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Manipulating saltmarsh microtopography modulates the effects of elevation on sediment redox potential and halophyte distribution

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Abstract

1. Halophyte distributions on saltmarshes are strongly related to elevation in the tidal frame. However, collinearity between elevation, the consequent inundation regime, and sediment waterlogging/redox potential obscures the proximate causes of distribution patterns. We sought to distinguish the effects of elevation *per se* from those of waterlogging by manipulating microtopography.
2. We experimentally manipulated elevation by ±15 cm at locations that spanned the elevation ranges of three saltmarshes recently reactivated by managed coastal realignment. Experimental plots were initially cleared of any vegetation. Elevation and sediment redox potential were determined for each plot. We planted five perennial species (*Armeria maritima*, *Atriplex portulacoides, Limonium vulgare*, *Plantago maritima* and *Triglochin maritima*) in half of the plots, recording survival over four years, and monitored natural colonisation of the other plots.
3. Overall, redox potential increased with elevation. Sediments were more oxidising in raised plots and more reducing in lowered plots. Redox reductions in lowered plots were in line with those that would be predicted from the overall redox/elevation relationship, but increases in raised plots were greater than predicted from elevation alone.
4. Plant colonisation and survival was poorer in lowered plots and, for most species, improved in raised plots. This poorer colonisation and survival can, in part, be attributed to the concomitant alterations in redox potential and elevation in the tidal frame, but microtopographic manipulation also had substantial independent effects on plant performance, including on the survival of all planted species and the colonisation of *Puccinellia maritima*, *Salicornia europaea* agg. and *Tripolium pannonicum*.
5. *Synthesis*: Microtopography can have effects on sediment chemistry and plant performance similar in magnitude to those of overall tidal elevation. Understanding how its effects modulate the relationship between tidal elevation, redox and other environmental conditions helps clarify the abiotic factors that fundamentally determine halophyte colonisation and survival. These results support the use of topographic manipulation to enhance the diversity of created saltmarshes.

1 INTRODUCTION

One of the striking features of coastal salt marshes is the structure imposed on their vegetation by the frequency and duration of tidal inundation (Chapman 1960). On a large scale, differential tidal inundation over an elevation gradient affects halophyte distribution and can be seen as vegetational or species zonation (e.g. Zedler *et al.* 1999; Bockelmann *et al.* 2002; Silvestri, Defina & Marani 2005). Superimposed on this, however, is local topographic variation relative to the marsh platform (creeks, pools and hummocks) that may also be an important influence, because of its effects on local drainage conditions (Crooks *et al.* 2002; Ewanchuk & Bertness 2004a; Brooks *et al.* 2015). The mechanisms by which submergence with seawater mediates plant distribution are complex; particularly important is the differing tolerance exhibited by species to the sediment hypoxia associated with sustained flooding. Anaerobic microbial respiration lowers sediment redox potential, releasing toxic reduced substances (Pezeshki & DeLaune 2012). Differing abilities of halophytes to produce aerenchyma and thus oxygenate their rhizospheres are critical to tolerating more reducing environments (Colmer & Flowers 2008).

The importance of absolute elevation in the tidal frame for sediment redox potential and species distributions has been well established from field measurements (Armstrong *et al.* 1985; de la Cruz, Hackney & Bhardwaj 1989; Castillo *et al.* 2000; Anastasiou & Brooks 2003). However, the interpretation of causality in these relationships from field observations is hampered by the strong correlations between elevation, redox potential and other variables, such as salinity. At a particular tidal elevation, there is some variation in other environmental conditions, which at least in part result from topographic position. For example, hummocks will be less waterlogged than local depressions or pools at the same elevation. Consequently, while the independent effects of these variables can be distinguished statistically (Davy *et al.* 2011), field experimentation is necessary to confirm causality. Some evidence derives from transplanting halophytes to lower-lying sediments with a more adverse redox potential (Bertness 1991; Castillo *et al.* 2000) but few studies have attempted to manipulate elevation experimentally (Fragoso & Spencer 2008; Kirwan & Guntenspergen 2012; Voss, Christian & Morris 2013; Kirwan & Guntenspergen 2015; Balke *et al.* 2017). Fewer of these have specifically addressed redox potential (but see Ewanchuk & Bertness 2004b; Varty & Zedler 2008) and they generally do not attempt to distinguish the effects of absolute elevation from those of local microtopography.

An investigation of the physico-chemical constraints on halophytes would ideally focus on the colonization of new salt marsh, when populations are sparse and interactions between them are minimal. Species interactions, positive and negative, become more important in more mature communities (Bertness & Ellison 1987; Castellanos, Figueroa & Davy 1994). However, the colonization of natural marshes tends to be at uniformly low elevation; in contrast, bare sediments at a wide range of elevation have been afforded by the reactivation of salt marshes as a result of managed coastal re-alignment, where sea walls have been breached and tidal regimes re-established (French 2006). Previous work has shown that some, mainly annual, species colonise managed-realignment marshes rapidly. However, many of the characteristic perennials may be dispersal-limited or suffer poor establishment (Mossman *et al.* 2012; Mossman, Davy & Grant 2012a; Sullivan *et al.* 2018). For these species, investigation of the effects of local topography on performance must involve planting.

Our work comprised a field experiment, with treatments distributed across three recently reactivated managed re-alignment marshes in the U.K. that embraced a wide range of tidal elevation. Topography was manipulated by raising or lowering the surface level of plots at locations across the tidal range of all three marshes. Plots were then either planted with container-grown halophyte plugs or allowed to colonise naturally. We sought to relate both the survival of planted populations and the recruitment to natural ones to local sediment redox potential. Our specific objectives were to: (1) distinguish the importance of relative elevation (in terms of local microtopography) from that of absolute elevation in the tidal frame for redox potential; (2) investigate the effects of elevation (both relative and absolute) and redox potential on the occurrence and abundance of naturally colonising species, and (3) on the survival of planted perennial halophytes.

2 MATERIALS AND METHODS

2.1 Study sites

Experimental plots were established at three managed realignment (MR) sites in south-eastern England, Brancaster in north Norfolk (52.96244^0 N, 0.63889^0 E), Freiston Shore in Lincolnshire (52.96443^0 N, 0.09364^0 E) and Wallasea, Essex (51.61532^0 N, 0.82833^0 E). The first two had tidal flow restored in September 2002, the last in September 2006. All were relatively new MR sites and the vegetation communities on adjacent natural marshes, the potential source of propagules, were similar to each other. There was no grazing by stock on the areas studied and no artificial seeding or planting had been conducted prior to the experiments.

2.2 Experimental design

In October and November 2009, ten groups of six 1 x 1 m plots were set up on each of the three MR sites. Each group contained two 'flat' (F) plots at the existing marsh elevation, two plots raised (R) by 15 cm from the marsh surface and two plots lowered (L) by 15 cm from the marsh surface (Fig. 1). Existing vegetation was removed from all plots. In each group, one set of plots (i.e. one raised, one flat and one lowered) was left to colonise naturally and the other set was planted with plugs of five perennial species thought to be slow to colonise (*Armeria maritima*, *Atriplex portulacoides, Limonium vulgare*, *Plantago maritima* and *Triglochin maritima* (Mossman, Davy & Grant 2012a)). Nomenclature follows Stace (2019).

Raised plots were established using sediment-retaining wooden frames (1 m x 1 m x 0.15 m), and transferring the top 15 cm of sediment from lowered plots, which were also reinforced with wooden frames. All vegetation was removed and the sediment in the raised plots allowed to settle naturally. Flat plots were established by removing all surface vegetation; where this involved removing turf, sediment from nearby but outside the group of plots (minimum distance of 5-10 m) was used to return the plot level to the same as the marsh surface. Placement of the groups of plots was stratified across the elevation gradient of each MR site, with plots haphazardly located along the gradient. Groups were a minimum of 25 m apart.

Seeds of the five perennial species were collected from natural marshes close to the MR sites in late summer and early autumn 2009. Seeds were mixed and so the origin of the material is not known. Seeds were given to British Wild Flower Plants, North Burlingham, UK, who germinated the seed and grew plugs outdoors in peat-free compost. Plugs were watered with tapwater until two weeks prior to anticipated field planting, when they were watered with 50% strength artificial seawater (TropicMarin® sea salt, Wartenberg, Germany).

In planted plots, ten plugs of each of the five species were planted in a regular grid, with individuals randomly assigned to a location. Plugs were watered with locally-collected seawater immediately after planting. Planting was undertaken at Brancaster and Freiston in May 2010. Planting at Wallasea was delayed until early August 2010, because of concern about the effects of a significant drought that occurred in May/June 2010, which coincided with the period of low tides around the summer solstice. However, by October 2013 there was no significant difference in survival of planted individuals between Brancaster and Wallasea, but overall survival at Freiston was significantly lower than at both Brancaster and Wallasea ($F_{2,493} = 97.3$, $P = 0.002$). We therefore consider there to be no effect of the timing of planting, but site was also included as a term in our analyses.

2.3 Field methods

Surviving planted individuals were counted at the end of the growing season each year from 2010-2013; data presented here are from October 2013 when survival had stabilised (Fig. S1). At the same time, any seedlings or established individuals of any of the five target species were counted in the unplanted plots; unplanted individuals of target species that had established in planted plots were also recorded. Colonisation in unplanted plots was also assessed by recording the presence and percentage cover of all vascular plant species to the nearest 5% (rare species were assigned a value of 1%).

Substrate redox potential at the centre of each experimental plot was measured in June, August, September and November 2010, April, August and October 2011, and October 2012 and 2013, using a combination redox electrode with an Ag/AgCl reference (BDH Gelplas, VWR, UK) and voltmeter (Hanna Instruments Ltd, Leighton Buzzard, UK) at 5 cm depth, left until a stable reading was achieved (up to 5 minutes). Values were corrected by adding the potential of the reference electrode (204 mV) with respect to a standard hydrogen electrode (Eh). The mean of these nine redox values in each plot was calculated and used in further analyses. The proportion of lowered plots that were full of water (i.e. ponded) was recorded in June and September 2010, representing the expected lowest (June) and highest (September) proportion due to the solstice and equinoctial tidal cycle. In October 2013, the surface elevation relative to the UK reference level (Ordnance Datum, Newlyn (ODN)) was measured at the four corners and centre of each plot (i.e. including the change in elevation due to the topographic manipulation), using a differential GPS (Topcon, Newbury, UK), with an accuracy of <2 cm and precision of <1.5 cm; the mean of these five measurements was used as the elevation of each plot. The three sites have differing tidal regimes and so direct comparison of elevation is not possible. In order to standardise elevations at the three sites to their respective positions in the tidal range, and therefore allow values to be compared across sites, they were expressed as tidal heights:

Tidal height = (Elevation relative to ODN – MHWN)/(MHWS-MHWN)

On this scale, 0 = mean high water of neap tides (MHWN), 1 = mean high water of spring tides (MHWS) (Mossman, Davy & Grant 2012b). MHWN (i.e. tidal height of 0) corresponds to approximately 600 inundations per year and MHWS (tidal height of 1) to 100 inundations per year, with an approximately linear relationship between tidal height and the number of inundations per year in this range (Fig. S2). Elevations of MHWN and MHWS were obtained from local tide gauges or Mossman *et al*. (2012b) and are given in Table S1.

2.4 Data analysis

By October 2013, 172 of the 180 plots remained (87 planted and 85 unplanted) and the data from these were used in the analyses; the eight other plots were destroyed at Freiston during site management. Redox potential (mean of nine measurements per plot) was compared between topographic treatments using ANOVA, with Tukey post-hoc test for pairwise differences using the R package *multcomp* (Hothorn, Bretz & Westfall 2008). Differences in redox potential between planted and unplanted pots were investigated using a paired Wilcoxon test. The effects of treatment and tidal height on redox potential was investigated using ANCOVA, with an interaction term added to test whether the relationship with tidal height varied between treatments.

Total survival of all planted individuals was modelled using a generalised linear model with binomial errors, with species as an explanatory variable. Significance of the whole model was tested by comparing to an intercept-only null model. Survival of individual species was modelled using binomial generalised linear models as a function of treatment, redox potential, tidal height of the surface of the plot (i.e. including the elevation change as a result of the manipulation) and site. These variables were scaled to have a mean of zero and standard deviation of one to aid comparison of coefficients (mean± SD of each variable given in Table S2). Although separate models were constructed for each species, as the scaling of explanatory variables was the same in each case, model coefficients can be compared across species. The independent effect of each explanatory variable was quantified using hierarchical partitioning, implemented using the R package *hier.part* (Walsh & Mac Nally 2013). The purpose of this analysis is to identify the independent additive effects of each variable. Similarly, the occurrence (presence/absence) of the most abundant species in the unplanted plots was modelled as a function of treatment, redox potential, tidal height and site, using generalised linear models; occurrence was selected for modelling as percentage cover data were zero inflated. The six species for which there was sufficient data to model were *Atriplex portulacoides*, *Puccinellia maritima*, *Salicornia europaea* agg., *Spartina anglica, Suaeda maritima* and *Tripolium pannonicum* (*Aster tripolium*). To visualise the effect of redox potential and tidal height, and explore their interaction, on plant survival in the planted plots and occurrence and percentage cover (arcsine transformed) in the unplanted plots, we constructed generalised additive models using the R package *mgcv* (Wood 2006), setting the maximum complexity of smoothed terms to three effective degrees of freedom. We then constrained predicted survival probabilities, occurrence and cover to fall within available environmental space.

Variation in survival in response to topographic manipulation treatment at different elevations was investigated using generalised linear models, with survival as a function of treatment and surrounding surface elevation, i.e. that of the flat plots, and the interaction between treatment and elevation.

3 RESULTS

3.1 Manipulation of microtopography significantly changed sediment oxygenation

Topographic manipulation significantly altered the sediment redox potential ($F_{2, 169} = 50.31$, $P < 0.001$, $R^2 = 0.37$; Fig. 1a), with redox potential being significantly reduced in lowered plots and increased in raised plots relative to flat plots. There was no significant difference in the redox potential between planted and unplanted plots (paired Wilcoxon test: V = 2100, $P = 0.432$). Overall, redox potential was driven by elevation and treatment ($F_{5,169} = 55.59$, $P < 0.001$, $R^2 = 0.62$). Elevation had a positive effect on redox potential ($\beta = 331.9 \pm 52.6$, t = 6.3, $P < 0.001$, Fig. 1b). This relationship between tidal height and redox was not significantly different between flat (control) and lowered plots (t = 1.5, $P = 0.144$) plots, but was significantly less steep in raised plots (t = 2.4, $P = 0.016$). The difference in redox potential between flat and lowered plots was marginally non-significant when the effect of tidal height was accounted for (t = 1.9, $P = 0.054$), but redox remained significantly higher in raised plots than in flat plots (t = 4.0, $P = 0.001$). Thirty percent of lowered plots were full of water in June and 97% were full in September.

3.2 Natural vegetation establishment

Eleven species had colonised the unplanted plots after four years (Table S3), with *Salicornia europaea*, *Tripolium pannonicum* and *Puccinellia maritima* occurring most frequently (72%, 71% and 62% of all plots respectively). Topographic manipulation influenced vegetation colonisation with 49% of lowered plots remaining completely unvegetated. In contrast, little bare ground remained in flat and raised plots after 4 years (Fig. 2). Natural colonisation of the five species selected for planting was poor, with the exception of *Atriplex,* which occurred in 45% of all unplanted plots (86% of raised plots) and at high abundance (Fig. 2c, j). *Limonium* colonised seven flat unplanted plots at Brancaster MR; all of these resulted from vegetative growth from plants adjacent to the plot, as determined by locating vegetative runners. No other planted species naturally colonised any unplanted plot. Four *Limonium* and three *Plantago* seedlings established in planted plots in the immediate vicinity of planted individuals that had set seed. Similarly, juvenile *Armeria* plants were found in five planted plots adjacent to planted individuals; no *Triglochin* seedlings were observed.

The occurrence and percentage cover of *Atriplex*, *Puccinellia, Suaeda* and *Tripolium* were associated with high elevations and high redox potentials (Fig. 3); elevation and redox potential were significant predictors of *Atriplex* and *Puccinellia* occurrence in the multivariate models (GLM, Table 1). In contrast, *Salicornia* occurred at all elevations and redox potentials but was most abundant at the lowest redox potentials. *Spartina* was highly influenced by elevation, being restricted to the lowest elevations (Fig. 3, Table 1), although it did not colonise the lowered plots (Fig. 2). Treatment had significant independent effects when elevation and redox potential were included in the models (Table 1). The lowered treatment had significant negative effects on the occurrence of *Puccinellia, Salicornia* and *Tripolium*, and the raised treatment also had a significant negative effect on *Puccinellia* (Table 1). The occurrence and abundance of *Atriplex* and *Suaeda* were highest in the raised plots (Fig. 2), although treatment was not a significant predictor when elevation and redox potential were included as predictors (Table 1).

3.3 Survival of planted individuals

Across all plots 35±2% (mean ± SE) of planted individuals survived to the end of the fourth growing season. However, there were significant differences in survival between species (χ^2=418.31, df = 4, P <0.001), with survival of *Armeria* (13±3% individuals) significantly lower than that of all other species. Survival of *Atriplex* (53±5%) and *Limonium* (49±4%) were significantly higher than that for *Triglochin* (33±4%) and *Plantago* (28±4%).

Survival of all planted species was significantly reduced in lowered plots compared to both flat and raised plots (average decrease in survival ranged from 71-81%; Fig. 4, Table 2). With the exception of *Triglochin*, survival of all species was significantly higher in the raised plots compared to flat ones (average increase in survival, excluding *Triglochin* for which there was no increase, ranged from 42-133%, Fig. 4, $P < 0.001$). This higher survival may be due to the higher redox potential in raised plots, with all species having higher survival at higher redox potential (Table 2) and survival of all species being poor at combinations of low elevations and low redox potentials (Fig. 5). *Armeria* was confined to both the highest elevations and redox potentials, not surviving at combinations of low elevation/high redox or at high elevation/low redox. In contrast, survival of *Limonium* and *Triglochin* was moderate (50% and 60%, respectively) in areas of high elevation/low redox. Similar to the patterns seen in the occurrence and cover of naturally colonising *Atriplex* (Fig. 3), survival of planted individuals was strongly influenced by redox potential (Table 2), with survival high (70%) in low elevation/high redox (Fig. 5).

There were significant independent effects of treatment on plant survival when tidal height and redox potential were accounted for (Table 2). There was a significant positive effect of the raised treatment on the survival of *Plantago* and *Atriplex*, the latter in contrast to no effect on its occurrence in unplanted plots, and a significant negative effect on survival of *Triglochin*. When manipulation was carried out low in the marsh (i.e. based on the elevation of the flat control plots), survival of all species was higher in the raised plots (Fig. 6, Table S4). However, *Atriplex* survival was very high in all raised plots irrespective of surface elevation. When manipulation was carried out higher on the marsh, the survival of *Limonium* and *Triglochin* increased in lowered plots to reach or exceed that of flat and raised plots.

There were significant effects of site for all planted and unplanted species except *Tripolium* (Table 1 & 2). The survival of all planted species was lower at Freiston compared to Brancaster (Table 2); survival of *Atriplex* and *Plantago* were significantly higher at Wallasea than Brancaster. The effects of site on the occurrence of unplanted species were more variable, although occurrence tended to be higher at Brancaster than at Freiston or Wallasea. The models accounted for high proportions of variance in survival or occurrence of most of the species. However, models for the occurrence of *Salicornia* and *Suaeda* accounted for <30% of variation, and in the planted plots variation in the survival of *Triglochin* explained by the model (40%) was lower than that of the other four planted species (61-78%) (Table 2).

4 DISCUSSION

Our manipulations of topography, raising and lowering the marsh surface by 15 cm, had substantial effects on plant survival and colonisation, both through changes in the position of plots in the tidal frame and redox potential, and independently of these. The magnitude of the effect of raising and lowering varied along an elevation gradient. Raising had the greatest effect when carried out at low elevations, with increased redox potential and survival of planted individuals. However, lowering had a negative effect on survival and colonisation across species at all but the highest elevations (Fig. 7).

By manipulating topography in the field across the whole elevation range, we had plots that could be at the same elevation but had differing topography (for example, a flat plot high in the marsh was at a similar elevation to a raised plot lower down the marsh (Fig. 1b)). This allowed us to distinguish the effects of position in the tidal frame from those of redox potential, as correlations between these variables were reduced, and to identify the independent effects of topography resulting from other mechanisms. These topographic manipulations altered the redox potential. Raising the local marsh level increased redox potential (mean increase 100 mV), across all three sites and all elevations in the tidal range, whereas local lowering of the marsh surface decreased redox potential (mean decrease of 71 mV); effects that were similar in magnitude to previous studies (Ewanchuk & Bertness 2004b; Varty & Zedler 2008). These changes in redox potential can only partly be explained by alterations in the elevation (and thus inundation regime) due to raising or lowering, as effects remained when elevation was accounted for, although for lowering this independent effect was marginally non-significant. The increased redox potential resulting from raising elevation relative to the surroundings is likely due to enhanced local drainage and hence sediment oxygenation. In contrast, lowering the surface reduced the redox potential and caused regular ponding in many plots. The latter suggests impeded drainage, which would have lowered redox potential. The adverse redox consequences of the lowering treatment were moderated somewhat at higher levels in the tidal frame, presumably because they were surrounded by higher ground and, therefore, received fewer inundations than flat ground at the same absolute elevation. Thus, the impact of the reduced drainage resulting from the lowering could have been partially offset by having fewer inundations.

Elevation in the tidal frame and redox potential had important effects on the natural colonisation of halophytes and the survival of planted individuals, confirming previous work (e.g. Chapman 1960; Davy *et al.* 2011). In general, redox potential was a more important predictor of the survival of planted species than elevation in the tidal frame. Remarkably, we found effects of local manipulations of elevation that were of similar magnitude to those of absolute elevation and redox potential, suggesting that microtopography is of greater importance in regulating halophyte distribution than previously recognised. In addition to the effects of topography on plant performance modulated through changes in elevation and redox potential, we found significant independent effects of the raising and lowering treatments. These independent effects may result from the effects of topography on unmeasured environmental variables. For example, there is substantial temporal variation in redox potential associated with tidal cycles (Armstrong *et al.* 1985) and our measures of redox potential may not have captured extreme events. The additional drainage may have resulted in droughting effects in some raised plots at high elevation. Permanent pooling of water in lowered plots may have prevented seedling establishment, and pooling of water and subsequent evaporation in high elevation-lowered plots could result in hypersalinity (Ewanchuk & Bertness 2004a). Such pooling may explain why approximately half of lowered plots remained completely unvegetated, even at moderate elevations. Topographic structures may also influence seed colonisation (Xie *et al.* 2018) though the provision of additional entrapment surfaces (Harper, Williams & Sagar 1965; Gage & Cooper 2005).

Natural colonisation of plots in the first four years was largely limited to six of the more fecund or well-dispersed species. A suite of perennial forbs common to the mid elevations of natural marshes (*Armeria maritima*, *Limonium vulgare*, *Plantago maritima*, *Triglochin maritima*) failed to colonise naturally, despite surviving as planted individuals. This failure to colonise likely indicates dispersal limitation, possibly as a result of low propagule availability (Mossman *et al.* 2012; Mossman, Davy & Grant 2012a). These species are rare or absent from saltmarshes restored through managed realignment (Mossman, Davy & Grant 2012a). Collectively, these findings highlight that differential colonisation rates will impact the development of vegetation communities, as initially poor colonisers fail to establish despite conditions being suitable for their survival. Planting is therefore recommended to establish populations of these species onto restored saltmarshes.

Although the niches (in terms of elevation and redox potential) of species revealed by this study are similar to those observed on natural marshes, there were some differences. Several pioneer species (*Suaeda*, *Tripolium*) colonised plots at higher elevations in the tidal frame than that observed in natural marshes. This result could be due to reduced competition in our plots, which were initially unvegetated, allowing species' distributions to better reflect their fundamental niche (i.e. where they can survive), whereas on a natural marsh they may be outcompeted (Sullivan *et al.* 2018). *Atriplex* was the only species sufficiently common as a natural colonist to allow us to compare the responses of planted and naturally colonised individuals. The ranges of elevation and redox were similar between surviving planted individual and natural colonists, but the distribution of naturally colonised individuals was more biased to higher elevation and redox, suggesting that environmental requirements for establishment of this species are more stringent than for adult survival (Beeftink *et al.* 1978; Mohamed 1998).

Generally, survival of planted species was high in raised plots, where redox potential was higher. However, in natural marshes, several of the planted forb species (*Limonium*, *Plantago*, *Triglochin*) are associated with pannes, depressed areas with low redox potential higher in the tidal frame (Ewanchuk & Bertness 2004b; Sullivan *et al.* 2018). These differences may reflect niche segregation induced by competition from the shrubby dominant, *Atriplex portulacoides*, which had very high survival in raised plots and is known to be associated with high redox potential (Crooks *et al.* 2002; Davy *et al.* 2011). The absence of low redox conditions on the mid-high marsh of managed realignment sites may therefore go some way to explain the rarity of *Limonium*, *Plantago* and *Triglochin* although they are also rare at sites 50-100 years after restoration (Mossman, Davy & Grant 2012a) where suitable environmental conditions do occur (Sullivan *et al.* 2018). These findings further indicate that planting schemes may be needed to establish populations of these species in restored saltmarshes.

Our models of species survival and occurrence explained relatively high proportion of the variance. We found significant effects of site in the distribution of species and this can only be attributed to other unmeasured factors, such as wave environments or nutrient availability. We found strong effects of elevation, which will be strongly correlated with inundation frequency and duration. However, both elevation and inundation regime are proxies for a suite of factors that directly influence plant physiology and ultimately occurrence, such as salinity, water availability and light availability (Janousek & Mayo

2013). Further exploration of how topography influences these would be valuable. Other unmeasured biotic factors, in addition to competition, may also have influenced the distribution of our species, such as differences in soil microbial communities or bioturbation by benthic invertebrates (Paramor & Hughes 2005).

Our systematic manipulations of microtopography in this experiment encompassed a wide range of tidal elevation and three geographically distinct sites. Consequently, the findings are likely to be robust. Sediment redox potential depended on overall elevation in the tidal range, and both factors were important determinants of plant colonisation and survival. Topographic manipulation altered inundation frequency and redox potential, and had separate independent effects on plant performance. But these effects were asymmetric and strikingly contingent on their context in the overall tidal range. In particular, we found that a small, local increase in elevation is able to ameliorate redox conditions sufficiently to facilitate the colonisation and survival of plants more typical of the mid-marsh even at the lowest marsh levels. Consequently, the presumed effects of local drainage conditions need to be recognised as modulating those of elevation in the tidal frame to explain patterns of saltmarsh vegetation (Crooks *et al.* 2002) and microtopography is of greater importance in driving halophyte distribution than previously recognised. The surface of natural saltmarshes is heterogeneous (Elschot & Bakker 2016; Lawrence *et al.* 2018). In contrast, those of restored saltmarshes lack topographic diversity (Masselink *et al.* 2017; Lawrence *et al.* 2018). Our results show that this lack of topographic diversity will limit their ecological diversity, so creation of microtopographic variation should be a greater priority during saltmarsh restoration.

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Data accessibility

Data available from the Dryad Digital Repository doi:10.5061/dryad.6c03bm4 (Mossman, Grant, & Davy, 2019).

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Author contributions

H.L.M, A.G. and A.J.D conceived and designed the study, and H.L.M. conducted experimental set up and data collection. All authors contributed to the analysis of the data, writing the manuscript and approved the final version.

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TABLES

Table 1. Coefficients (±SE) of generalised linear models of the occurrence of the six most abundant species that established in unplanted plots (n=90 plots). Occurrence was assessed in October 2013, 48 months after experimental set up. Coefficients are relative to the flat treatment in Brancaster. Significant effects in **bold**. ▪ *P*<0.1;* *P* <0.05*;* ** *P* <0.01; *** *P* <0.001. Independent effects (Ind Eff) were calculated with hierarchical partitioning.

	Atriplex		***Puccinellia***		***Salicornia***		***Spartina***		***Suaeda***		***Tripolium***	
	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)
Tidal height	**2.78 (1.14)** *	29.1	**3.22 (1.36)** *	20.3	-0.76 (0.48)	4.8	**-1.80 (0.71)** **	15.0	0.42 (0.41)	20.0	0.77 (0.48)	19.4
Raised treatment	0.82 (0.69)	18.2	**-3.4 (1.26)** **	35.0	-0.57 (0.45)	77.4	0.82 (0.50)	65.5	0.47 (0.35)	35.2	0.0 (0.0)	65.4
Lowered treatment	-0.53 (0.57)		**-4.54 (1.48)** ***		**-1.67 (0.45)** ***		-11.77 (1183)†		-0.45 (0.40)		**-1.35 (0.36)** ***	
Redox potential	**4.86 (1.71)** ***	41.8	**3.98 (1.69)** *	16.9	0.28 (0.36)	3.0	-1.56 (0.92) ▪	8.8	0.4 (0.31)	20.9	-0.02 (0.48)	14.6
Freiston	-0.52 (0.57)	11.0	-1.44 (1.03)	27.8	**-0.80 (0.36)** *	14.7	-1.02 (0.49) ▪	10.6	-0.15 (0.31)	23.9	0.22 (0.40)	6.0
Wallasea	**-2.84 (1.13)** *		**-5.23 (1.94)** *		-0.26 (0.34)		**-0.85 (0.44)** *		**0.72 (0.33)** *		-0.11 (0.37)	
Total variance explained (%)	72.8		76.4		26.0		51.9		27.2		38.8	

† Parameter estimate effected by separation – *Spartina* was absent from all lowered plots

Table 2. Coefficients (±SE) of generalised linear models of survival of planted individuals (proportion of individuals planted, n=10 per species per plot (n=90 plots)). Surviving individuals were counted in October 2013, 36-41 months after planting. Coefficients are relative to the flat treatment in Brancaster. Significant effects in **bold**. * *P* <0.05; * *P* <0.01; *** *P* <0.001. Independent effects (Ind Eff) were calculated with hierarchical partitioning.

	Armeria		***Atriplex***		***Limonium***		***Plantago***		***Triglochin***	
	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)
Tidal height	**0.49 (0.25) ***	29.0	-0.05 (0.21)	16.9	**-0.44 (0.15) *****	14.1	**0.55 (0.15) *****	27.2	0.08 (0.13)	12.8
Raised treatment	-0.04 (0.14)	10.7	**1.07 (0.19) *****	45.0	0.03 (0.12)	31.0	**0.27 (0.11) ***	29.1	**-0.25 (0.09) ***	39.8
Lowered treatment	**-0.57 (0.24) ***		**-1.09 (0.14) *****		**-0.93 (0.12) *****		**-0.75 (0.17) *****		**-0.86 (0.12) *****	
Redox potential	**2.73 (0.45) *****	35.9	**2.01 (0.22) *****	35.9	**1.71 (0.18) *****	35.3	**0.97 (0.21) *****	26.9	**0.59 (0.16) *****	16.9
Freiston	**-1.60 (0.24) *****	24.4	**-0.46 (0.14) ****	2.3	**-1.15 (0.12) *****	19.6	**-0.24 (0.12) ***	16.8	**-0.63 (0.10) *****	30.6
Wallasea	**-0.18 (0.13)**		**0.27 (0.14) ***		-0.13 (0.11)		**0.64 (0.11) *****		**-0.69 (0.10) *****	
Total variance explained (%)	75.1		73.3		63.1		61.2		34.8	

FIGURES

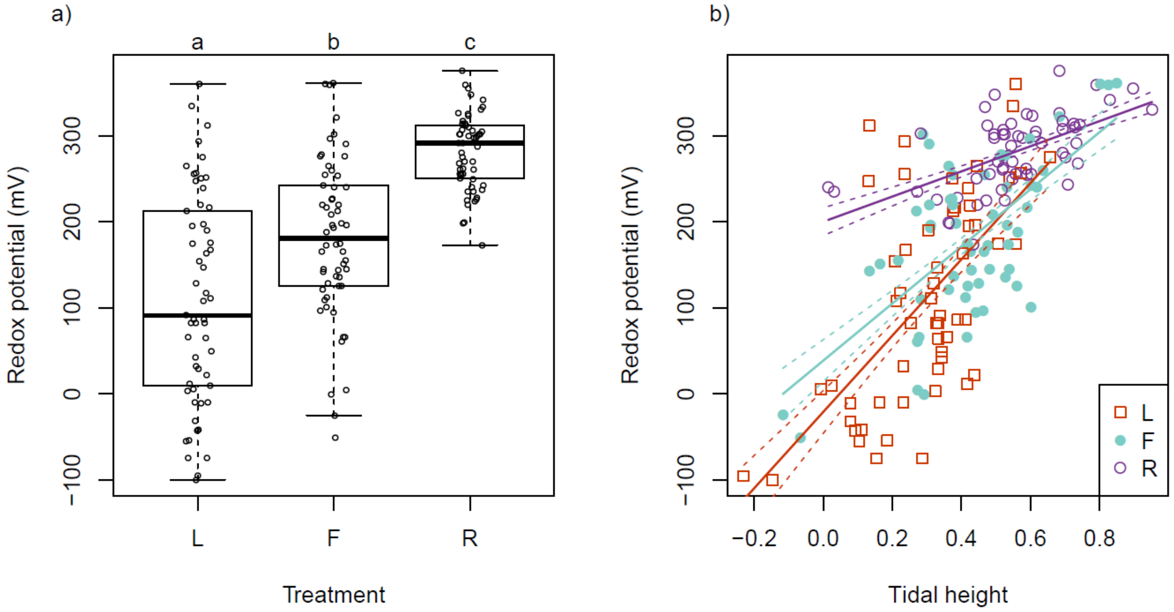

Fig. 1 (a) Sediment redox potential in planted plots with differing topographic treatments; (b) Variation in redox potential with tidal height in experimental plots. N = 172 plots. Each data point is the mean of nine values per plot taken between June 2010 and Oct 2013. L=lowered, F=flat (level with marsh surface) and R= raised. Manipulating topography across the elevation gradient of our marshes provided plots that could have the same elevation but different topography.

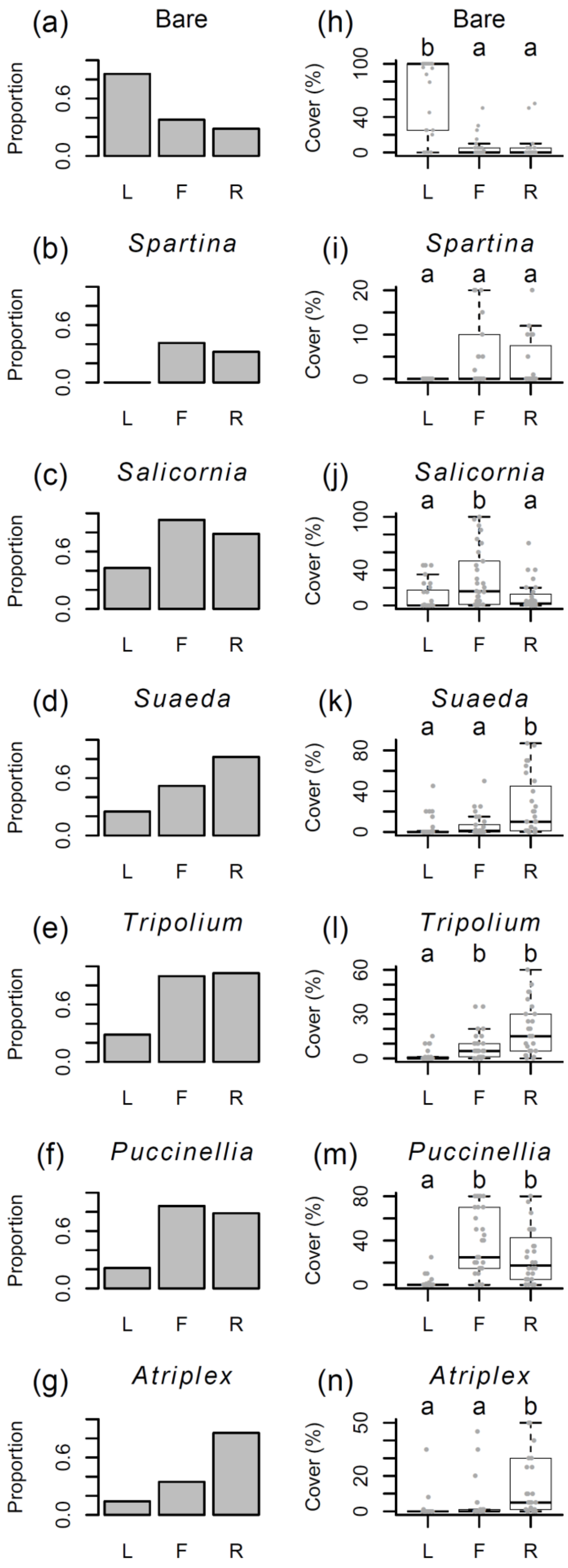

Fig. 2. (a-g) Proportion of unplanted plots with bare ground and the most abundant colonising species, and (h-n) percentage cover of bare ground and the most abundant colonising species. L=lowered, F=flat (level with marsh surface) and R= raised. Plots were sampled in October 2013, four growing seasons after the experiment was set up. Species ordered by the median elevation (from lowest to highest) that they occurred at on natural marshes from Sullivan *et al*. (2018).

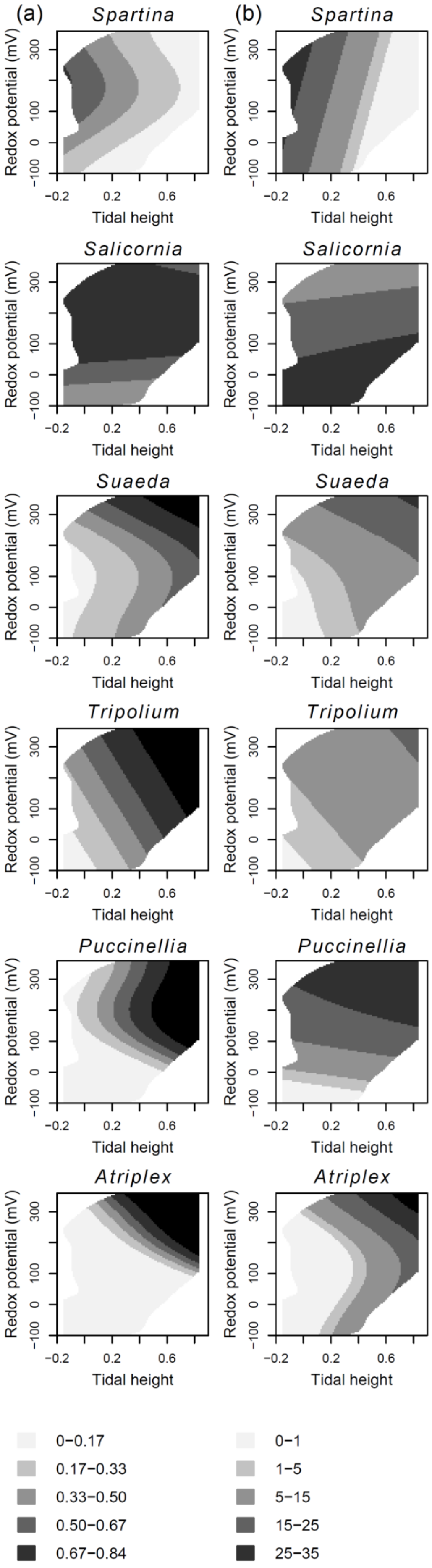

Fig. 3. Relationship between redox potential and tidal height and (a) the probability of occurrence and (b) the percentage cover (arcsine transformed) of the commonest species in unplanted plots. Contours show the predicted probability from generalised additive models. Contour lines have been clipped to the area of data availability as shown in Fig 1b. Darker colours indicate higher occurrence or cover. Species ordered as in Fig. 2.

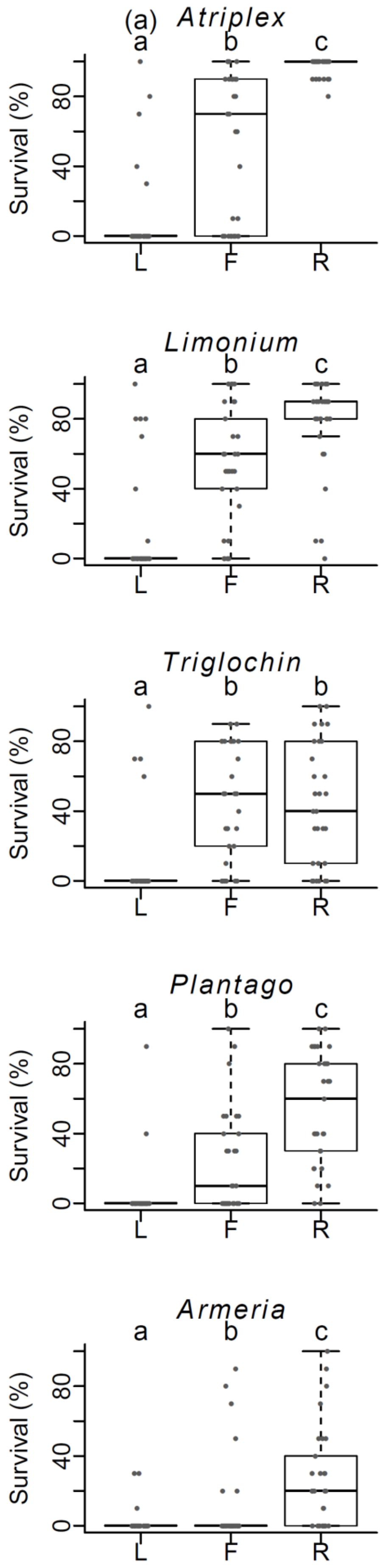

Fig. 4 Mean ±SE proportion (%) of planted individual surviving in October 2013, 36-41 months after planting, in differing topographic treatments. L=lowered, F=level with marsh surface (control) and R= raised. Differing letters indicate significant differences between treatments (GLM *P* <0.001, Tukey post hoc test). Species ordered by the median elevation (from lowest to highest) that they occurred at on natural marshes (from Sullivan *et al.* 2018); *Armeria* was not modelled by Sullivan *et al.* (2018), so its average elevation was taken from our data.

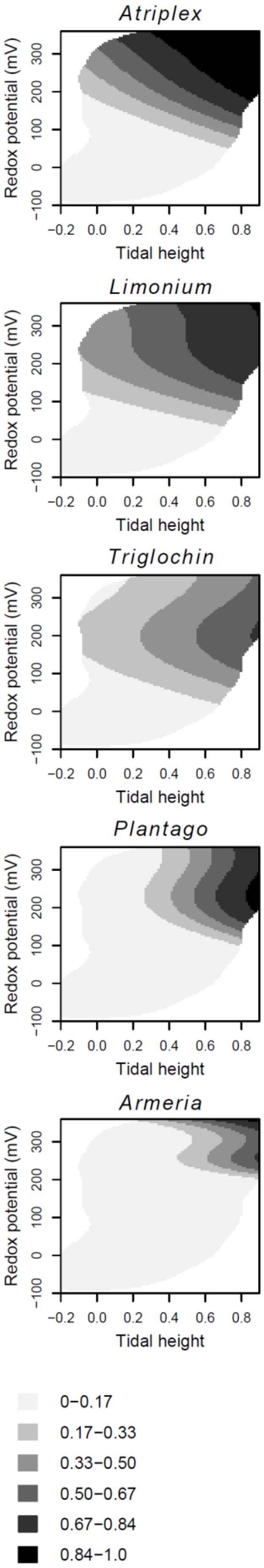

Fig. 5. Relationship between redox potential and tidal height and the proportion of surviving planted individuals in planted plots. Contours show the predicted probability from generalised additive models. Contour lines have been clipped to the area of data availability. Darker colours indicate higher probability of survival. Species ordered as in Fig. 4.

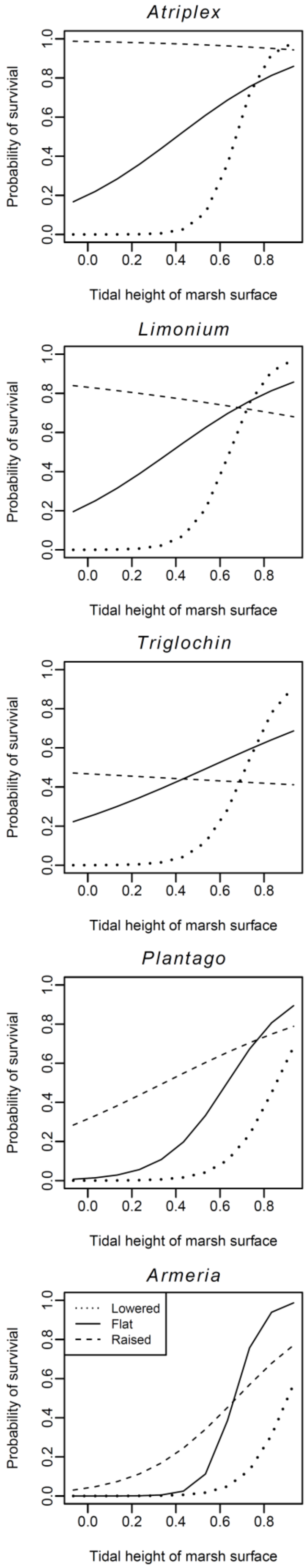

Fig. 6. Variation in the response to topographic manipulation treatment with elevation of marsh surface. Response curves are from generalised linear models of survival as a function of treatment and surrounding surface elevation, i.e. that of the flat plots, and the interaction between treatment and elevation. Model coefficients are provided in Table S4. Species ordered as in Fig. 4.

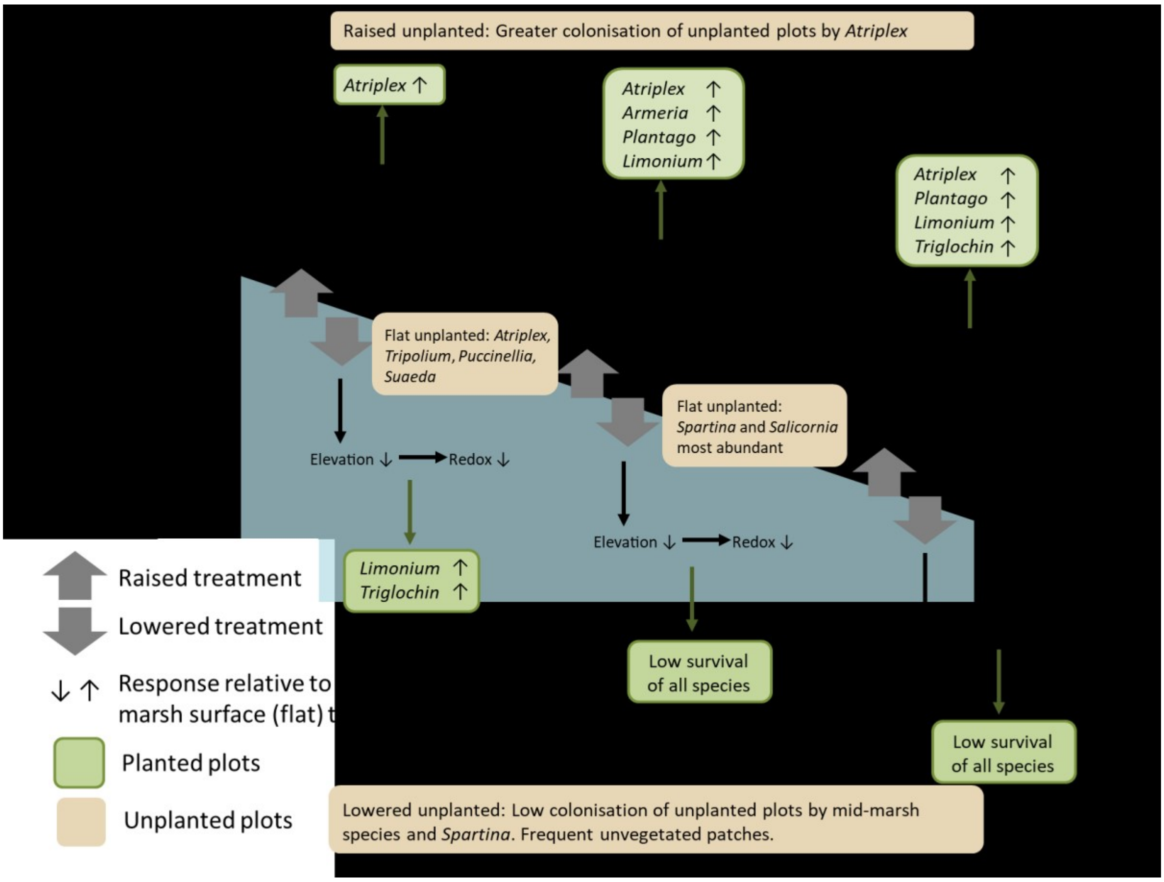

Fig. 7. Schematic diagram of how topographic manipulation (raising and lowering plots by ± 15 cm from the marsh surface) alters the elevation, redox potential and their relationship, and the consequences of this on plant survival and colonisation. Lowering plots reduces redox potential but the reduction is no greater than would be predicted from the change in elevation (although the latter is marginally non-significant). In contrast, raising plots at low and mid-marsh elevations increases redox potential more than the increase that would be predicted from the change in elevation alone.