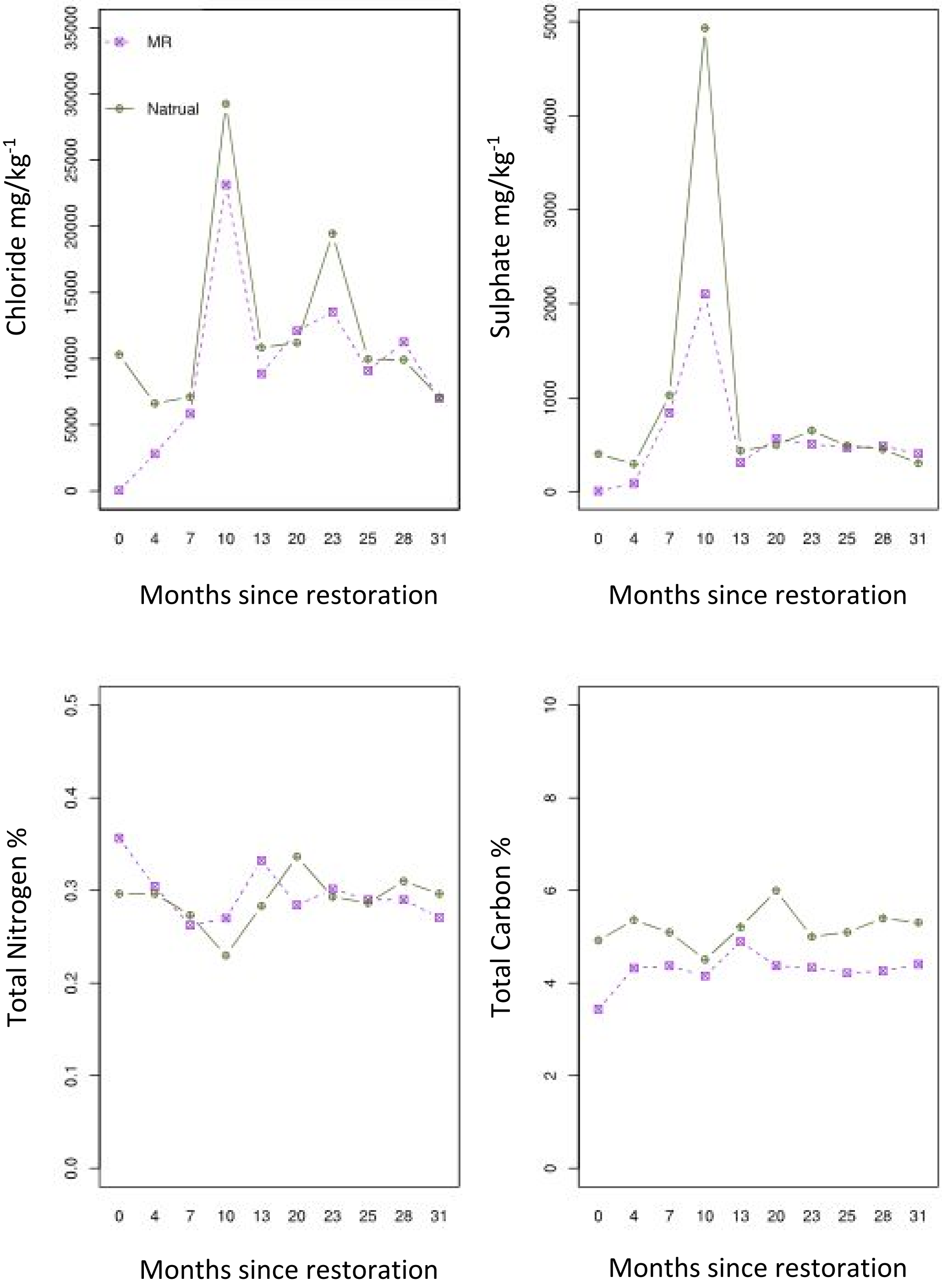


Figure 4-3 Mean for each sampling visit between the Natural saltmarsh (green) and MR site (purple dashed). Plot generated via interaction plots using two-way combinations of factors. Plots clockwise from top left: Chloride, Sulphate, Total Carbon and Total Nitrogen.

The drivers of each soil property during this study was inconsistent (Table 4-1). Two of the nutrients, both forms for bioavailable Nitrogen (Nitrate and Ammonium) seemed dominated by the roles of temporal factors such as seasonality and time since restoration. This differed however to possible less dynamic total nitrogen and carbon that was driven by spatial factors of former land-cover and elevation of the quadrats (Table 4-1). All the other properties can include Chloride, water content and Phosphate were dominated by a mix of spatial and temporal factors.

Table 4-1 Summary of significant drivers within analysis of variance models of the effects of former landcover (arable, disturbed, grass ley and pasture), season (spring, summer, winter and autumn), elevation (initial and sedimentation adjusted) and months (time since restoration) for each of the soil properties. p < 0.01 = ** and p < 0.05 = *

Soil properties	***Landcover***	***Season***	***Elevation***	***Months***	***Summary***
Nitrate		*		**	temporal
Ammonium		**		**	temporal
Phosphate			**	**	mix
Magnesium		**	**	**	mix
Water %	*	**	**		mix
Organic Carbon	**	*	**	**	mix
Chloride		**	**	**	mix
Sulphate	*	**	**	**	mix
Total N			**		Spatial
Total C	**		**		Spatial
Model summary					
Df	1	3	13	6	
Residuals	124				

4.3.2 Accretion

We found notable periods of accretion, particularly in the second spring (t = 20), and very clear dewatering in all former land uses in t = 10, 23 and 25 (summer months) (Figure 4-4). It is worth noting that the natural saltmarsh also experienced similar periods of both accretion and erosion during this 31-month study, suggesting potential hydrodynamic impacts of managed realignment on existing saltmarshes, which may also explain some of the variation seen in Figure 4-2 and 4-3. By the end of the study however there was far higher levels of accretion in the MR than the natural marsh, with a peak sedimentation level of 246 mm within the “Disturbed” land use during the 20th month since restoration. In the natural marsh we saw the opposite and in fact after 31 months the accretion in far less drastic < 40 mm. Pasture and Disturbed experienced the highest rates of sedimentation (between t = 13 and t = 20). Average accretion rates within the MR site were approximately 4.2 cm yr $^{-1}$.

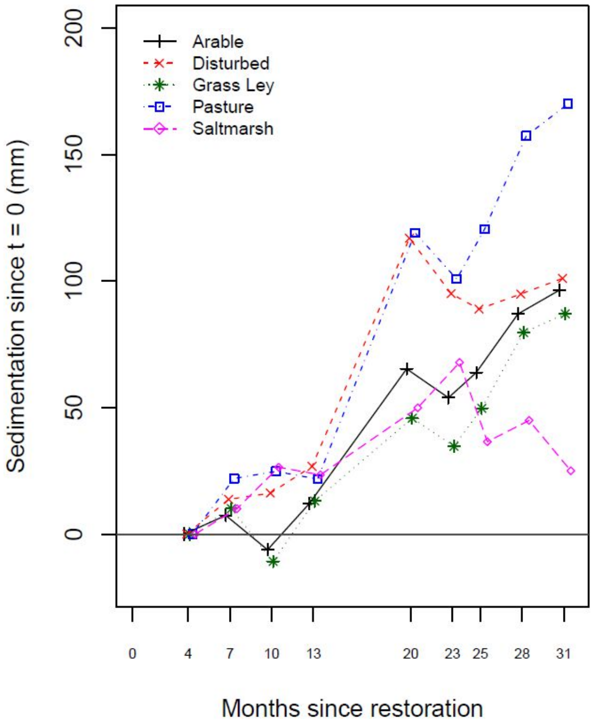


Figure 4-4 Total sedimentation (mm) since the initial (t=0) last visit on land-uses of the Steart Marshes managed realignment site and the reference natural saltmarsh.

4.3.3 Soil ordination, and the roles of time, space and land use.

In Figure 4-5, we present the NMDS for pre-restoration (t = 0, months), the initial post restoration time point (t = 7), the second spring (t = 20) and the third spring visits (t = 31, months). From the t = 0 to t = 7 there was not a significant correlation between the ordinations ($m^2 = 0.88$, $p = 0.32$). As the restoration process continued a strengthening and significant collation develops between the spring samples t = 7 and t =20 ($m^2 = 0.39$, $p = 0.001$) and between t =20 and t = 31 ($m^2 = 0.59$, $p = 0.002$).

Within the ordinations we find that initially the soil properties of the saltmarsh (yellow) is separate from the land-uses within the MR scheme drive mostly by increased Chloride, Ammonium, Magnesium and Sulphate. When the MR is introduced to the effects of flooding much of this difference is lost and variation within the saltmarsh itself becomes alongside huge variation in the MR in first spring (t = 7). By the proceeding spring (t = 20) most of the MR land uses have begun to cluster apart from arable (red) that remains more akin to the agricultural reference (orange) and driven by Ammonium. At the final sampling visit variation in the MR and natural saltmarsh is broadly similar though it is worth noting that throughout the time series one of the saltmarsh plots remains distinct from all the others, this is the mudflat or lowest part of the natural reference. This is an interesting finding as we may have expected this quadrat to be most convergent with the MR due to the pooling and accretion present in the MR.

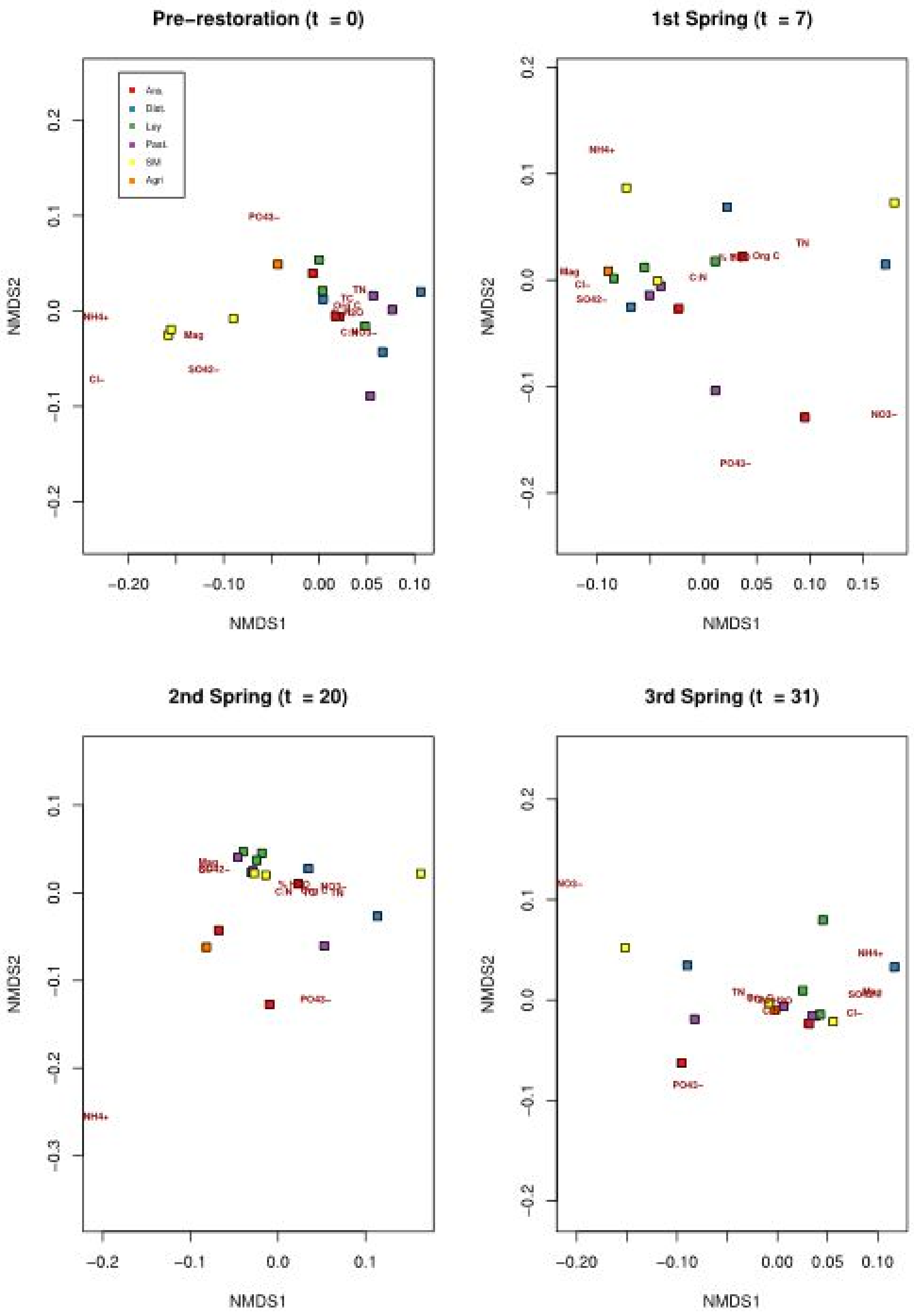


Figure 4-5 NMDS of soil parameters in the natural saltmarsh, agricultural reference and four former land uses (arable, disturbed, grass ley, pasture) on the managed realignment site. Soil parameters included in the NMDS were; Chloride, Sulphate, Nitrate, Phosphate and Ammonium concentrations, and percentage soil moisture content, total Nitrogen, total Carbon and the C:N ratio.

4.3.4 Drivers within the development

Despite starting conditions being different, we found that during restoration (t = 4 to 31), land use no longer presented significant effect on the developing soil conditions during the three years after restoration (PERMANOVA: F = 2.51, p = 0.079). Indeed, by the end of sampling, there was not a significant difference between the natural marsh and MR in terms of nutrient composition (PERMANOVA: F = 0.002, p = 0.997). We also found the initial elevation of the quadrats had no significant influence on the soil chemistry (PERMANOVA: F = 3.02, p = 0.07). Interestingly, the current elevation, which included the sedimentation adjustments per visit, was significant (PERMANOVA: F = 0.449, p = 0.02). A full table or results for the PERMANOVA analysis is provided in section 4.6, Appendix 4-2. Finally, when individual soil parameters were tested for the effects of land use and elevation, we found that only total Nitrogen differed significantly between the arable and other former land uses, Table 4-2.

Table 4-2 Summary of the linear mixed effects model for total Nitrogen on the Steart managed realignment site, with land use and elevation including sedimentation (current elevation) (site was included to account for repeated measures)

Fixed effects	*Estimate*	*S.E.*	*Df*	*t value*	*p*
Arable	0.730	0.220	9.38	3.311	< 0.01
Disturbed	-0.028	0.062	6.74	-0.460	0.659
Grass Ley	0.117	0.065	6.93	1.795	0.116
Pasture	-0.027	0.062	6.76	-0.442	0.671
Elevation ± sedimentation	-0.094	0.046	9.53	-2.017	0.072

4.4 Discussion

Our results demonstrate that differences in prior land use do not result in differences in soil chemistry following restoration. However, the elevation of the quadrats including recent sedimentation was a significant factor on soil chemistry. Few previous studies have investigated the role of prior land use in marsh development. Garbutt *et al.*, (2006) found higher plant colonisation in cereal stubble fields compared to ploughed and cultivated, although this was short-lived. They also did not study soil chemistry or account for changing elevation (via sedimentation) in their relationships. Ploughing is thought to alter sub-surface sediment properties, such as porosity, reducing sediment drainage (Spencer *et al.*, 2017). Three of the land uses in our study have experienced long term ploughing or major disturbance during site construction, and we found that redox potential was lower in the managed realignment compared to the natural marsh. While land use activities during reclamation can influence marsh development, e.g. altered topography (Chapter 2) and sub-surface sediment structure, we find that this is not reflected on plant-available nutrient concentrations. This is likely to be due to increased sedimentation covering the previous agricultural surface, thus reducing its influence. With no impact of former land use on the developing soil chemistry, it is important to recognise it is the nutrient levels in the fresh sediment or estuarine waters that must dictate the observed conditions. Therefore, the timing of restoration and location of the MR site will drive the soil chemistry at least for the first two and half years of development.

In our study we observe massive seasonal variation in the soil chemistry (Figure 4-2), but with no trend over time. In a similar but shorter study with fewer soil variables, Blackwell, Hogan and Maltby, (2004) observed comparable variation but only in Ammonium, and not in the other soil properties they measured. Interestingly, our long-term study allows us to detect that this variation in multiple soil properties did in fact tail off over time, thus demonstrating the value of long term studies. We also find similar temporal patterns in the natural marsh as in the MR, further strengthening the need for spatial and temporal reference to soil development studies. During the first spring and summer ($t = 7$ and 10) of restoration, typically the periods of maximum plant growth, we found very high concentrations of Sodium, Chloride and both Nitrate and Phosphate. These enhanced concentrations will favour pioneer species that can tolerate the salts and outcompete mid marsh species when in competition due peaks in nutrient conditions (Emery, Ewanchuk and Bertness, 2001; Pennings, Grant and Bertness, 2005). Evaporation rates are known to be higher on bare ground and at the higher elevations present in the Steart MR site, so potentially causing increased concentrations. However, these high concentrations were also observed on the well vegetated natural marsh. We can hypothesis this is due to repeated sedimentation and de-watering events leaving behind concentrated nutrients, and we have observed evidence of this in thin laminations of sequential deposition (Appendix 4-3).

Initial quadrat elevation was not a significant driver of variation in soil chemical composition. However, when we adjusted the elevation by sequential sedimentation measurements we find it is an important predictor. Sedimentation per se is also has an important impact on marsh development as accretion between years of greater than 2 cm begins to have an impact on seedling survival (Bouma *et al.*, 2016). Our average sedimentation rate on the MR site of 4 cm per year far exceeds this, possibly explaining why we see very limited vegetation colonisation at our quadrats (pers. obs.). Differential sedimentation is known to occur in topographic features, such as depressions and hillocks (Elschot and Bakker, 2016). As a result, increasing elevational heterogeneity through topographic features could result increased nutrient variation and possibly more niches.

To conclude, in contrast to our earlier hypothesis, land use only had an impact on soil conditions prior to the breach. We did however observe a catastrophic impact of tidal flooding on the early soil-forming nutrient conditions in the MR. As the sediment was deposited the role of former land use was removed and replaced with the importance of both seasonality and alterations in elevation. Soil nutrient concentrations and composition in the MR site at the end of our study were not different from those on natural marshes, therefore, if the same plant communities do not develop post t = 31 we must assume there further yet unexplored drivers of these plant communities outside of elevation, nutrient dynamics and time.

Acknowledgements

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4.6 Appendix

Appendix 4-1 Kruskal-Wallis analysis of the effects of difference between the MR and natural marsh and within the MR at selected time points.

Df = 1	**t = 0**		**t = 4**		**t = 7**		**t = 20**		**t = 31**	
	χ2	p	χ2	p	χ2	p	χ2	p	χ2	p
Nitrate	3.52	0.06	4.68	0.03 *	0.18	0.66	1.02	0.31	0.57	0.44
Ammonium	7.50	0.01 *	0.02	0.88	1.51	0.21	0.86	0.35	0.33	0.56
Phosphate	2.12	0.14	0.02	0.87	3.52	0.06	1.90	0.16	2.08	0.14
Magnesium	6.75	0.01 *	1.68	0.19	0.02	0.88	0.02	0.88	0.33	0.56
Water %	5.33	0.02 *	1.02	0.31	0.00	1.00	0.02	0.88	0.08	0.77
Organic C	2.52	0.11	0.33	0.56	0.33	0.56	0.08	0.77	2.52	0.11
Chloride	6.75	0.01 *	1.68	0.19	0.18	0.66	0.00	1.00	0.02	0.88
Sulphate	6.75	0.01 *	2.52	0.11	1.02	0.31	0.85	0.47	0.08	0.77
Total N	1.03	0.31	0.01	0.94	0.88	0.34	0.64	0.42	2.79	0.09
Total C	3.00	0.08	4.68	0.03 *	1.02	0.31	3.00	0.08	2.30	0.12
Ratio	4.68	0.03 *	1.33	0.24	0.18	0.66	0.33	0.56	0.00	1.00
Redox					2.57	0.10	0.52	0.46	1.14	0.28

Appendix 4-2 PERMANOVA analysis of the effects of former land-use (arable, disturbed, grass ley and pasture), elevation (initial and sedimentation adjusted) and time (continuous and between visits) between the MR and natural marsh and within the MR.

MR vs Natural saltmarsh	***Df***	μ^2	***F***	R^2	***p***
Pre-restoration (t = 0)					
Former land-use	3	1696.9	4.25	0.614	0.012 *
Residuals	*8*	*399.63*			
Pre-restoration (t = 4 to 31)					
Former land-use	3	241041585	2.51	0.067	0.079
Between visits (time)	8	409208238	5.44	0.305	0.001 *
Months since restoration	1	23581181	0.23	0.002	0.617
Elevation	1	298226061	3.02	0.027	0.073
Elevation ± sedimentation	1	482049416	4.99	0.449	0.025 *
Residuals	*94*	*59858246*			
Land use with MR					
Pre-restoration (t = 0)					
Former land-use	1	253343408	278.45	0.955	0.002 *
Residuals	*13*	*909820*			
Final survey (t = 31)					
Former land-use	1	39668	0.002	< 0.001	0.997
Residuals	*13*	*17620837*			

Appendix 4-3 Descriptions of sampling permanent quadrats at Steart marshes (MR) and adjacent agricultural and natural saltmarsh reference areas.

MR land use	*Ele.*	*Typical quadrat soil conditions during restoration*	*Photography (Appendix 4-4)*
Arable	4.04 to 5.54m	Strong elevation gradient present. Highest plot rarely flooded with terrestrial vegetation still present at t=31. Mid and low elevation plots typically waterlogged in winter months. Friable and de-watered in summer. Distinct anoxic layer ~15 cm deep with rotting vegetation in first/second year at two lowest quadrats.	Soft sediment in winter. Summer dewatering. Anoxic black substrate.
Disturbed	4.09 to 5.06m	Variable conditions with land use. Disturbed high extremely rarely flooded if ever. Disturbed low with signs of alternating scour. Disturbed hump well vegetated in local vicinity but the quadrat itself was unvegetated and accreting rapidly.	Significant accretion and summer drying. Collonistion on high ground.
Grass Ley	4.56 to 5.26m	Strong elevation gradient present. Lowest quadrat (C) very poorly drained with pooled water for first year of restoration. The higher quadrats showed evidence of flooding into the second year and minimal sedimentation. Moderate and lower quadrats showed signs of colonisation.	Winter accretion. Examples of rotting vegetation.
Pasture	4.65 to 4.70m	Land-use typically waterlogged in winter months and entirely de-watered in summer with signs of laminations and soil friability and salt deposits. Broadly homogenous in the land use, some added drainage near Pasture C (near creek head). Clear anoxic layer ~15 cm deep and rotting vegetation in first year.	Pooling in winter / salt deposit in summer. Erosion in fresh sediment.
References			
Saltmarsh	3.03 to 5.05m	Some signs of seasonality. The mudflat (lowest elevation) quadrat dewatered and became laminated in the summer months like the MR land uses. However, the mid and upper elevations present remained vegetated and moist. Observable migration of drainage pathways along the estuary and periodic sedimentation inputs.	
Agricultural	5.35m	Remained short grazed grass for the entire sampling campaign with some signs of seasonal variability in the texture with loss of moisture in summer and autumn months.	

Appendix 4-4 Matrix of photography taken of the four land uses within Steart MR top to bottom (Arable, Disturbed, Grass Ley and Pasture). Photographs of the land uses separated by typical winter, summer and sedimentation / anoxia examples (left to right). (Photographs taken by Peter Lawrence and Hannah Mossman).

5 Surface complexity in saltmarsh: a driver for vegetation community diversity and redox potential

Abstract

Restoration of saltmarshes does not create plant communities like those on natural reference sites, even many years after restoration. Elevation and redox potential are key drivers of vegetation colonisation, but alone are not sufficient to account for these differences. Relative elevation (topography) can alter local environmental conditions and thus potentially vegetation colonisation, but its role is poorly understood. The role of elevation, redox potential and local topography as drivers of vegetation diversity were investigated in four natural saltmarshes and four restored through managed realignment (MR), plus one area where topographic manipulation has been conducted post-restoration.

Here for the first time we provide multiple site evidence that plant composition is spatially more homogenous on MR sites (indicating lower beta diversity) than natural marshes, and this is reflected in equally homogenous environmental conditions at local scales (elevation and redox). For land manages we also provide the first evidence that topographically manipulation can result in greater heterogeneity in environmental conditions and vegetation diversity.

Supporting these findings, we investigate the drivers upon vegetation communities behind results suggesting that MR marshes have lower redox potential and reduced topographic variability (rugosity). Here we find that there are different mechanisms driving vegetation diversity in MR than natural sites. Plant diversity on MR sites is driven predominantly by redox potential, which in turn is almost entirely driven by elevation. In contrast, natural saltmarsh diversity was driven by a more complex relationship of elevation, redox and local topography.

Limited topographic diversity may impair restored sites attaining vegetation communities similar to those on natural sites. The greater diversity in the topographically manipulated area indicates the potential for post-restoration surface manipulation as a management tool to encourage increase plant diversity at restored sites.

5.1 Introduction

The restoration of coastal ecosystems, such as saltmarshes, is an important activity if we are to maintain the services they provide in the face of sea level rise, erosion and economic development (Cooper, Cooper and Burd, 2001; Tian *et al.*, 2016). The goal of this restoration process is to mimic the biological and physical properties of a natural site (Copeland, 1999; European Parliament and the Council of the European Union, 2000). One method of creating new saltmarshes is through the deliberate breaching of sea defences, allowing parcels of land to be reconnected with the sea; a process known as managed realignment (MR). However, MR has had limited success in creating the same biological and physical characteristics as natural sites. For example, Mossman, Davy and Grant (2012) have shown that mature restored marshes (> 100 years old) still exhibit different plant community characteristics to natural marshes (see also Section 1.2.1).

To encourage natural vegetation to develop in restored saltmarshes we need an understanding of the environmental drivers of plant communities, and how these vary between MRs and natural marshes. Elevation in the tidal frame is probably the most important factor determining the distribution of saltmarsh plants because species vary in their tolerance of the ecophysiological the pressures associated with tidal inundation (Colmer and Flowers, 2008; Janousek and Mayo, 2013). Other environmental factors that also influence the distribution of plants, such as redox potential, vary across the elevation gradient, but these relationships are inconsistent (Davy *et al.*, 2011). Local topography (scales of several meters) may influence redox potential, for example, poorly drained depressions at high elevations may be waterlogged (Varty and Zedler, 2008), leading to low redox potential (Pearsall and Mortimer, 1939; Fiedler, Vepraskas and Richardson, 2007). However, the links between redox potential and 'local' topographic attributes have not been widely studied, with topography an understudied variable in saltmarsh plant ecology.

The topography of restored sites is less complex in comparison to natural saltmarshes (Chapter 2), and this might impact vegetation colonisation (Masselink *et al.*, 2017). Our current understanding of the effect of topography on plants is however focused primarily upon coarse topographic features, such as creeks or pools. For example, some species, such as *Triglochin maritima* and *Salicornia* spp., are associated with pools (Davy and

Bishop, 1991; Bakker *et al.*, 2002), whilst others, such as *Atriplex portulacoides*, are found on creek banks (Chapman, 1950). While features such as creeks are clearly important, these are not the limits of topography as there is variation in the surface elevation of the marsh plateaux (Brooks *et al.*, 2015), where many plant communities occur, but the magnitude and effect of this is poorly understood. Differences in topography may have an important influence on the spatial arrangement of plant communities, with diverse topography across the marsh plateaux linked to greater spatial turnover in plant species. However, differences in the diversity between locations (beta diversity) is rarely considered in assessing the success of habitat restoration (Passy and Blanchet, 2007). To summarise, we know elevation has a direct impact on plant communities but is imperfectly correlated with other drivers of saltmarsh plant communities, such as redox potential. However, little is currently known about the relationships between local topography, elevation and redox potential, or if these three drivers act independently or in conjunction with each other to drive the communities present in natural marshes. Furthermore, is not understood if these relationships are the same in restored marshes which we may expect are different as communities are typically also different. Finally, the spatial arrangement of variation in these properties is poorly understood making designing for natural conditions on local scales impossible.

As MR sites lack equivalent biological characteristics, management and design practices have been developing to try improving the design or intervene post restoration. If topographic diversity is linked to plant diversity, manipulation of topography may encourage more natural communities. Evidence from one restored site (Abbotts Hall, Essex) suggests that topographic manipulation can enhance local heterogeneity in surface elevation (Brooks *et al.*, 2015). However, the effectiveness of these interventions on plant and other environmental characteristics are poorly understood.

Here we investigate the role of elevation and local topography as drivers of saltmarsh plant richness and diversity, in four restored and four natural saltmarshes. Furthermore, we investigate the role of elevation and topography as a driver of redox potential, and its implications for plant richness and diversity. We establish the spatial heterogeneity in elevation, redox and vegetation in natural and MR sites. Finally, we assess the effectiveness of topographic manipulation at one restored site in terms of aiding a more natural arrangement of marsh conditions and vegetation.

5.2 Methods

5.2.1 Study sites

We selected four MR sites along the east coast of the UK, varying in age from 6-21 years. Sites were selected for geographic proximity to natural saltmarsh, practicalities in sampling and for consistency of species pool between sites. Furthermore, none of the sites had evidence of current grazing by livestock or widespread erosion. The sites were Tollesbury (51.7671 N; 0.8378 E, age at sampling = 21 years), Orplands (51.7191 N; 0.8631 E, age at sampling = 21 years), Freiston (52.9623 N; 0.0898 E, age at sampling = 14 years) and Deveaux (51.8564 N; 1.2478 E, age at sampling = 6 years). Immediately adjacent (< 500 m) to each MR, we sampled an area of natural reference marsh in an identical manner. Additional to the MR and natural references, we also studied an area of topographically manipulated land within one MR site (Freiston), where topographic manipulation (TM) was conducted as part of management intervention. The manipulations at Freiston occurred 12 years after restoration, and 2 years prior to sampling. The topographic manipulation included the creation of shallow creeks and pannes and small hillocks, and in places, infilling creeks. The scale of these manipulation varied in size from approximately 1m by 5m micro creek extensions, to the largest hillock of c. 10 m^2, with the aim of creating a more heterogenous surface than the rest of the MR site. This resulted in a total of nine areas sampled (four MR, four natural and one TM), across four sites.

5.2.2 Survey design

In order to quantify differences in local vegetation composition and environmental conditions, we established a fractal sampling scheme, similar to that of Brooks *et al.*, (2015). In each area (natural, MR and TM), we established one 50 x 50 m grid, with sampling points at every 10 m (labelled alphabetically A to AJ). Eight of these points were randomly selected (C, G, P, Q, S, AA, AD and AH) and additional sampling points in the four cardinal directions were established 1 m and 2 m from the central point creating a cross formation with nine sampling points inclusive of the formally established position. This resulted in 100 sampling points per grid, with good replication across all horizontal distances, from 1 - 72.5 m.

To quantify the local topography of each sampling point, the elevation was measured at 1 m distances (horizontally) from each sampling point in the four cardinal directions. A further elevation measurement was obtained in the central location of each 10 m square within the 50 x 50 m grid to add further topographic detail. This sampling strategy resulted in a total of 100 sampling points (quadrats, redox and soil) and 365 elevation observations per grid. The grids were established haphazardly on the marsh, avoiding artificial features (walls, paths etc.). Grids were orientated from A to AE in the direction of the estuary i.e. largest channel or breach.

5.2.3 Field methods

At each sampling point, data on vegetation, soil conditions and elevation were collected. A single 0.25 m^2 quadrat was placed at the centre of each sampling point, obtaining abundance (% cover) of all higher plant species and bare ground. Species cover was estimated to the nearest 5%, with occasions where a species was present but in less than 5% cover it was assigned 1% cover. The 0.25 m^2 sized quadrat was selected to ensure no overlap in quadrats within the nested plots (1 m spacing) and as this size has proven an effective size for studying saltmarsh plant communities (Zedler *et al.*, 1999; Mossman *et al.*, 2012). The redox potential at the centre of each quadrat was measured with a Campbell Scientific calibrated ORP Probe (-700 to +1100 mV), at a soil depth of approximately 5 cm, left until the reading stabilised (~ 5 mins). Prior to field work, the probe was calibrated with Zobells solution.

Elevation relative to the UK reference mean sea level (Ordnance Datum Newlyn, ODN) was measured at each location using a differential GPS (Trimble R10, Sunnyvale, CA), with typical accuracy of < 1 cm and precision of < 1 cm in both horizontal and vertical dimensions. Using the four elevation measurements taken 1 m from each sampling point, we derived two topographic indices: rugosity and relative elevational position. Rugosity was calculated as the standard deviation of elevation of the central and surrounding four points. The relative position of the quadrat to its local surroundings was calculated by subtracting from it the mean of the point and its four nearest neighbours (1 m max distance), modified from Wilson and Gallant, (2000). The resulting value, herein called relative elevational position (REP), is measured in metres and can be either negative or positive, reflecting small scale concave or convex features respectively.

Elevation above ODN was converted to the local datum (relative tidal height (RTH)), where, 0 equates to mean high water neap and 1 mean high water spring tide level, to enable comparisons between sites as tidal variation can change dramatically over small geographic distances (Mossman, Davy and Grant, 2011).

5.2.4 Data analysis

All analysis for this study was performed in R Studio version 1.1.414 (R Development Core Team, 2011). Shannon-Wiener diversity and richness per quadrat, omitting bare earth, was calculated using R package ‘vegan’ (Oksanen *et al.*, 2013). Linear models (LM) were used to test for differences in elevation, redox, topographic measures and species composition between natural and MR marshes, whilst accounting for site effects by using site as a fixed effect.

The factors affecting the species diversity and richness (at quadrat level) in natural and MR marshes separately, were examined using a linear model and generalised linear model (GLM) with a Poisson distribution respectively, with RTH, rugosity, REP and redox as explanatory variables. Similarly, we examine the drivers of redox potential using LM with RTH, rugosity and REP as the explanatory variables. In these analyses, data were pooled from sites because we were interested in the drivers of species richness, diversity and redox potential across sites. All species present in the dataset had a UK distribution that covered all sampling sites (Botanical Society of Britain & Ireland, 2018), thus ensuring comparable diversity scores between sites.

As collinearity between environmental variables is expected, correlation within the explanatory variables (RTH, REP, rugosity and redox) was examined using Pearson correlation tests. Significant correlations were found between all variables except redox and rugosity, although most were weak. Only the relationship between RTH and redox was strong (rho = 0.58), Table 5-1.

Table 5-1 Summary of Pearson correlations between explanatory variables. Asterisks denote statistical significance where p < 0.05

	Rugosity	REP	Redox
Relative topographic height (RTH)	-0.25 *	0.23 *	0.58 *
Rugosity (s.d. of elevation)		0.08 *	-0.03
Relative elevational position (REP)			0.16 *

Due to this collinearity, we used hierarchical partitioning (HP) in the package 'hier.part', with a log link function, to identify the independent effects of the explanatory variables in the LM / GLMs described above.

We wanted to quantify the patterns in surface elevation, redox potential and vegetation community variation over different distances in natural, MR and TM marshes. To do so, we calculated the differences in elevation (n = 66430), redox and vegetation communities (Jaccard dissimilarity) (n = 4950). For each plot, these differences were plotted against the horizontal distances between points, using local polynomial regression fitting (LOESS) to visualise the relationships, with boot-strapping to calculate the mean and upper/lower confidence intervals (97.5% and 2.5%). In the calculation of Jaccard dissimilarity, bare earth was included the measure cannot be calculated where no species are present we wished to know the difference between quadrats with no species and those of most diversity, ultimately this provides a maximum value of local dissimilarity. Finally, Mantel tests were employed with 100 permutations to test for correlations in the distance matrices between the elevation, redox and vegetation dissimilarities within each type of marsh.

5.3 Results

Overall, species diversity and richness were significantly higher in natural marshes than in the MR sites (diversity, $t = -5.681$, $p < 0.01$ (Figure 5-4); richness, $t = -5.031$, $p < 0.01$). However, there was a significant effect of site. At Freiston, species diversity and richness were higher in the MR than on the natural, and diversity was marginally higher at Orplands MR than the natural site (Figure 5-1). Relative tidal height was significantly higher in natural marshes ($t = -9.025$, $p < 0.01$), although Freiston MR was slightly higher than the natural site. Redox potential was significantly higher in natural sites ($t = -7.118$, $p < 0.01$) overall, but very variable between sites (Figure 5-1) and the mean was higher at Orplands and Freiston MRs compared to the natural sites. Rugosity was consistently and significantly higher ($t = -1.366$, $p < 0.01$) in all the natural marshes compared to MR sites (Figure 5-1). There was no significant difference in REP between marsh types, however there were more observations of flat or hollows (score below 0) in MR sites, compared to typically higher values (scores above 0) in natural marshes, suggesting localized hills were more dominant in natural sites (Figure 5-1).

Table 5-2 Summary of topographic, environmental and species richness and diversity, measured at each restored (MR) and natural site surveyed. Mean (µ) and standard deviation (s.d.) for the tidal height adjusted elevation (RTH), redox (mV), derived microtopography (rugosity and relative elevational position (REP) and plant species diversity (Shannon-Wiener) and richness. Toll = Tollesbury, Orp. = Orplands, Frei = Freiston and Dev = Devereaux

Site	***RTH***		***Redox (mV)***		***Rugosity***		***REP (m)***		***Diversity***		***Richness***	
	µ	s.d.	µ	s.d.	µ	s.d.	µ	s.d.	µ	s.d.	µ	s.d.
Toll.												
Nat.	0.54	0.40	95.95	77.9	0.15	0.16	0.019	0.14	0.88	0.48	3.40	1.74
MR	0.38	0.13	-90.42	156.3	0.03	0.07	<0.001	0.04	0.56	0.54	2.41	1.39
Orp.												
Nat.	0.85	0.24	65.73	108.4	0.11	0.10	0.018	0.11	0.85	0.57	3.56	1.96
MR	0.79	0.17	79.40	108.6	< 0.01	< 0.01	0.003	<0.01	0.87	0.49	3.51	1.52
Frei.												
Nat.	0.54	0.13	35.18	91.9	0.05	0.08	<0.001	0.07	0.82	0.44	3.17	1.41
MR	0.59	0.25	95.03	66.8	0.02	0.03	<0.001	0.03	1.25	0.42	4.98	1.33
TM	0.62	0.14	-24.5	174.9	0.04	0.03	-0.002	0.05	0.81	0.55	3.13	1.70
Dev.												
Nat.	0.61	0.36	127.15	86.4	0.07	0.10	0.005	0.09	1.32	0.43	5.25	1.71
MR	0.40	0.39	-30.38	222.0	0.03	0.03	0.004	0.02	0.33	0.43	1.83	1.63
Nat.	**0.63**	**0.33**	**82.00**	**97.9**	**0.09**	**0.12**	**0.01**	**0.11**	**0.97**	**0.52**	**3.84**	**1.90**
MR	**0.54**	**0.30**	**14.07**	**167.1**	**0.02**	**0.04**	**0.01**	**0.02**	**0.75**	**0.59**	**3.18**	**1.90**

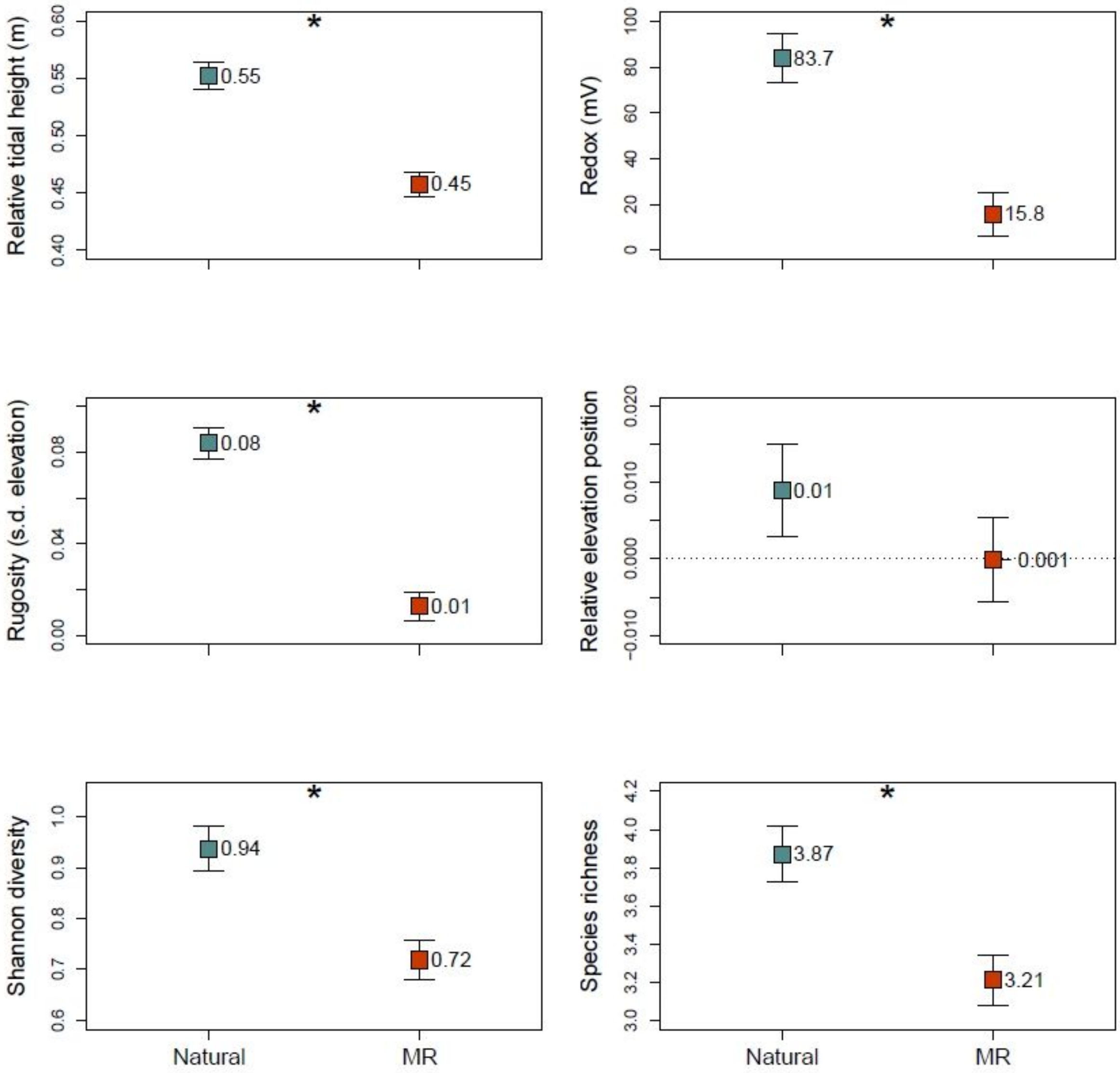

Figure 5-1 Comparison (mean ± SE) of quadrat level elevation, redox potential, topography (rugosity, relative elevational position) and species richness and diversity between restored (MR) and natural saltmarshes. Mean and SE were calculated via linear models (generalized linear model with a Poisson distribution for species richness), accounting for site as a fixed effect. Letters indicate significant differences ($p < 0.05$) between natural and MR marshes. Dotted horizontal line in relative elevation position indicates a threshold between a positive position (e.g. a hillock) and a negative position (e.g. a depression).

5.3.1 Do natural and MR have different drivers of species diversity, richness and redox?

Relative tidal height, rugosity, REP, and redox potential predicted 33 % and 28 % of the variation in species diversity in natural and MR marshes, respectively (Table 5-3). There were differences in which explanatory variables were important between the MR and natural models, confirmed by Hierarchical Partitioning (HP), which provides estimates of the independent contribution of the terms within each model. We found that both rugosity and redox had significant effects on species diversity in both natural and MR systems. However, RTH and REP were also significant drivers of species diversity in natural marshes (Table 5-3).

Table 5-3 Summary of the relationships between the dependent variables vegetation richness and diversity and redox, and the explanatory variables relative tidal height (RTH), rugosity, relative elevational position (REP) and redox (only for vegetation models) in natural and restored (MR) saltmarshes. Linear models (LM) were used to test for the relationships of vegetation species diversity and redox potential, and a generalized linear model (GLM) with Poisson distribution used to test for relationships of species richness. Values are the modelled estimate and those in brackets are the standard error. Asterisks indicate significance levels, p < 0.05 = * and p < 0.01 = **.

	Explanatory variables				***LM***			
	RTH (SE)	Rugosity (SE)	REP (SE)	Redox (SE)	R^2 (%)	df	F	p
Div.								
Nat.	0.18 (0.09) *	- 1.22 (0.23) **	0.77 (0.27) **	0.001 (< 0.01) **	32.9	(4,395)	48.3	**
MR	0.20 (0.15)	- 1.82 (0.66) **	1.79 (1.01)	0.001 (< 0.01) **	27.7	(4,388)	37.1	**
Redox								
Nat.	70.04 (16.98) **	-151 (43.89) **	325 (49.41) **	-	29.8	(3,396)	56.13	**
MR	491 (18.86) **	-98.65 (132.94)	7.42 (201.65)	-	64.3	(3,389)	233.3	**
Rich.					**GLM**			
Nat.l	0.32 (0.12) **	- 1.36 (0.31) **	0.85 (0.35) *	0.002 (< 0.001) **	AIC			
MR	0.25 (0.16)	- 3.34 (1.38) *	2.32 (1.36)	0.002 (< 0.001) **	1526.9			

All four environmental factors had significant independent effects on species diversity in natural saltmarshes (RTH 25%, Rugosity 26%, REP 12% and Redox 38%), whereas on MR sites vegetation was driven by only Redox (58%) with only a minor contribution from surface rugosity (6%) (Figure 5-2). The independent predictors of species richness were very similar to those for species diversity, see Appendix 5-1.

Substantially more variation in soil redox was explained in MR saltmarshes (64 %) compared to natural ones (30 %) (Table 5-3). Much like the models of species diversity, there were differences in which explanatory variables were significant between the natural and MR models. Within the natural marsh, RTH, rugosity and REP were all significant explanatory variables (Table 5-3), having independent contributions of 43%, 13% and 43%, respectively (Figure 5-2). In contrast, rugosity and REP were not significant predictors of redox potential in MR marshes, where only RTH had a significant independent contribution (99%).

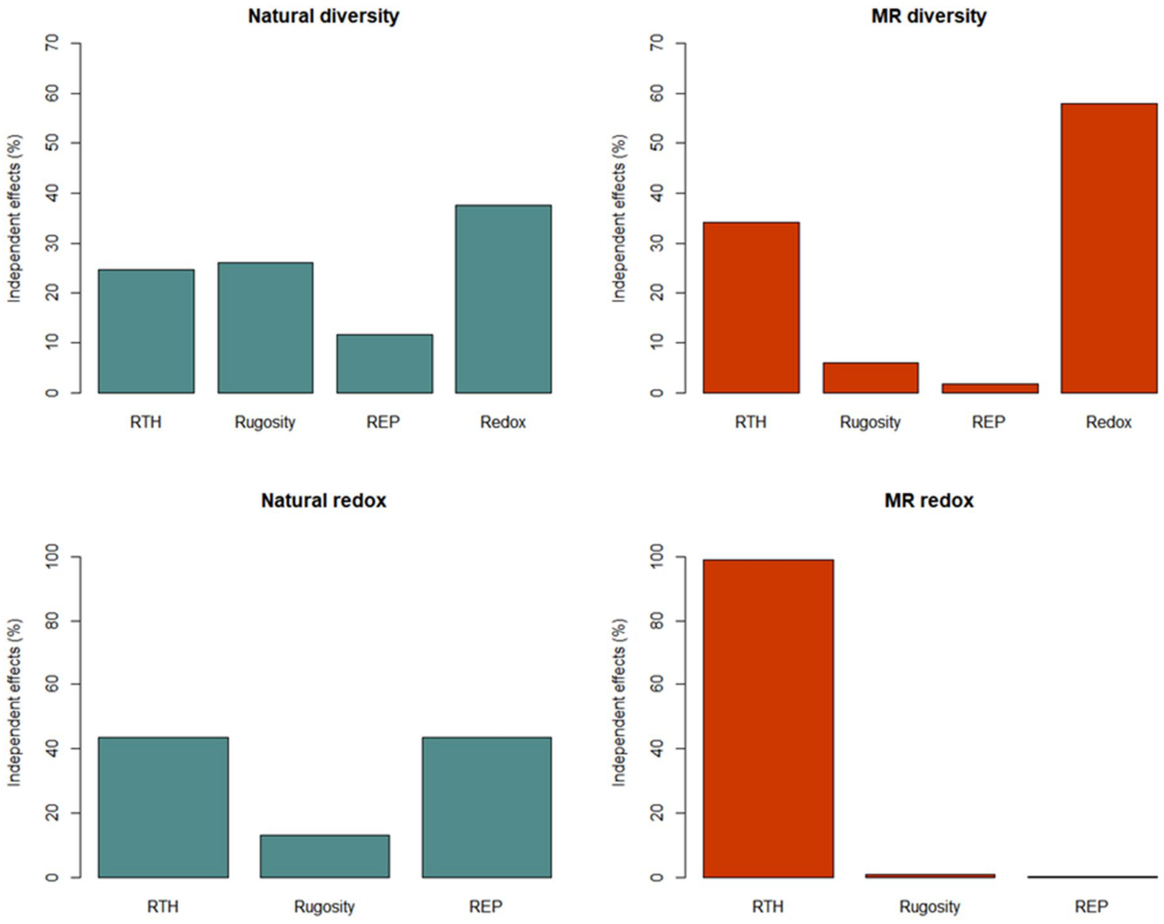

Figure 5-2 The natural and restored (green and orange plots respectively) independent effects in of the explanatory variables (RTH, Rugosity, REP and Redox), calculated using hierarchical partitioning for the prediction of response variables vegetation diversity and soil redox potential (top row and bottom row respectively).

5.3.2 Is there variation in saltmarsh homogeneity between sites?

The spatial heterogeneity of three components of the saltmarsh, elevation (structure), redox potential (chemical) and species diversity (biological) was measured. Heterogeneity in elevation was greater in natural saltmarshes than in MR sites, with the greatest differences at small spatial scales (0–20 m, Figure 5-3, top row). In two of four sites (Tollesbury and Freiston), the natural marsh was consistently more heterogenous in surface elevation at all spatial scales.

In natural saltmarshes, the heterogeneity in redox potential was consistent across spatial scales and between sites (Figure 5-3), with an average difference of approximately 90 mV between sampling points. In contrast, MR sites were more varied, with variation at three of the four sites being greater than on natural marshes, particularly at distances > 40m.

Trends in vegetation dissimilarity (Jaccard) between quadrats followed very similar patterns as those of elevation heterogeneity. This is supported by the Mantel tests, where elevation had consistently the strongest correlations with Jaccard dissimilarity for both natural and MR sites (Table 5-4). In all four natural sites there was higher vegetation dissimilarity at a scale of 0–20 m than in the MR sites, with both Tollesbury and Freiston natural sites possessing greater heterogeneity across the entire spatial sampling range. Differences in vegetation and elevation were weakly correlated with distance in natural marshes but more strongly correlated in MRs (Table 5-4), indicating that the gradients in the environment and plant communities were longer in MRs than in natural marshes.

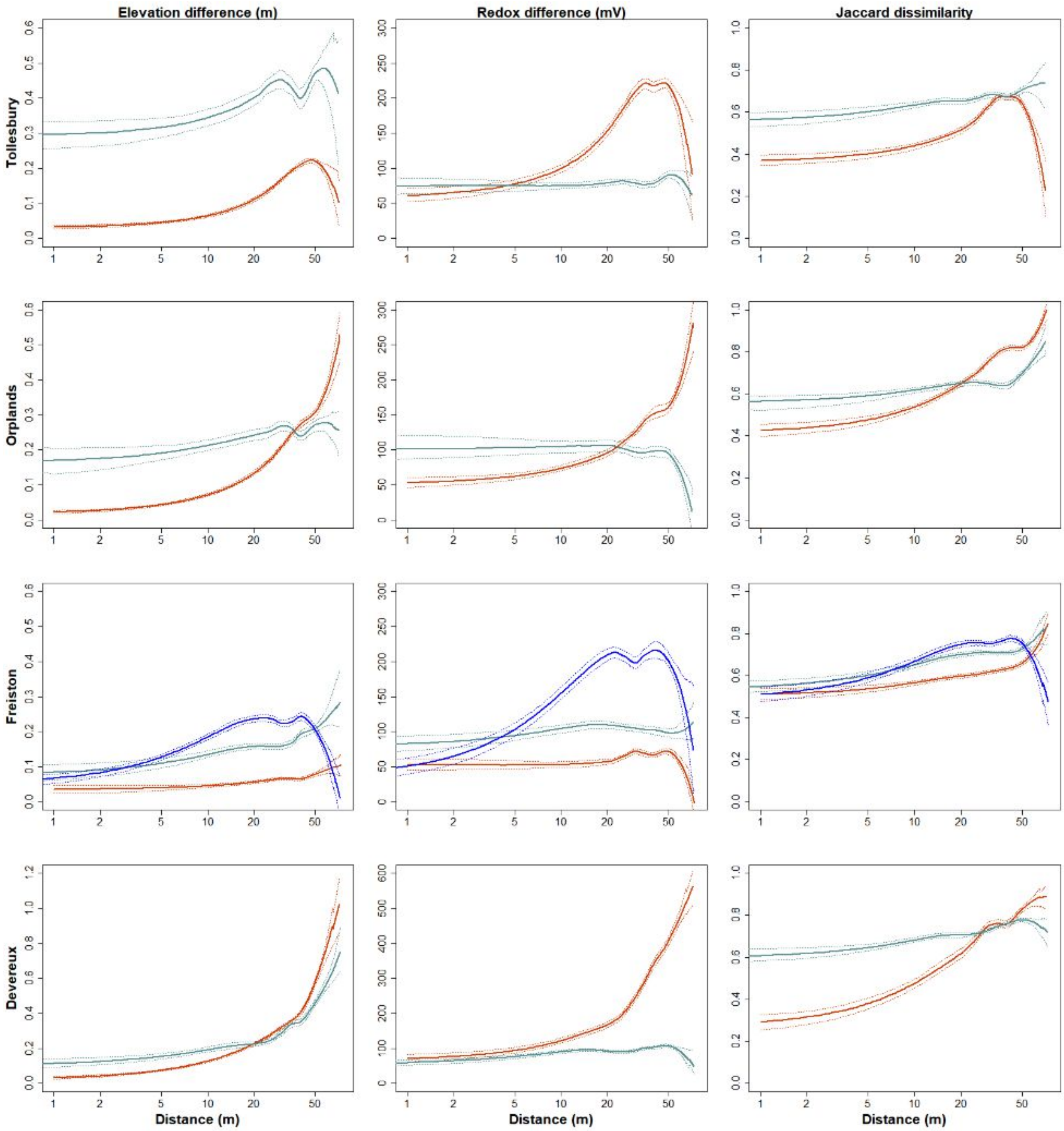

Figure 5-3 Heterogeneity of elevation, soil redox and vegetation diversity across spatial scales in natural saltmarsh (green) and restored saltmarsh (orange), and an area at one site that had experienced topographic manipulation (blue). Solid lines are LOESS regressions fitted to all pairwise differences in e.g. elevation and the distance between the two sampling points. Dotted line shows upper and lower confidence intervals (97.5 and 2.5 %) for each relationship. Note that Devereux (bottom row) scales for redox and elevation heterogeneity are different to the other sites.

Table 5-4 Correlations (Kendall's tau) between Jaccard dissimilarity (left side) matrices and matrices of elevation, distance and redox potential, and correlations between redox difference and both elevation and distance matrices. Values presented are Mantel r statistic, based on 100 permutations; all p values = 0.0099.

p = 0.0099	***Jaccard diss. matrix vs.***			***Redox diff. matrix vs.***		***Distance diff vs.***
	Distance	*Elevation*	*Redox*	*Distance*	*Elevation*	*Elevation*
Tollesbury						
Natural	0.066	0.519	0.256	0.034	0.356	0.064
MR	0.238	0.503	0.381	0.211	0.413	0.336
Orplands						
Natural	0.091	0.296	0.215	-0.018	0.225	0.086
MR	0.302	0.542	0.287	0.250	0.395	0.417
Freiston						
Natural	0.084	0.184	0.113	0.003	0.132	0.136
MR	0.128	0.150	0.098	0.051	0.174	0.146
MT	0.071	0.275	0.377	0.102	0.249	0.067
Deveraux						
Natural	0.143	0.346	0.159	0.053	0.177	0.323
MR	0.228	0.459	0.288	0.288	0.383	0.454

5.3.3 Effectiveness of topographic manipulations

There were clear indications that topographic manipulations at Freiston resulted in a more natural heterogeneity in elevation and redox potential. There was a concurrent marked increase in vegetation dissimilarity at distances of >5 m compared to the MR (blue line in Figure 5-3), resulting in vegetation heterogeneity more like natural marshes. Differences in vegetation and elevation were more weakly correlated with distance in the topographically manipulated area compared to the MR (Table 5-4).

5.4 Discussion

This study shows that quadrat-level diversity (alpha) and richness is higher on natural marshes compared to MR sites. The differences in richness found between natural and MR that are very similar other studies, with a reduction in richness from natural to MR quadrats of 22 % shown both here and by Garbutt and Wolters, (2008). These results indicate that diversity is very likely to be lower at any given sampling point within a MR site, despite the majority of the species pool being present at a site level (Mossman, Davy and Grant, 2012). This suggests that MR must lack proportional representation of some species spatially, and thus are less heterogeneous in terms of vegetation at local scales (further supported by our LOESS regressions in (Figure 5-3); until now, comparisons of within-site environmental heterogeneity have never been studied. Along with vegetation diversity and richness, MR sites also have significantly lower elevation and redox potential. These findings mirror those of Garbutt *et al.*, (2006), who also found MR sites tend to have low elevations; and Brooks *et al.*, (2015) who, also, demonstrate a differences in soil redox potential. Possibly most interestingly, we show that MR sites have reduced surface topography compared to natural saltmarshes, which is consistent with results from the analysis of remote sensing derived data at site-scales (Chapter 2) and that topography is a key driver of natural diversity.

These differences in the local topography between natural and MR sites are reflected in the key drivers of plant diversity. The more diverse structure of natural marshes resulted in local topography acting as an important driver of plant richness and diversity. In contrast, MR sites have a typically flatter surface, whereby MR diversity and richness is driven almost entirely by redox potential and elevation. Furthermore, topography was a key driver of redox potential on natural marshes, but not in restored saltmarshes. This suggests that topography may act as both a direct and indirect driver (via redox) of vegetation. Its direct effects might be felt on vegetation communities through reduction of seedling survival in depressions due to high levels of sedimentation (Bouma *et al.*, 2016), or via the increased accumulation of salts in flat, water collecting areas with high evaporation (Largier, Hollibaugh and Smith, 1997; Hladik and Alber, 2014), or via droughting pressure on raised humps. It is quite likely that these impacts are felt most strongly as early stages of regeneration and establishment where plants are most vulnerable to mortality, thus intervention that intervenes prior to germination periods would be most timely.

Topography was more heterogeneous at local scales on natural marshes than on MR sites, indicated both by the higher mean local rugosity (Figure 5-1) and greater differences in elevation between sampling points on natural sites (Figure 5-3). In contrast, there were stronger relationships of local topography with elevation and distance (indicated by stronger Mantel correlations) in MR sites, suggesting local topography was associated with other factors. Elevation on natural marshes varies over short spatial scales, whereas MR sites had smoother gradients over the same distances (Figure 5-3). Over these distances (0-72.5 m), topographic heterogeneity was an important driver of plant community heterogeneity. The results demonstrated that pairs of quadrats with more dissimilar elevations also had more dissimilar species compositions, and as natural marshes were more topography diverse this resulted in natural marshes having more heterogeneous plant communities. In contrast, MR sites had more homogenous vegetation, only approaching the heterogeneity of natural marshes at the largest spatial scales. This is the first time that differences in the heterogeneity of plant diversity between restored and natural saltmarshes has been shown.

These differences in the heterogeneity of plant communities on restored marshes are important because beta diversity *per se* is desirable in establishing equivalent habitat to natural saltmarshes, yet it is not commonly studied (Passy and Blanchet, 2007). Differences in diversity between natural and restored marshes are likely to impact the provision of ecosystem services. However, it is unclear how the importance of plant diversity varies with spatial scale. For example, species are known to differ in their interaction with wave energy (Möller *et al.*, 2014), but is unknown how the arrangement of species across the marsh impacts wave attenuation. Likewise, plant diversity enhances sediment stability at the scale of a sediment core (Ford *et al.*, 2016), but it is not known how the arrangement of species with different root morphology across the marsh affects erosion dynamics.

The greater environmental heterogeneity in natural marshes could enhance species coexistence through spatial niche partitioning (Chesson, 2000). In this, variation in the environment tips the balance of competitive interactions in favour certain species differentially over space (Amarasekare, 2003). Although we did not test whether the differences in environmental conditions were sufficient to alter competitive interactions, it is likely that they would be, given the relatively subtle variation in the niches of different saltmarsh plant species (Sullivan *et al.*, 2017). However, our results suggest a not so subtle difference in environmental conditions, with differences in the site means of redox of over 60 mV between natural and restored sites (Figure 5-1). In addition, MR and natural sites have very different spatial patterns in redox potential, whereby natural marshes are relatively consistent, but MR have variation of 600 mV over distances of 70 m (Figure 5-3). The potential for environmental heterogeneity to enhance the local-scale coexistence of species may be especially high in saltmarshes where several dominant species (e.g. *Atriplex portulacoides, Puccinellia maritima* and *Spartina anglica*) spread by vegetative growth (Chapman, 1950; Hill, Preston and Roy, 2004). The expansion of clones of these species is likely to be limited in natural marshes by encountering patches of unsuitable environmental conditions, whereas the more homogenous environment in restored marshes is likely to allow them to expand more widely as their niches are continuously connected on a flat surface. The potential for topographic heterogeneity to create more niches for plants and thus increase diversity is illustrated in Figure 5-4.

This highlights the potential importance of the landscape-scale arrangement of niches. Further work is needed to see if diversity patterns can be predicted from modelling the spatial arrangement of niches and to test if the fragmentation of niches is important in constraining dominant species.

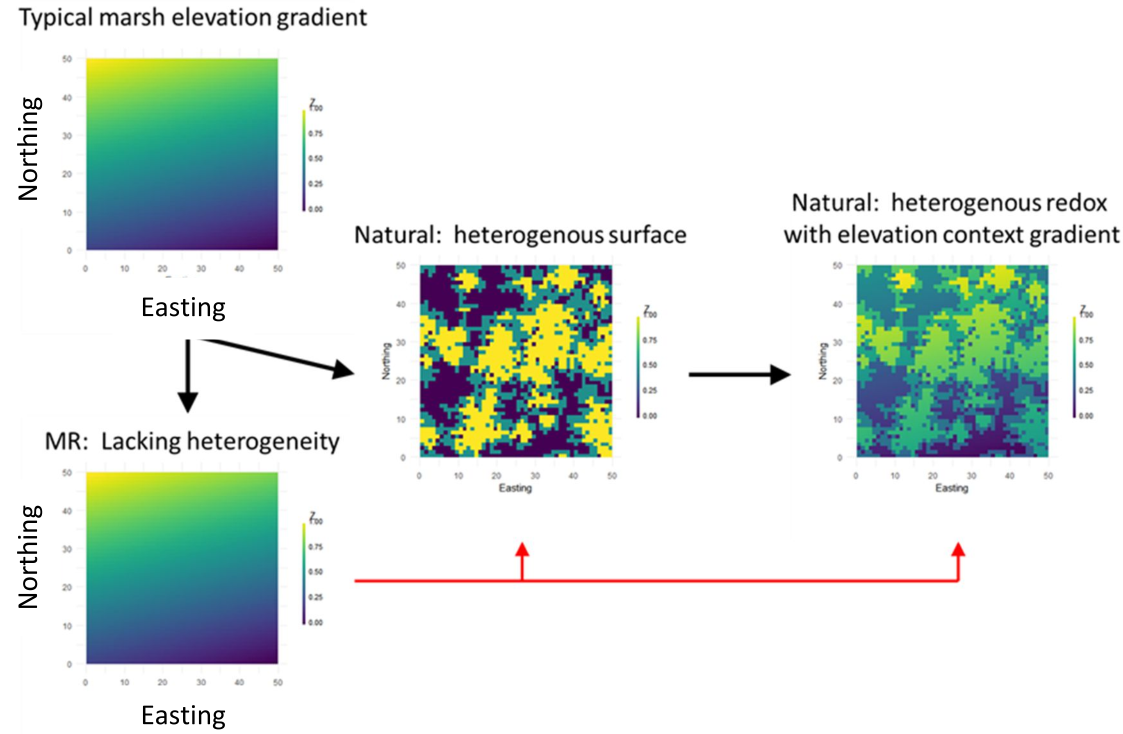

Figure 5-4 Hypothetical relationships between elevation and topographic in MR and natural marshes and their relationship with heterogeneity in redox potential. The top left shows an elevation gradient. MR sites lack topographic heterogeneity and so maintain the elevation gradient only (bottom left). In contrast, natural marshes contain localized topographic heterogeneity (central image). When this is combined with the underlying elevation gradient (right image), there is a complex pattern elevation that reflects both the surface heterogeneity and elevation gradient present. If the green colour was to represent the niche of a dominant species, such as *Atriplex portulacoides*, the species is isolated in patches on the natural marsh by sizable barriers unsuitable habitat that may prevent vegetative spread; this is not the case in the managed realignment (bottom left).

Implications for restoration management

The results show that topography is important in driving vegetation diversity and its spatial patterns. Manipulation of topography thus could be a useful management tool for increasing diversity on restored sites. At one site where this has been conducted subsequent to restoration, we found that the areas of topographic manipulation led to a surface topography more like natural marshes (at scales of >2 m) and more importantly similar vegetation (at scales of >5 m). The manipulations at Freiston were only 2 years old at the time of sampling so further monitoring is required to demonstrate the effectiveness of such features over time. Our results suggest that there is a higher proportion of convex (hillock) features on natural marshes (supported by the results in Chapter 2). The typical disparities in elevational heterogeneity between natural and MR marshes tends to be 10 cm or more, particularly on local scales from 0 - 20 m. To increase heterogeneity by this much, restored sites would require enhanced topographic heterogeneity much larger than existing features. These enhancements may be formed via combinations of features, such as hillocks with a peak at least 50 cm vertically taller than the marsh surface within a 10 m^2 area. Alternatively, a series of undulations 10-20 cm vertically and separated by distances of 1-2 m would increase heterogeneity by the same magnitude. Subtle features of this size should not be underestimated in enhancing local diversity where it can be preserved as 10 – 20 cm vertical change can generate significant, community altering environmental conditions (Cahoon and Reed, 1995; Varty and Zedler, 2008). As undulations in terrain require less vertical change, it would perhaps be preferable to use such alteration where sedimentation is lower. Lower sedimentation occurs both at the upper elevational zone and upon hillocks (Elschot and Bakker, 2016). As such it may be preferable to use of hillocks (convex) instead of pannes (concave), that will also increase REP values, currently lower in MR (Figure 5-1).

Restoration that has involved using bunds to encourage sedimentation and targeting more natural successional processes has resulted in vegetation more similar to natural marshes (Van Loon-Steensma *et al.*, 2015). This may be due to the creation of more similar environmental conditions, including the development of topographic features as the sediment builds up. In contrast, some areas of MR sites are created at levels already suitable for colonisation (Mossman *et al.*, 2012) but may have more homogenous surfaces due to former agricultural practices, such as ploughing. More natural topography may not re-establish here due to different accretion and erosional processes (e.g. hard sub-surface layers (Spencer *et al.*, 2017). These sites are not aided in reaching similar topography through post-restoration management, relying on the initial design to generate similar environmental conditions, which do not appear to be successful.

In conclusion, it is likely that in both natural and created saltmarshes environmental heterogeneity creates more niches and thus increased plant diversity across various spatial scales. However, current MR design does not allow for the localised heterogeneity that could increase diversity. Our results lend support to suggestions that future MR site selection and design may require post-restoration intervention and certainly the continued monitoring to facilitate design practice.

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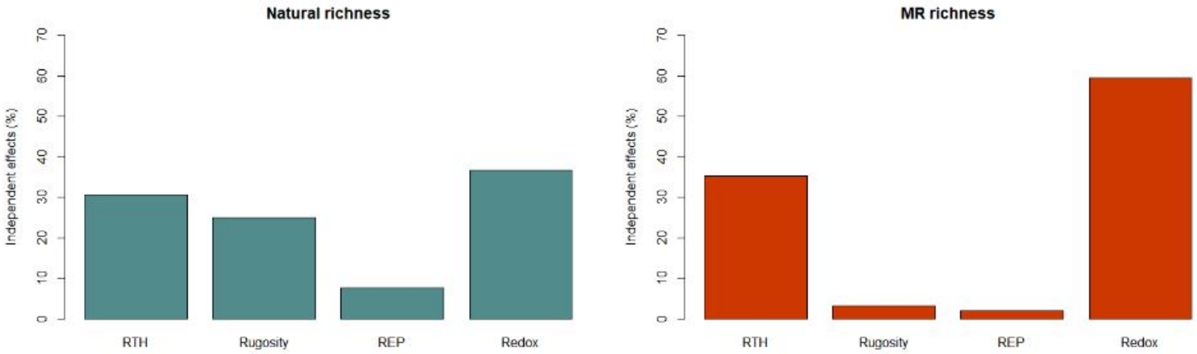
5.6 Appendix



Appendix 5-1 Bar plots of the independent effects of the explanatory variables from hierarchical partitioning in predicting species richness. Asterisks indicate significant terms from the GLMs.

6 Discussion and synthesis of PhD

6.1 General conclusions

Saltmarsh habitats are an important and valuable coastal ecosystem. Due to historic losses saltmarsh restoration is critical to replace lost habitat and becoming an important way of managing the coastline for the future, whilst fulfilling legal obligations to counter losses. Thus far there is little evidence that restored systems reach the same biological characteristics expected by law (Mossman, Davy and Grant, 2012). Many avenues of research have investigated differences between natural and managed realignment (MR, restored) systems in the parameters known to affect the development of natural saltmarsh, such as the provision of appropriate elevation, accretion and salinity gradients (Bertness and Ellison, 1987).

On local scales we know surface texture can impact soil conditions, such as salinity and waterlogging (redox potential) (Varty and Zedler, 2008), and that these soil properties can indicate different communities of saltmarsh species (Silvestri, Defina and Marani, 2005; Davy *et al.*, 2011). However, until now nobody has attempted to characterise the whole of a saltmarsh in terms of the topographic characteristics nor the development of soil conditions on a MR site. Further to this, very few papers have attempted to unite multiple physical and chemical characteristics and how these relate to the biological communities in either natural or restored saltmarshes.

In this Chapter 1 of this thesis I discussed the roles of lesser-studied factors that play critical roles in the development of a natural saltmarsh. Here I hypothesised that an interplay might exist between topography, redox and nutrient dynamics, and that these could improve our elevation-focused current understanding of plant zonation in saltmarsh. To investigate the importance of these I posed several questions:

1. What is a typical topographic characteristic of natural saltmarsh and MR sites, and do they differ?
2. What is a typical nutrient concentration saltmarshes and MR schemes, and do these also differ?
3. How, and in what direction, do MR soils develop against natural and agricultural baselines?
4. Does former land use, time or elevation play the biggest role in MR soil development?
5. What relationships exist between elevation, topography and redox potential, and what are the effects of these have on vegetation diversity?

Topography on restored saltmarshes is reduced at both site and plot scales compared to natural marshes (Chapters 2 & 5). Managed realignment sites, as a result, are flatter, concave in nature, wetter and with fewer creeks than natural marshes; this is more like the agricultural land that they likely derived from. This difference may be due to the impacts of former agricultural activities, e.g. ploughing, removing the topography that existed prior to reclamation, which originated from saltmarsh. MR sites that were formally reclaimed for shorter periods of time may therefore have lost less of their topography than those reclaimed for centuries. Freiston MR site for example, was only reclaimed for approximately 20 years, and it had a more similar suite of characteristics to its natural marsh, including elevation, redox and rugosity, than other sites that had been reclaimed longer (Chapter 4). Although this may warrant further investigation, identifying the date of initial reclamation is extremely difficult due to the large time gaps in historic maps, thus losing temporal resolution. The flatness of the MR sites will tend to allow uniform flow across the marsh surface, and this may impede the ability for hydrological processes to create its own drainage pathways within the substrate – perhaps further exacerbated as MR sites are typically dissected by few very large creeks, rather than a more dendritic network (Chapter 2). The issues surrounding reduced hydrological flow are best observed in regulated tidal exchange sites, where flow is highly controlled (Masselink *et al.*, 2017). Former agricultural land use can also reduce the hydrological processes that would assist the development of topography (via erosion and deposition) as compaction and other structural changes to the sediment can lead to layers of impermeability, reduced porosity and increased shear strength (Crooks *et al.*, 2002; Tempest, Harvey and Spencer, 2015; Spencer *et al.*, 2017).

Reduced surface topography on MR sites results in the dominance of redox potential (as a function of elevation) becoming the sole driver of plant diversity. This differs from natural marshes where the drivers of plant diversity on a local scale are more complex, with equal roles of elevation, topography and redox. This would suggest therefore that in MR there is heightened impact of redox potential and thus we may expect a MR to conform better to expected niches of redox potential of saltmarsh species (Sullivan *et al.*, 2017); this warrants further investigation.

Previous research has identified that MR and natural marshes have different vegetation communities (Mossman, Davy and Grant, 2012). However, the spatial distribution of communities, and how this impacts the diversity within a site (Beta diversity) is rarely studied in any restored system, and never in saltmarshes. The results from Chapter 5 indicate that restored saltmarshes are more homogenous in terms of community structure and that vegetation turnover spatially (beta diversity) is at its most different between natural saltmarsh and MR sites at localised scales (0 – 20m). These differences in spatial structure between MR and natural marshes relate to the topography present in each system. Without the added topography present in natural marshes, MR sites contain a smaller number of elevational niches but each covering a larger area and thus also likely more connected. Here, the opportunity of colonising species to dominate large and linked patches in MR is not hindered by complex terrain and barriers to expansion, such as unfavourable niches. This may explain why older restored marshes can still be dominated by the early colonisers (Mossman, Davy and Grant, 2012). Habitat and niche connectively in saltmarshes and MR schemes on local, moderate or site scales has never been studied and warrants further investigation. Also, yet to be studied are the consequences of homogenous vegetation created via the expansion of a few individuals into the large area of a given niche. Given the potential expanse of just a few individuals, there may be low genetic diversity on restored sites (Edge, unpublished data), potentially leading to less resilience to cope with changing conditions or disease.

Unsurprisingly, soil conditions between former agricultural land uses prior to tidal inundation were different. However, after three years this was no longer the case and so other factors must have superseded the former land use in the development of this soil. Previous research has shown that there are differences in soil structure between natural and restored marshes as a result of agricultural activities (Spencer *et al.*, 2017), but nobody thus far has compared the impact of these different types of agricultural activities to each other. Although there may be differences in the sub-surface soil structure (Spencer *et al.*, 2017), we know some MR sites can accrete rapidly, and seasonally and spatially differently within a site (Chapter 4; (Elschot and Bakker, 2016; Oosterlee *et al.*, 2017). The signature of former land use appears to be lost under the input of freshly deposited marine sediment, with no difference in most soil conditions between restored and natural marshes (Chapter 3 & 4). This result suggests that there may be very little leaching of nutrients from the agricultural soils in to the newly deposited sediment or very little mixing/reworking, resulting in distinct layers (Tempest, Harvey and Spencer, 2015), with an interface of trapped, rotting vegetation between the two (Chapter 4). As a result, the impact of former land use on surface soil chemistry is negligible, but there may be an impact of this distinct interface in changes to other properties, such as lower redox potential (observed in Chapter 4) or trapped water. Investigation of this would require further sampling with deeper cores. However, the depth of fresh sedimentation can often exceed that of typical plant rooting depth (8 cm) (Chapter 4); (Garbutt *et al.*, 2006), and so the relevance of deeper cores may be hard to interpret in terms of plant colonisation.

Soil conditions at the managed realignment at Steart were similar to those on natural marshes after 31 months. Sedimentation rates were high in our plots (c. 4 cm year^{-1}), but are in line with those on other managed realignment sites (e.g. 2.3 cm year^{-1} at Tollesbury (Garbutt *et al.*, 2006), and between 0.1 and 10 cm year^{-1} at Lippenbroek (Oosterlee *et al.*, 2017). This high sedimentation rate may be the reason for the delayed plant colonisation observed in our plots. This, combined with the high variability in soil conditions observed in the first year of restoration, highlights the importance of monitoring site development beyond the first three years, and possibly delaying the start of monitoring until as late as year 2.

In our study we adjusted the temporal resolution and breadth of nutrients monitored at a newly restored saltmarsh compared to the shorter term study of (Blackwell, Hogan and Maltby, 2004). This extended duration of the study allowed us to detect both the first-year peak in variability of soil characteristics, also observed by Blackwell, Hogan and Maltby, (2004), and the convergence of the MR site conditions to that of natural saltmarshes in terms of variation and concentrations in the whole suite of properties sampled. Temporal sampling is rarer than spatial sampling (Chapter 3). However, our focus on temporal development in the site constrained our spatial sampling. It is possible that a greater number of samples within the elevations or land uses would have given more power to detect differences and allowed us to have investigated the relationships within land uses and between environmental conditions (e.g. elevation and nutrient concentrations). So, due to the strong spatial and temporal variability observed in nutrient concentrations, we would strongly recommend that any future sampling effort either 1) is focused on understanding relationships in specific points in time (e.g. growing season) with many replicates of years and within spatial contexts; or 2) aims to quantify temporal stochasticity and its drivers, e.g. local weather, nutrient inputs or external sediment input, as this sedimentation dominates nutrient concentration development on restored sites.

In order to provide context to the nutrient concentrations at Steart, a baseline was required to understand the current nutrient levels within saltmarsh habitats. A systematic literature review of saltmarsh nutrient concentrations (Chapter 3) found that there was not a clear picture of the nutrient status of saltmarshes, due to inconsistent analytical methodology, incomplete reporting of methodologies and large numbers units presented. Our knowledge of saltmarsh nutrients may be improved through the establishment of a set of guidelines setting out recommended methods and units for presentation. Despite these challenges, we found that natural saltmarshes are typically Phosphate-enriched, unlike restored marshes. However, N:P ratios tend to be lower, than those that potentially have detrimental effects (Chapter 3; (Deegan *et al.*, 2012). This suggests that any enrichment of Nitrogen could pose a significant impact as it is detrimental on its own and is its effect is enhanced by presence of excess Phosphate (Sundareshwar, 2003), which we know to already be in natural marshes.

6.2 Future directions

The results presented in Chapter 2 and 5 suggest that there is a very strong and significant role of topography in the development of saltmarsh diversity. However, current knowledge is limited to correlative studies, such as this one, or small scale manipulations (e.g. Mossman *in prep*; Varty and Zedler, 2008; Wigand *et al.*, 2016). We need an understanding of the consequences of topographic manipulations in circumstances that mirror those that are practically possible to create in a MR scheme. More medium scale manipulations, such as that at Freiston MR, should be conducted and these should seek to test a variety of topographic features at all elevations within a site. In addition to this, we should seek opportunities to work with coastal engineers to modify site design before restoration, or work with site managers post-restoration to manipulate existing sites. Early evidence from this thesis suggests that manipulation may be beneficial and, as a result, with limited opportunities to influence site design (because there are not many sites), it is important to trial large-scale topographic manipulations whenever possible. To evaluate the cost effectiveness of differing topographic designs, any trials should be monitored regularly and consistently for vegetation colonisation and longevity of the features, e.g. erosion or sedimentation.

The importance of soil nutrient concentrations on the development of MR sites and in natural saltmarsh zonation remains a significant knowledge gap. There is evidence of Phosphate enrichment in many natural saltmarshes (Chapter 3). However, current understanding of the effects of such enrichment from experiments is still based on very high levels of N and P, and not the critical tipping point between different ratios of these, or the concentrations at which they become detrimental. Experimentation should focus on manipulating the N:P ratio at different concentrations. This is possibly best achieved in laboratory conditions to control remaining soil properties. Such design would also allow other stressors to be tested, e.g. those that will alter with climate change (temperature, sea level and CO_2) and how this will influence interspecific competition in existing saltmarsh. Furthermore, nutrient experiments tend to administer doses once or constantly. This thesis found evidence of high temporal variability in nutrients and this should also be incorporated into experiments.

Nutrient concentrations were highly variable between estuaries, within sites, through time and were poorly correlated with other environmental properties, such as redox potential and elevation (Chapters 3 & 4, Lawrence, unpublished data). This makes the interpretation of their independent relationships with plants or other variables difficult to predict, and their integration into models of the environment or plant communities very challenging. As a result, the optimisation of field and laboratory effort may be better spent investigating possible proxies for these soil properties. For example, can conductivity accurately predict the proportions of total anion and cations in the soil? It maybe not just the use of a single variable or measurement that can act as an effective proxy. Indeed, this study showed total Nitrogen was more stable temporally and spatially removing some of this challenging variability. It is worth investigating therefore, if factors such as total Nitrogen, in conjunction with other properties such as redox, may be able to act as an effective proxy for many other soil properties. Since understanding of nutrient status is poor yet so important for ecosystem resilience, the development of quick and easy to measure proxies would allow for the rapid assessment of status, globally. In addition to proxies, a standardised set of methodologies for nutrient measurement should be developed to allow a global study of nutrient status.

The ability to predict plant zonation through the use of species distribution modelling and spatial analysis can assist with better plant community convergence between restored and natural systems (Brudvig, 2017; Brudvig *et al.*, 2017). This analysis could identify areas where edaphic conditions are detrimental and where there are niches suitable to specific species that are slow to colonise, thus informing the design of future compensatory habitat. Elevation, soil moisture, redox potential and salinity have been used with some success in predicting plant communities (Moffett, Robinson and Gorelick, 2010; Sullivan *et al.*, 2017), but such models have not been fully exploited in restored systems to predict restoration success or guide management. Furthermore, topography and its link to redox potential, such as locally low or high terrain, have yet to be included in such models. The role of redox potential is particularly important in managed realignments, where it is currently the dominant driver of vegetation diversity. Incorporation of topography into niche models may increase their ability to predict species distributions.

The results in this thesis indicate that in MR sites redox potential is driven by elevation and not by topography. However, this was found over a limited elevation range and this did not hold in natural marshes. A first step would be expanding sampling to encompass a wider sample both spatially and over elevations on restored and natural sites. This redox dataset should then be modelled as a function of elevation and topography; crucially both elevation and topography can be derived from remote sensing data, allowing scaling up. This approach will allow construction of high resolution redox potential maps, which can in turn be used to predict plant distribution. Prediction of plant communities could be used on a restored site prior to restoration, or under different sedimentation, sea level rise or topographic manipulation scenarios.

While the above modelling would increase our understanding of the physical niche of a given species, a key aspect has not been accounted for is the differential dispersal and colonisation abilities of species, and their interactions with each other. Currently our knowledge of species coexistence is limited to abiotic drivers and there is much overlap between species in tolerances (Sullivan *et al.*, 2017). A recent development in community ecology is joint species distribution models (Pollock *et al.*, 2014), and these could be used to investigate the potential facilitative and competitive interactions between species within shared niches. This would move forward our understanding of the communities a found in managed realignments since many appear to be dominated by a few species.

The results of this thesis found that homogenous environmental conditions leads to homogenous plant communities and I have hypothesised that this is due to large connected niches that allow vegetative spread of dominant species. This hypothesis requires testing. One way to do this would be to investigate the genetic similarity to identify if the patches are clonal, and thus the mechanism of spread. If this mechanism was supported, we may be able to hinder the dominance of one species within a niche by planting or encouraging other species that share the niche.

6.3 Implications for restoration

The results of this thesis suggest that MR sites currently lack the same abiotic drivers of vegetation community development in natural saltmarshes. The results also show that time since restoration does not lead to a trajectory towards similar topographic characteristics. As such, the only means to achieve similar physical drivers is via the creation, prior to breaching, of substantially more topographic manipulations than previously used. The results suggest than convex, hummock-like features are rare in MR schemes, that there are less dendric creek networks reaching the upper marsh and finally that they are typically flatter. Manipulations of the surface topography to create features similar to those in natural marshes is needed, as it will help drive the establishment of more natural vegetation and reduce dominance of specific species.

Opportunities to aid restoration is not limited to pre-restoration design. Encouragingly for site managers, post restoration manipulations have provided some extremely encouraging results in altering soil redox potential and driving plant diversity towards a more natural community composition. We also found that the impact of the restoration of tidal flooding within MR sites in the first year is so overwhelming that site managers, and policy makers should consider that a site does not appear to settle chemically and physically (sedimentation) for at least a year after restoration. Observations of site development in the first year could provide an indication of longer-term topographic development or loss. We observed large areas of de-watered fresh sediment in the first summer, which was hard underfoot (although this is elevation and weather dependent), and this time period also coincides with high variability in soil chemistry and is prior to large-scale vegetation establishment. It is therefore proposed that this is an ideal time to continue or aid further topographic development, based on the prior observations. Additional to this site managers can begin to appraise the longevity of depressions at low and moderate elevations within MR site, that may be filling in and are thus losing value for money. At this time point it may be possible to use the newly deposited sediment as a resource to create further topography, e.g. hillocks, small banks, and levees that encourage drainage development, thus reducing the expense of sourcing earth for these features prior to restoration.

As we find topography is particularly lacking at local scales on restored sites, it may not necessarily be a requirement to use large-scale, heavy plant and machinery to create post-restoration topography, and could possible be completed by site managers and with smaller plant. Finally reserving funding for intervention within this time window may also allow the investigation of dedicated, landscape sensitive planting or seeding programs. The success or failure of these experiments within topographically designed niches for those species will prove extremely informative about potential of such targeted planting in the future.

6.4 References

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